Disturbance History and Decline of American Chestnut

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ABSTRACT

Invasive diseases can interact with other disturbances and the environment to affect host population decline, realized niche, and interspecific interactions. In my dissertation, I sampled oak-chestnut forests first sampled for vegetation composition 66-89 years ago and conducted a field experiment to evaluate the effects of variance in environment, in invasive disease prevalence, in logging history, and in deer browsing on the abundance, realized niche, and survival of a declining host tree in southwestern Virginia, USA. The disease and host I studied were American chestnut (*Castanea dentata*) and chestnut blight (*Cryphonectria parasitica*), a disease introduced in the early 1900's that received national attention due to chestnut's timber value and ubiquity.

Two sources of mortality studied here, in addition to chestnut blight, had significant effects on chestnut abundance and survival. Current chestnut abundance was significantly lower in areas where pre-blight chestnuts were logged than in areas where they were not logged. Since chestnut is highly palatable to deer, high levels of deer browsing significantly increased chestnut mortality rate, which affects its interactions with other understory species.

Pre-blight chestnut abundance was not predictive of post-blight chestnut abundance. Multiple regressions of principal components representing the environment with pre-blight and current chestnut abundance demonstrated that chestnuts are now more restricted to areas with slopes and aspects receiving high light (southern to western facing slopes) and xeric species than pre-blight chestnut was. When assessing a study area with larger variation in elevation, chestnut abundance was also related to elevation and moderately acidic soil pH. Although chestnut blight was predicted to be less prevalent in environments where chestnut abundance was higher, this prediction was not supported. Chestnut blight prevalence was not significantly related to any measured environmental variable, was independent of chestnut density, and infected an average of 15% of chestnuts, regardless of chestnut abundance. This work highlights the drastic change in chestnut's interactions with the environment now that chestnut blight is endemic across its range and the need for a better understanding of chestnut blight's spatiotemporal dynamics.

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DISSERTATION INTRODUCTION

In today's globalized economy, introductions of invasive species are increasing. One class of threat is introduced pathogens that are novel to susceptible native hosts. In forest ecosystems, invasive pathogen introductions that cause widespread native tree mortality and dieback can have pervasive impacts at the population, community, and ecosystem level. For example, the loss of a stand of dominant canopy trees alters nutrient cycling, vegetation composition, and interactions between species that depend on it for food and higher order consumers (Franklin et al. 1987, Castello et al. 1995, Ellison et al. 2005, Loo 2009). Some recent forest pathogen or pest introductions include: sudden oak death (*Phytophthora ramorum*) in North America (Rizzo and Garbelotto 2003); the emerald ash borer (*Agrilus planipennis*) on ash (*Fraxinus spp.*) in North America (Haack et al. 2002); hemlock woolly adelgid (*Adelges tsugae*) on hemlock (*Tsuga spp.*) in North America (Kizlinski et al. 2002); *Raffaelea lauricola* on plants in the *Lauracae* family, vectored by the recently-introduced ambrosia beetle (*Xyleborus glabratus*), in southeastern North America (Moser et al. 2009); *Sirococcus clavigignenti-juglandacearum* on butternut (*Juglans cinearea*) in North America (Loo 2009); powdery mildew fungi (*Erysiphe spp.*) on a variety of hardwood families in Europe (Heluta et al. 2009); pine wilt nematode (*Bursaphelenchus xylophilus*) in Europe and east Asia (Ridley et al. 2000, Schrader and Unger 2003); and, *Ceratocystis fimbriata* on *Eucalyptus* *spp.* and *Acacia mearnsii* in South Africa and Congo (Ridley et al. 2000, Wingfield et al. 2001). Such disease introductions pose major challenges to conservationists and forest managers.

Invasive disease infections can interact with other agents of mortality and with the environment to affect population decline, realized niches, and interspecific interactions. Studies of the long-term effects of invasive disease introductions are unusual because few forests with disease introductions have been endemic and monitored more than a few decades.

My general goal is to explore the long-term effects of an invasive disease, chestnut blight (*Cryphonectria parasitica*), on the host plant American chestnut (*Castanea dentata*) to better understand where and how long the host is expected to persist in southwestern Virginia and to understand what other sources of mortality interact with chestnut blight to affect host abundance and persistence. Chestnut blight was the first major invasive forest disease with widespread repercussions in the United States (Freinkel 2007). Introduced from Asia in 1904, the chestnut blight, which infects trees in the genus *Castanea*, caused range-wide dieback of a common tree of high timber value in eastern deciduous forests, the American chestnut. Chestnut blight prevents nearly all afflicted chestnuts from reaching reproductive age. The pathogen cannot infect belowground tissues, so a tree can produce new sprouts from its root collar following infection and dieback of the stem.

Chestnut rarely reproduces in the wild and does not disperse vegetatively or through seeds. Thus, populations are restricted to locations where the tree has persisted through re-sprouting since initial chestnut blight infection.

Because of chestnut blight's national attention and pervasive impact, chestnut forests were the location of classic studies in forest ecology addressing community and disturbance ecology (Braun 1950, Keever 1953, Whittaker 1956, Day and Monk 1974, Lorimer 1976, Shugart and West 1977, McCormick and Platt 1980). These early studies of chestnut blight by American forest ecologists were focused predominantly on what tree species would "replace" the chestnut after chestnut went extinct. Recently, ecologists have focused on understanding how invasive disease such as chestnut blight may interact with environment, land use, or other disturbances to affect the host distribution and its community (Paillet 1988, Foster 1992, Holdenrieder et al. 2004, Kauffman and Jules 2006, Fei et al. 2007, Crowl et al. 2008, Elliott and Swank 2008, Antonovics 2009). Here, I examine how the environment, logging history, and deer browsing interact with chestnut blight to affect chestnut abundance, niche contraction, and survival in Giles and Craig Counties, VA, in the southern Appalachian Mountains, USA.

By the late 1800's, more accessible timber resources were depleted, railroad lines into the interior Appalachians were built, and the post-Civil War recession allowed timber barons to buy large tracts of land in the Appalachian Mountains because many people moved to urban areas with more jobs, which allowed for large-scale logging operations in the Appalachians (Davis 2000). Logging of chestnuts peaked in the early 1900's (Freinkel 2007). In an attempt to curb the spread of chestnut blight and to prevent loss of large, valuable chestnuts due to chestnut blight infection, land managers and private landowners were advised by local and federal government agencies to cut chestnut trees, preemptively or immediately following blight infection (Murrill 1908, Carleton 1913, Gravatt 1914, Kelley 1924, Gravatt 1925, White 1930, Baxter and Gill 1931). In my first chapter, I explore the effects of logging history on chestnut abundance and whether environmental variation in chestnut can be explained by spatial variation in chestnut blight prevalence. Chestnuts were more abundant on sites that had not been selectively logged for pre-blight chestnuts. Chestnut presence was more likely at high elevations (857±33 m). Chestnut abundance was greater at high elevations (>1000m) and on acidic soils (pH 4–5). Contrary to my expectations, chestnut blight prevalence was not correlated with any measured environmental variable. Rather, 15.1% of all chestnut stems were infected with blight regardless of chestnut density. Thus, this study suggests that higher chestnut abundance is not due to lower mortality from the chestnut blight, although the temporal dynamics of blight infection and stem recovery were not within the scope of this study. This chapter showed that local rates of chestnut population decline differ between locations with different chestnut logging histories.

The century-long decline of chestnut provides a unique opportunity to study niche contraction and population decline in response to a pathogen invasion on a large spatiotemporal scale. My second chapter explored spatiotemporal variation in American chestnut survival over an eighty-year period in response to the introduction of an invasive pathogen, chestnut blight, and identified changes by comparing its current realized niche with its original niche. Two study areas sampled for chestnut volume and abundance before blight invasion in southwestern Virginia, U.S.A., were re-sampled, and measures of topography, soil chemistry, and forest composition were taken. Pre-blight chestnut abundance was not significantly correlated to current chestnut abundance, suggesting that chestnut survival rate was not constant across stands. A principal components analysis was used to represent the variation in environment variables. Relationships between pre-blight chestnut abundance and current chestnut abundance were analyzed with multiple regressions of principal components representing environmental variation. Principal components that were significantly related to pre-blight chestnut abundance were not the same as those components significantly related to current chestnut abundance, indicating a shift in chestnut's niche. Further, significant slope differences were found between linear models of pre-blight and current chestnut abundance with two principal components that were highly related to a gradient in solar insolation, and in mesic to xeric species, indicating a shift in chestnut's niche toward dry sites on southern to western facing slopes. Post-blight chestnut abundance was most closely related to principal components representing habitats with high *Quercus montana* basal area. If survival rates remain constant at the average rate for the last 80 years, *ceteris paribus*, 53% of all sampled stands are expected to be extinct in 224 years, and 95% extinct in 1103 years. This chapter provides evidence that chestnut is being constrained to a portion of its former niche following chestnut blight introduction because of spatial heterogeneity in survival rate.

My third chapter explores the effect of deer browsing on chestnut and striped maple (*Acer pensylvanicum),* a co-dominant understory tree that is less palatable to deer and more resilient to deer browsing. White-tailed deer (*Odocoileus virginiana*) are selective browsers that have increased across eastern North America since the early 1900's when restoration efforts began (McShea et al. 1997), and their effects on forest ecosystems remain less studied in the southeastern than in the northeastern United States (Russell et al. 2001). Across the study area, deer densities are very high (Knox 1997, Rearick et al. *in review*), and chestnuts have been declining while striped maples have been increasing in abundance (Parker et al. 1993). In this study, fenced exclosures monitored for four years from 2006-2009 were compared to unfenced plots to determine the effects of white-tailed deer browsing on the growth and mortality of these two co-dominant understory trees. Diameter, height, number of stems, mortality rate, and blight prevalence were measured annually over the four-year period. Results showed that chestnut stem number and survival rate were significantly positively affected by the fencing treatment, while striped maple growth in number of stems per plot decreased slightly and striped maple mortality rates were not different between fenced and control plots. These results indicate that deer browsing did not affect striped maple growth and mortality significantly but strongly affected chestnut sprouting and mortality rate. There was a trend of higher blight prevalence in the control than in the fenced plots, suggesting that browsing increases chestnut sprout susceptibility to chestnut blight, a result that merits further study.

My dissertation work highlights the importance of considering the effects of interactions between an invasive pathogen and disturbances, such as logging and deer overabundance, and between the pathogen and the environment, thus posing new limits on the host's realized niche. My examination of the effects of chestnut blight, logging, deer browsing, and environmental variation on chestnut survival, abundance, and niche contraction provides an excellent example of the effects of multiple disturbances and of landscape variation on a tree hosting an invasive pathogen.

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CHAPTER 1

The effects of logging and disease on American chestnut

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ABSTRACT

Disturbance histories drive spatiotemporal patterns of species distributions, and multiple disturbances can have complex effects on these patterns of distribution. The introduction of the chestnut blight (*Cryphonectria parasitica* (Murril.) Barr.) to the eastern United States in the early 1900s coincided with an increase in logging, thus presenting an ideal situation for studying the effect of two disturbance events, logging and disease. The purpose of this study was to compare chestnut (*Castanea dentata*) abundance and the prevalence of chestnut blight among (1) sites that were and were not logged for chestnuts during the blight pandemic and (2) sites that varied in time since the last logging event. Current chestnut abundance and chestnut blight prevalence were assessed in areas where chestnut was known to occur before the blight. Elevation, soil pH, slope, aspect, age of canopy trees, and presence or absence of chestnut stumps indicating selective logging of chestnuts were recorded at each site. Chestnuts were more abundant on sites that had not been selectively logged for pre-blight chestnuts. Chestnut presence was more likely at high elevations (857 m ± 33 m). Chestnut abundance was greater at high elevations (>1000 m) and acidic soils (pH 4 to 5). Chestnut blight prevalence was not correlated with any measured environmental variable. Rather, 15.1% of all chestnut stems were infected with blight regardless of chestnut density. Thus, higher chestnut abundance is not due to lower mortality from the chestnut blight, although the temporal dynamics of blight infection and stem recovery were not within the scope of this study. This research shows that local rates of chestnut population decline differ between locations with different chestnut logging histories. Chestnut site preferences are better understood within the context of history, and thus teasing apart the effects of disease, logging, and environment will result in more successful chestnut restoration efforts.

INTRODUCTION

Forests are characterized by complex disturbance histories that drive spatiotemporal patterns of species distributions and functional processes. Traditionally, plant ecologists have viewed climate and topography as the major variables that limit plant species distributions (Curtis and McIntosh, 1951; Whittaker, 1956; Bray and Curtis, 1957). It is now clear that anthropogenic and natural disturbance history must also be considered before forest spatiotemporal patterns and processes can be clearly understood (Shugart and West, 1977; Pickett and White, 1985). For example, logging is known to affect species composition and forest nutrient cycling (Chapin *et al.*, 2002). The effects of multiple disturbances can result in forest spatiotemporal patterns that are different than any single disturbance alone (Veblen *et al.*, 1994; Busby *et al.*, 2008; Garbarino *et al.*, 2009). Specifically, land-use and disease can result in divergent outcomes in population responses and in the re-growth of individuals (Veblen *et al.*, 1994; Kizlinski *et al.*, 2002; Latty *et al.*, 2004; Vepakomma *et al.*, 2010). A disease epidemic causing large-scale tree mortality results in the removal of or change in a species' function within the ecosystem, in the addition of large amounts of coarse woody debris through tree-fall, and in increased light due to opening of canopy gaps (Franklin *et al.*, 1987). These environmental changes affect inter-specific interactions and may also feedback to affect the disease and the host species.

The chestnut blight (*Cryphonectria parasitica* (Murril.) Barr.*)* was the first invasive tree disease to capture national attention in the United States because it affected a valuable and ubiquitous lumber species, the American chestnut (*Castanea dentata* (Marsh.) Borkh.) (Freinkel, 2007). The chestnut blight, introduced from Asia, was identified in 1904 in New York City, and spread throughout the range of the American chestnut during subsequent decades. The spread of chestnut blight occurred during a period of increased timber harvesting in the eastern United States. In the 1920s and 1930s, when the front of the blight pandemic was sweeping across Virginia (Clapper and Gravatt, 1943), demand for chestnut lumber also increased. Landowners were strongly encouraged to cut any chestnuts on their land, first in an attempt to halt disease spread, and later to profit from chestnut lumber before the opportunity was lost (Murrill, 1908; Carleton, 1913; Gravatt, 1914; Kelley, 1924; Gravatt, 1925; White, 1930; Baxter and Gill, 1931). Today, the chestnut blight is endemic, with surviving chestnuts re-sprouting from pre-blight root stocks until re-infection with the blight, after which all above-ground parts of the stem eventually die. The blight does not directly infect and kill roots of the chestnut, although the root system can decline and die following blight infection as a result of inadequate photosynthate production. Almost a century after the blight invaded, chestnuts are declining but not extinct, and their persistence varies across sites of different topographies, soils, and disturbance histories. This scenario is ideal for a study of the long-term effects of logging and disease on host-pathogen interactions, differential tree mortality, and population decline.

Both logging and tree disease remove trees from the canopy and cause dieback via different mechanisms having distinct effects on the environment and inter-specific interactions. Logging can influence pathogen infection rates and thus host species mortality, resulting in complex effects on forest processes such as nutrient cycling, decomposition, and interspecific competition (Lewis and Lindgren, 2000; Kizlinski *et al.*, 2002; Latty *et al.*, 2004). Furthermore, timber harvesting can lead to the homogenization of stand age or species composition, and a decrease in structural diversity may facilitate disease spread (Hebard, 1982; Smallidge *et al.*, 1991). Young trees often have different disease susceptibility than older trees, and thus a younger stand can harbor different rates and patterns of disease spread (Veblen *et al.*, 1994). A relationship between land use and chestnut decline has been indicated in previous studies, but results on the magnitude and direction of the effect differ between studies (Hebard, 1982; Schwadron, 1995; Paillet, 2002; Fei *et al.*, 2007; Elliott and Swank, 2008). Interestingly, with the exception of Hebard (1982), none of these studies measured chestnut blight prevalence, which has a major influence on chestnut decline. It is clear that land use impacts chestnut survival, but the effects of different land use types and their varied timing and intensity are still unclear in the literature.

In addition to an increase in forest disease in North America, cleared land has been returning to forest over the past half-century (Foster *et al.*, 1997). Understanding the individual and combined effects of tree disease and logging will inform forest management and will improve conservation of species declining because of disease, such as the American chestnut. Most studies in disturbance ecology emphasize the effect of one disturbance event rather than characterizing the effect of multiple disturbances. This study will assess the long-term effects of multiple disturbances on host population dynamics and pathogen prevalence. Specifically, the questions addressed in this study were: (1)

Do areas selectively logged for chestnut have different present-day chestnut abundance than areas not logged for chestnut? (2) Does timing of logging (stand age) have long-term effects on chestnut abundance? (3) How does chestnut blight prevalence vary across sites of differing chestnut densities, environment, and history?

METHODS

Study Area

This study was conducted in Giles and Craig Counties, VA, in the Ridge and Valley Physiographic Province of the southern Appalachians of the eastern United States (N 37° 12’ 38” to N 37° 22’ 5”; W 80° 26’ 1” to W 80° 39’ 2”). Bedrock geology in this region varies between limestone in the valleys, sandstone on the ridges, and shale on steep slopes. Average annual temperature is 10.8°C, and average annual precipitation is 101.6 cm (Swecker *et al.*, 1985). Elevation of the study area was between 544 and 1302 m. Most of the study area is Jefferson National Forest, but sections of the study area are on private lands.

Field Methods

Two historical datasets, pre-dating chestnut blight infection in the region, were used to choose sites to re-sample where chestnuts were known to have occurred before the blight: (1) Forest communities covering 22 sites near Mountain Lake Biological Station (MLBS) sampled by station students during the years 1934-1941; (2) Timber cruises of 21 tracts owned by the Craig-Giles Iron Company (CGIC) in 1918. Areas re-visited were in the Jefferson National Forest (JNF), on MLBS land, or on private lands adjacent to JNF or MLBS. The original MLBS studies were conducted on land that had been timbered and, in most cases, burned, while the timber cruise was conducted on land that was a mix of virgin timber and previously cleared land, according to notes in the survey. Most of the land included in the CGIC timber cruise was also burned in the 1920s or 1930s, according to1937 USFS aerial photographs. Only 15 plots (<4%) were located on land that was being used for agriculture in 1937. Thus, agriculture was not an important aspect of land clearing across the study area. Rather, most land clearing was a result of a combination of timbering and burning.

The MLBS studies gave detailed descriptions or maps of the original study plot, but only one plot was permanently marked and thus re-located exactly. For the other 21 study sites, precision varied but only areas that were clearly in the same original stand on the same slope were used. The CGIC timber cruise included a topographical plat map that allowed exact re-locations of the original sampling areas.

Each original sampling area was re-sampled. In 2008 and 2009, chestnut density and site environment were measured on three to ten non-overlapping 0.04 ha circular plots. Plots were usually 150 m apart within a site. In cases where the original sampling site was so small that <3 plots fit into the sampling area at 150 m spacing, spacing between plots was reduced to 50 m. In large sampling areas where >10 plots were to be sampled at 150 m spacing, the spacing between plots was increased to 300 m. The CGIC sampling areas ranged from 8.2 to 1121 ha, in contrast to MLBS areas ranging from 0.1 to 7 ha. In especially large CGIC sampling areas (>55 ha), all of which occurred in JNF, stands designated as the USFS management units (5-81 ha) were selected as a sub-sample within each sampling area. Selection of these stands was based on their canopy composition, the stand age in the USFS Jefferson National Forest Stand Information database, and their accessibility by USFS road. All categories of canopy composition were sampled once in each tract, unless the canopy composition was unlikely to have ever harbored chestnut (e.g., *Tsuga canadensis, Pinus pungens*). Stands that were established between 1900 and 1918 were considered unlikely to have been forested when the timber cruise was conducted and thus were discarded as potential sample sites. In 2007, 11 MLBS study sites were sampled with a different re-sampling method than 2008 and 2009. Four randomly selected transects (500 m^2) were sampled for chestnut abundance throughout the original study area that was re-located, as well as sampling the original 100 m^2 quadrat as closely as possible. After the 2007 field season, this sampling method was replaced with the more efficient regularly-spaced circular plot sampling method used in the rest of the MLBS study sites and all of the CGIC tracts. In the MLBS area, 121 plots were sampled on 22 sites. In the CGIC area, 289 plots were sampled on 21 tracts.

In each 0.04 ha plot, four soil samples were taken to 10 cm depth, each 5.5 m from the plot center in the four ordinal directions, and combined into one plot sample to measure soil pH. In 2007, soil samples were taken in the 10 m x 10 m quadrats but not along transects. Slope was measured with an Abney level, and aspect was measured with a compass. Elevation, latitude, and longitude were measured with a handheld GPS allowed to average for at least 10 minutes.

In each plot (circular, transect, or quadrat), two randomly-selected canopy trees of any species that could be cored (not hollow, rotten, diseased, or excessively crooked) were sampled with an increment borer to calculate year of establishment of the stand. Cores were taken at stump height (60 cm above the ground) rather than breast height to more accurately estimate the age of the tree. At each plot, chestnut wood, if present, was identified by the ring porous structure of the wood, the lack of large rays (as occur in oaks), and the distinctive patterning of the parenchyma cells in the early wood (Hoadley, 1990). Dead chestnut was recorded as either a fallen log with no indication of logging, or a flat stump, indicating selective logging of chestnut. Chestnut wood indicating chestnut logging history was only recorded in 2008 and 2009.

Tree cores were used to calculate time since the last stand-level logging event.

In each sample unit, all chestnut stems above breast height were measured for DBH and height. If a clump of chestnuts sharing a root did not contain a stem above breast height, the tallest stem of the clump was measured (this was uncommon on most sites). Stems within 1 m of each other were designated as the same genet from the same original root following the findings of a genetic study of chestnuts at MLBS (Stilwell *et al.*, 2003). Any stems with chestnut blight conidial pustules were noted as infected with the chestnut blight.

The center of each 0.04 ha plot was used as the center for variable radius sampling of canopy basal area. A 4.59 basal area factor (BAF) wedge prism, which is generally used in mixed hardwood forests of the Appalachians (Zeide and Troxell, 1979; Wiant *et al.*, 1984; Packard and Radtke, 2007), was used to select overstory trees to measure and record forest species composition. On especially steep slopes (>15% grade), the Cruiser's Crutch (Forestry Suppliers, English Model) at 4.59 BAF was used instead of the wedge prism because it accounts for error due to slope. The distance to borderline trees, meaning trees that were difficult to determine using the wedge prism if they were within the variable sampling radius, was measured in order to ascertain if they should be included in the sample. Only very large trees (>48.4 cm dbh) fell outside of the 0.04 ha plot boundaries. Trees <10 cm DBH were not used in data analysis for calculation of basal area per hectare because the wedge prism method is known to have increased error at low DBH by inflating the density of small trees (Packard and Radtke, 2007). The DBH of trees that were within the sampling radius of the wedge prism was recorded.

Laboratory Methods

Soil samples were frozen until analysis was performed. Before analysis, soils were air-dried for 24 hours and sifted through 2 mm mesh. A 2:1 (by mass) water to soil slurry was prepared, and pH was measured with a calibrated pH meter (Thermo Orion Model 420A) (Watson and Brown, 1998).

All cores were mounted and then sanded with increasingly finer grit sandpaper to 600 grit. Only complete cores that had a clear inner ring, defined as a clear semi-circle that showed that cores had reached the center (though not necessarily the pith) of the tree, were used. This year of tree establishment was averaged across the two cores in each plot, and from here on will be referred to as year of establishment.

Data Analysis

In all analyses, slope and aspect were converted to a measure of solar insolation following McCune and Keon (2002). This transformation puts aspect on an ordinal rather than a cardinal scale and incorporates steepness of slope in the calculation of solar radiation, unlike the similar conversion for heat load index. Spatial autocorrelation of variance in number of chestnuts between plots was tested with a Mantel test using the function mantel.rtest in the “ade4” package in R, across all plots visited in 2007, 2008, and 2009 (Crawley, 2007). A variogram was created using the “variog” function in the spatial library in R to plot variance in number of chestnuts per plot with spatial distance between plots.

A generalized linear model of number of chestnut genets with chestnut logging as a two-state class variable, in addition to continuous independent variables solar insolation, soil pH, elevation, canopy basal area per hectare, and year of establishment, was analyzed using PROC GENMOD in SAS v. 9.1 (SAS Institute, Cary, NC). Errors were assumed to be Poisson distributed, and the model was corrected for overdispersion by dividing the deviance by the degrees of freedom using the SCALE = DEVIANCE option in the MODEL statement. Three plots with extremely high z-scores (4.32, 5.03, and 7.71) for number of chestnut genets were deleted as outliers, leaving a total of 130 plots for analysis. Four additional missing values due to poor quality cores left a total of 126 plots in the analysis (83 not logged and 43 logged).

To understand the effects of environment and canopy stand age on chestnut presence, a logistic regression with forward selection of independent variables was used to determine the effect of year of establishment, solar insolation, elevation, canopy basal area per hectare, and soil pH in predicting chestnut presence using PROC LOGISTIC in SAS v.9.1 (SAS Institute, Cary, NC). Nine plots were deleted due to missing values because of poor quality cores, leaving 353 plots in the analysis (130 with chestnut present and 223 with chestnut absent) covering both MLBS and CGIC sampling areas.

Sites in both MLBS and CGIC areas with chestnut present were analyzed for the canonical correlation of environmental variables with chestnut abundance in PROC CANCORR SAS v.9.1 (SAS Institute, Cary, NC). There were 140 sites with chestnut present in the analysis, but 3 sites were not used because of missing estimates of year of establishment. Number of chestnut genets was positively skewed and therefore was transformed to natural logarithms to meet assumptions of normality.

The same 140 sites were then analyzed for the canonical correlation of chestnut blight prevalence with the environmental variables. Blight prevalence was transformed by taking the arcsine of the square root of blight prevalence to meet assumptions of normality.

To determine whether blight prevalence was density dependent or density independent with respect to chestnut stem density, a stepwise multiple regression was used to determine if number of chestnut stems infected with blight was better predicted by total number of chestnut stems per 0.04 ha, indicating density independence, or by including the square of total number of chestnut stems per 0.04 ha, indicating density dependence using PROC REG (SAS Institute, Cary, NC, USA). Data from 2007, 2008, and 2009 were pooled, covering both MLBS and CGIC areas, so there were 405 plots in this analysis.

RESULTS

405 plots were sampled. They ranged in elevation 544-1302 m, in solar insolation 0.50-1.07 MJ cm^{-2} yr^{-1}, in year of establishment from 1778 to 1999, and in soil pH 3.00-5.98. Number of chestnut stems per hectare varied from 0 to 3775, and number of chestnut genets per hectare varied from 0 to 1900. Chestnut tree remains, indicating whether or not chestnuts had been selectively logged, were found at 129 of the 405 sites. Spatial autocorrelation between variance in number of chestnut genets per plot and spatial distance between plots was weak but significant ($r = 0.049$, $p = 0.024$, $n = 405$). The variogram showed a peak in autocorrelation at 4000 m, which is close to the average distance between stands of 3013 m. The variogram showed another peak at 17.5 km, which is close to the distance between the MLBS study area and the centroid of the CGIC study area. The MLBS study area is higher in elevation than the CGIC study area, which accounts for the second peak seen in the variogram.

In a generalized linear model of the dependence of chestnut abundance (number of chestnut genets per 0.04 ha) on the continuous environmental variables (elevation, solar insolation, soil pH, canopy basal area per hectare, and average year of establishment) and on the binary variable chestnut logging history, chestnut logging history was the only significant independent variable (X^2 = 5.32, p = 0.021, df = 119) (Fig 1). There was no significant difference between year of establishment in chestnut logged or unlogged sites. Mean year of establishment dated to 1916 in the chestnut logged sites (median = 1930, ranging 1807-1982). Mean year of establishment dated to 1919 in the unlogged sites (median = 1931, ranging 1778-1974).

In the logistic regression of chestnut presence or absence, the only significant environmental variable among elevation, solar insolation, soil pH, and average year of establishment was elevation (X^2 = 9.76, df = 1, p = 0.0018; Fig 2). There was good model fit using elevation as the sole predictor (X^2 = 3.84, p = 0.43, df = 4). Elevation was not significantly correlated with any other environmental variable using Pearson's correlation, although solar insolation and soil pH were almost significant (respectively, r = 0.099, p = 0.055; and r = 0.097, p = 0.063). In the model without the environmental predictors, the model was not a good predictor because the null model of the logistic curve fitting the data was rejected (X^2 = 13.50, p = 0.019, df = 5). The full model including elevation found 62.0 % of predictions of chestnut presence were concordant with the observed data. The odds ratio estimate was 1.002, indicating that for every 1 m increase in elevation, the odds of chestnut being present are 1.002 times greater (Tabachnick and Fidell, 2007).

On sites where chestnut was present, the canonical correlation between chestnut abundance and the same five environmental variables was 0.53 and was significant ($F_{5, 130} = 10.16$; $p < 0.0001$; Table 1). The environmental variables with highest canonical coefficients on the first canonical variate with chestnut abundance in the analysis were elevation (0.909), soil pH (0.601), and canopy basal area (0.322) (Table 1 and Fig 3). The assumption of linearity between the independent variables and the response variables was tested by comparing a linear regression of each independent variable with the dependent variable (chestnut genet abundance) to the quadratic regression. In no case was the quadratic regression a better fit to the data.

The canonical correlation of the same environmental variables with chestnut blight prevalence was 0.25 and was not significant, although the p-value was low ($F_{5, 130} = 1.73$; $p = 0.132$; Table 1). Canopy basal area per hectare was very strongly correlated to blight prevalence in this analysis ($r = -0.992$). The assumption of linearity in this canonical correlation was also tested in the same way as described in the previous paragraph. In the multiple regression analysis, only the linear relationship between number of blighted genets and total number of genets was significant ($F_{2, 402} = 568.41$, $p < 0.0001$; Fig 4). The mean square error for the linear model was 2.053, and the mean square error for the quadratic model was 1.930. Dividing the linear model's mean square error by the quadratic model's mean square error yields an F statistic of 1.064, showing that the quadratic model was not significantly better than the linear model. Overall, 15.1% of the total genets were infected with chestnut blight.

DISCUSSION

The purpose of this study was to understand the effects of logging and the chestnut blight on the current distribution of the American chestnut in southwestern Virginia, USA. Chestnuts were more abundant on sites that had not been selectively logged for pre-blight chestnuts. However, canopy stand age (as indicated by year of establishment) was not shown to affect chestnut presence or its abundance. Chestnut presence was more likely at high elevations, and chestnut abundance was strongly correlated with elevation and soil pH. Chestnut blight prevalence was not found to be correlated with these or any other environmental variables. Rather, chestnut blight showed a distribution independent of chestnut density, with 15.1% of all stems infected with blight regardless of chestnut density. Thus, despite the fact that I found that chestnut abundance is greater at higher elevations and higher acidic soil pH, my data do not suggest that this higher abundance is due to lower mortality from the chestnut blight because chestnut blight prevalence was not lower at these sites.

Selective logging of the chestnut during the blight pandemic has often been suggested as the reason why so few trees free of blight are found today (Kelley, 1924; White, 1930; Clapper and Gravatt, 1943). This study indicates that chestnut abundance was significantly lower on sites that had been selectively logged for chestnut than on sites that had not been logged for chestnut. This result is consistent with a study by Elliott and Swank (2008), whose data suggest lower chestnut abundance was found in areas where a higher basal area was removed in a selective logging event of oak and chestnut in the 1930s. The lack of difference in stand age (as indicated by year of establishment) between chestnut logged and unlogged sites could be for three reasons: (1) Selective logging events were not detected by the stand age because old and young trees are more likely to co-occur on a site than after a more extensive cut (Oliver and Larson, 1996); (2) Most of these sites were burned in the 1920s or 1930s, according to USDA 1937 aerial photographs, notes in the MLBS studies, and communication with local residents in the area; and (3) If the oldest stems in forests dominated by chestnut were chestnut stems, then the trees cored in this study would have been those that were released by the chestnut death rather than regeneration that occurred as a result of the logging event.

There was no relationship between canopy stand age and chestnut presence or abundance. Characterizing logging history at the landscape scale is extremely difficult, because sites vary in the number of times they were logged *before* the last logging event, in the intensity of logging (high-grade to clearcut), and in the history of other disturbance events such as fire or storm damage. Other studies at the stand scale have suggested an effect of logging or clearing on chestnuts. Hebard (1982) found that blight epidemics erupted 10 years after a clearcut, indicating increased susceptibility to or transmission of chestnut blight once the chestnut stems reach 10 years of age. In contrast, Paillet (1988) and Schwadron (1995) found higher chestnut abundance on fields abandoned (presumably with young chestnut seedlings) immediately prior to blight introduction to the area, indicating a positive effect of land clearing. However, Fei et al. (2007) found the opposite to be the case with fewer chestnuts on previously agricultural land. My study uses average canopy tree age as a gauge for time since last clearing, but other details on land use history prior to 1937, such as pasturing, agricultural crops, or multiple lumbering events, were not available. Giles and Craig Counties were settled in the late 1700s and early 1800s. At that time, land was cleared for lumber and agriculture simultaneously. Timber harvesting, when not clearing land for agriculture, was usually selective. Pastures encompassed cleared and wooded land, so that livestock often ranged across wide unfenced areas (Davis, 2000). It was not until the early to mid 1900s that clear-cutting trees for the sole purpose of acquiring lumber became a prevalent practice in the southern Appalachians (Davis, 2000). Although most of the sites I studied were too high in elevation to have experienced tillage, many were cleared or timbered, either selectively or commercially clearcut, multiple times.

Sites were also subjected to livestock grazing, at varying degrees of intensity, which depended on number of livestock owned and distance from the owner's farm. In addition, all sites have some history of burning, though the intensity and frequency of these fires are generally not recorded. Thus, the effects of logging and land clearing on chestnut persistence may be site-specific and highly complex, which could obscure any relationship between timing of last logging event and chestnut abundance.

The timing of logging may influence the magnitude of chestnut decline. Chestnut stems are less susceptible to the blight when young (Milgroom and Cortesi, 2004), so forests that were young when the blight invaded may have experienced lower blight infection. However, one could argue that younger roots would have a less developed system that could not re-sprout as easily following dieback (Harmon *et al.*, 1983). In such a scenario, older forests would have a greater number of chestnut sprouts surviving after blight infection and die-back. The physiology of chestnut root-shoot dynamics with age, especially allocation to growth or defense, has not been studied well (but see Zon 1904). The effect of timing of logging on chestnut persistence merits more study because of logging's known effects on light reaching the understory, homogenization of age and species composition, and the age of the pre-blight chestnuts at initial blight infection.

Elevation was found to be an important predictor of chestnut presence and also strongly correlated with chestnut abundance, and soil pH was also strongly correlated with chestnut abundance. Other studies of chestnut abundance have not found elevation to be a significantly correlated variable but also did not compare chestnut abundance across sites of such a wide range of elevations (Stephenson *et al.*, 1991; Fei *et al.*, 2007). This increase in chestnut abundance with increasing elevation would be reversed at some maximum elevation for chestnut. Chestnut's ideal elevation is likely different across variation in latitude. Stephenson *et al.* (1991)and Fei *et al.* (2007) did not measure soil pH, but Fei *et al.* (2007) did find that chestnut presence was associated with local geology. In particular, presence differed between sandstone ridges and limestone slopes, and these bedrock geologies are tightly coupled with soil pH in this region. Chestnut does not grow as well on more basic, limestone soils (Russell, 1987). All the soils sampled in this study were acidic, but chestnut showed a preference for a higher soil pH (4 to 5) within this range (Fig 3).

Canopy density, estimated by basal area per hectare of canopy trees, has an important effect on understory trees. This variable was weakly correlated with chestnut genet abundance and with blight prevalence. Sites with high chestnut abundance also had high canopy basal area, especially at high elevations. Greater chestnut abundance on shady sites may be because chestnut's shade tolerance allows it to outcompete other understory trees, or because chestnut blight's infection rate is lower on shady sites. The strong trend that chestnut blight was less prevalent on sites with high canopy basal area supports the second hypothesis. This result is supported by a study by Griffin (1992) that found that mesic sites with high canopy basal area also had high chestnut survival. However, Griffin *et al.* (1991) showed that in young forests (13 or 19 year-old clearcuts), chestnut survival was inversely related to canopy basal area. Clearly, canopy density affects chestnut mortality. However, other variables may interact with this effect. In this study, chestnut abundance was highest on high-elevation sites with moderate soil acidity and high canopy basal area.

I expected that chestnut was more abundant in specific environments because chestnut blight was less prevalent in these environments. In this study, for example, I found that chestnut was more likely to be present and was more abundant at high elevations. Thus, I expected chestnut blight to be less prevalent at high elevations. However, this study did not support this prediction. Chestnut blight prevalence was not significantly related to elevation or any other environmental variable. In fact, number of chestnut blight infections did not appear to be dependent on chestnut density. No study has compared chestnut blight prevalence across stands of varying chestnut density before this study. A stand-level study at MLBS found that likelihood of chestnut blight infection of a healthy stem was not related to distance to the nearest infected stem (Milo, 2009). The dispersal distance of chestnut blight is probably quite large because the spores are dispersed by wind and birds, so if spores in this area are ubiquitous, probability of infection could be related to factors other than distance from infection. Although chestnut blight has been identified with and without pycnidia or stroma on scarlet oaks (*Quercus coccinea*) and possibly could be present on other oaks (Torsello *et al.*, 1994), signs of spore dispersal on tree species besides chestnut were never observed in this study area. It seems more likely that the major source of blight inoculum in this area is other infected or recently dead chestnut stems, but the epidemiological importance of blight's ability to grow on other species merits further study.

This study shows that disease and logging affect chestnut abundance today, suggesting different rates of decline in chestnut populations in locations logged for chestnut and not logged, so that population numbers are different eighty years following these disturbances. Chestnut abundance and decline are better understood within the context of history, and thus teasing apart the effects of disease, logging, and environment will result in more successfully planned chestnut conservation efforts. Chestnut blight transmission rate, spatial spread, and temporal dynamics are not understood in historical or contemporary settings. Better prediction of chestnut blight infection is an important future direction in understanding chestnut mortality and in managing chestnut restoration. Chestnut has been declining since blight introduction, and this decline varies spatially. This study suggests that this spatial variance in chestnut's decline is not due to variance in chestnut blight prevalence. However, given blight's known effect on chestnut decline, chestnut blight's patterns of infection are likely temporally complex, and chestnut's ability to recover and re-sprout also likely varies spatiotemporally. Study of spatiotemporal patterns of blight infection and chestnut recovery across different environments in a landscape would provide valuable information on minimizing chestnut mortality due to blight. Multiple disturbances can have long-term impacts of plant distribution different from the effect of one disturbance alone. Further studies of multiple disturbances are important for predicting spatiotemporal patterns of forest composition.

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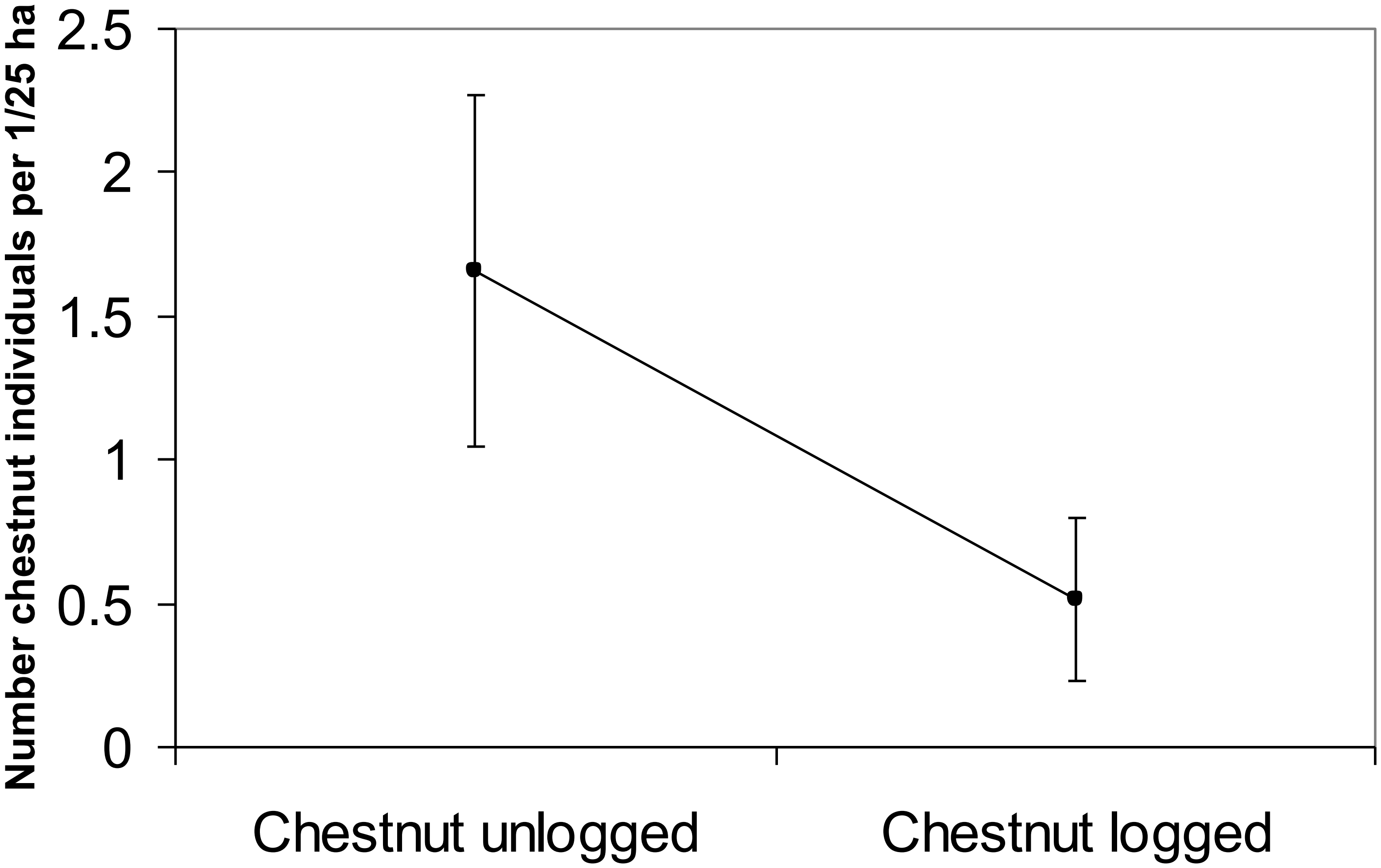
TABLES

Table 1. Canonical correlation of environmental variables with chestnut abundance Elevation and soil pH were most correlated to chestnut abundance. Canopy basal area was most related to chestnut blight prevalence, although the canonical correlation was not significant. Correlations >0.30 are bold-faced.

Variable	**Standardized correlation with number of chestnuts**	**Canonical coefficient**	**Standardized correlation with blight prevalence**	**Canonical coefficient**
Canopy basal area	**0.322**	0.326	**-0.992**	-1.018
Elevation	**0.909**	0.812	0.060	-0.022
Soil pH	**0.601**	0.235	-0.015	0.132
Solar insolation	0.231	0.078	0.168	0.002
Year of establishment	-0.023	0.083	0.146	-0.046

FIGURES



Number chestnut individuals per 1/25 ha
2.5
2
1.5
1
0.5
0
Chestnut unlogged
Chestnut logged

Figure 1

Figure 1. Chestnut genet abundance with Selective Logging History. Comparison of number of chestnut genets in sites where pre-blight chestnuts were logged and sites where pre-blight chestnuts were not logged. The class variable of chestnut logging was the only significant variable affecting number of chestnuts, as determined by a generalized linear model of environmental variables' effects on chestnut abundance. Error bars are 95% Confidence Intervals.

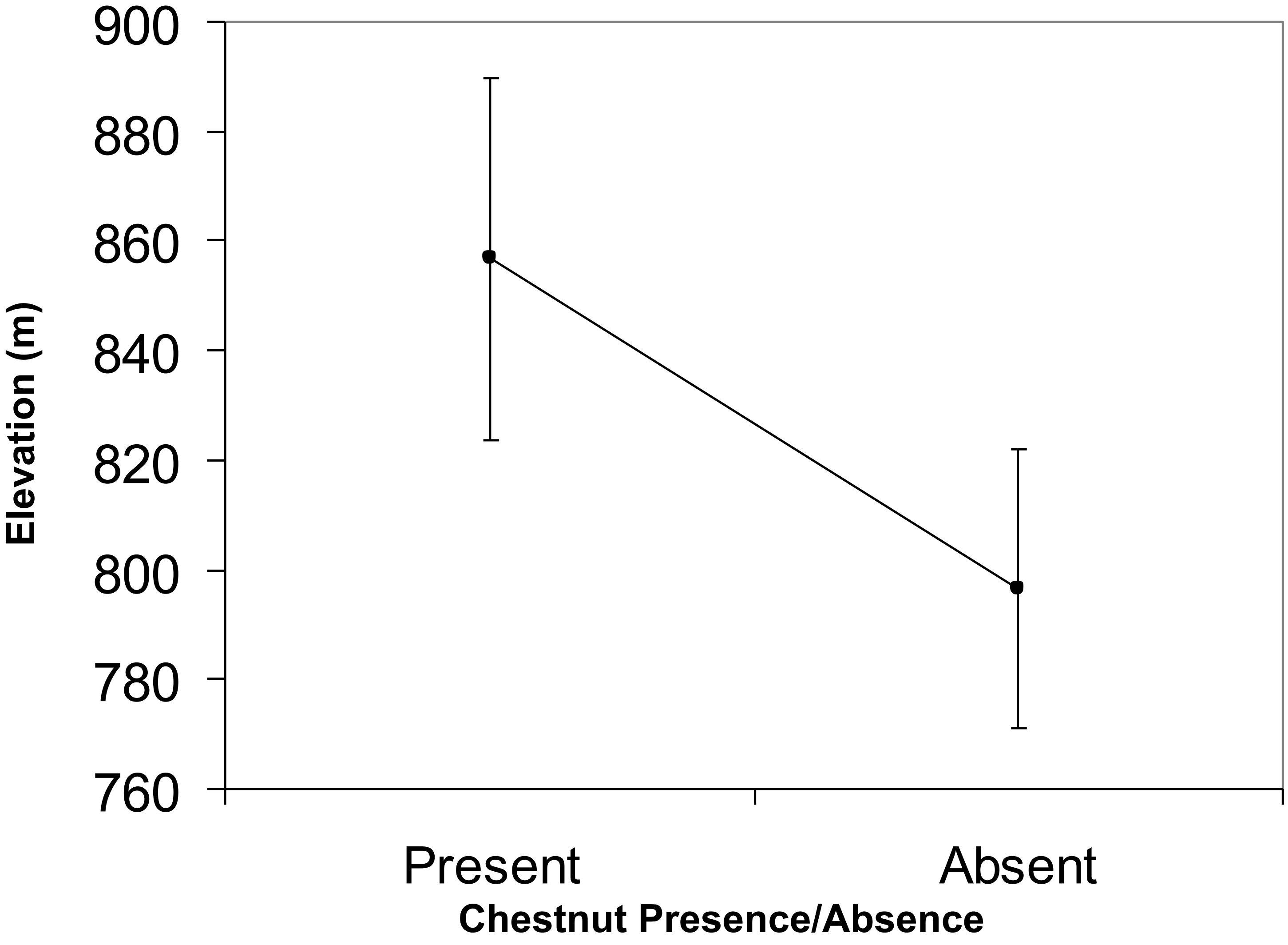
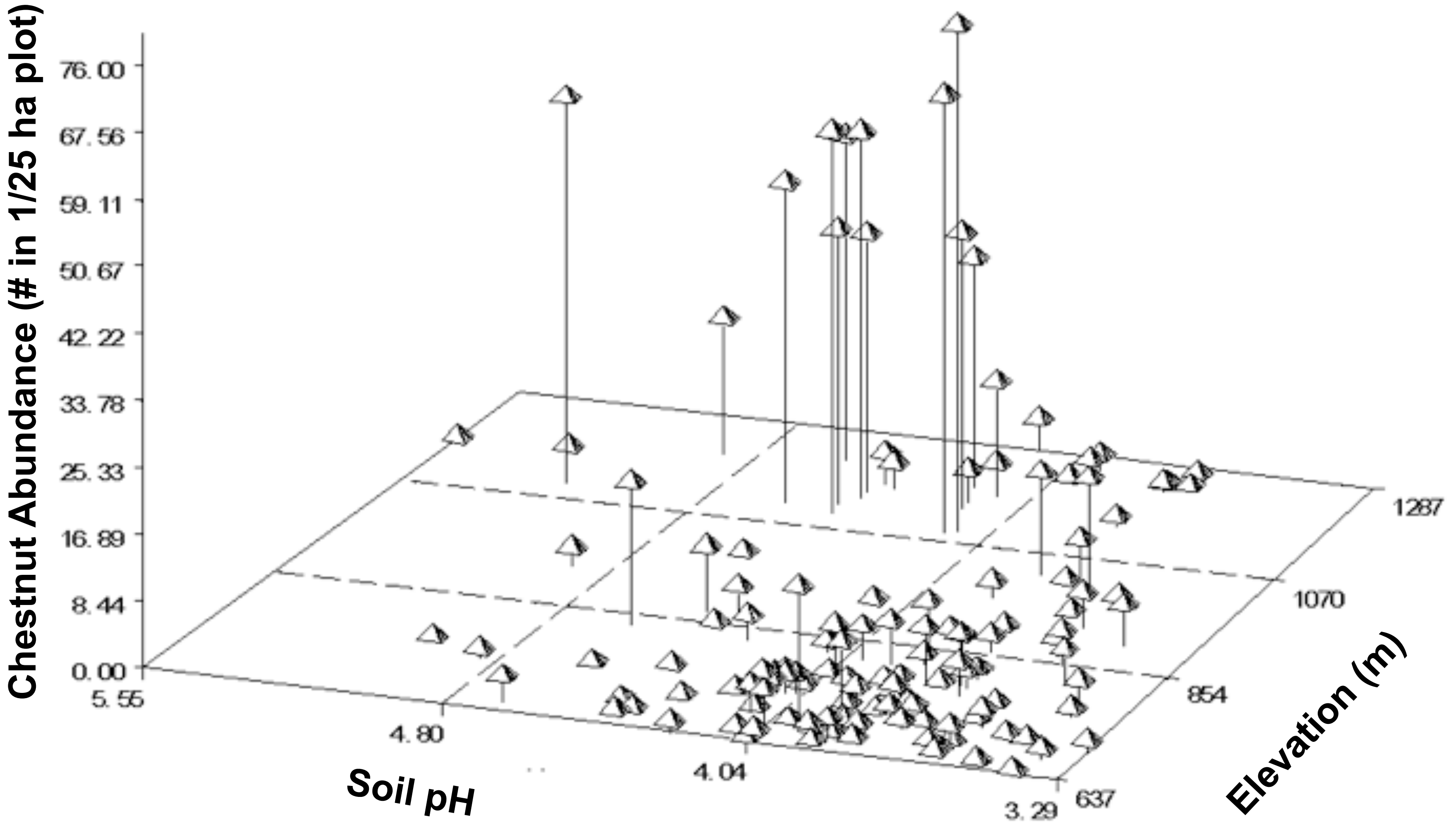

900
880
860
840
820
800
780
760
Elevation (m)
Present
Absent
Chestnut Presence/Absence

Figure 2

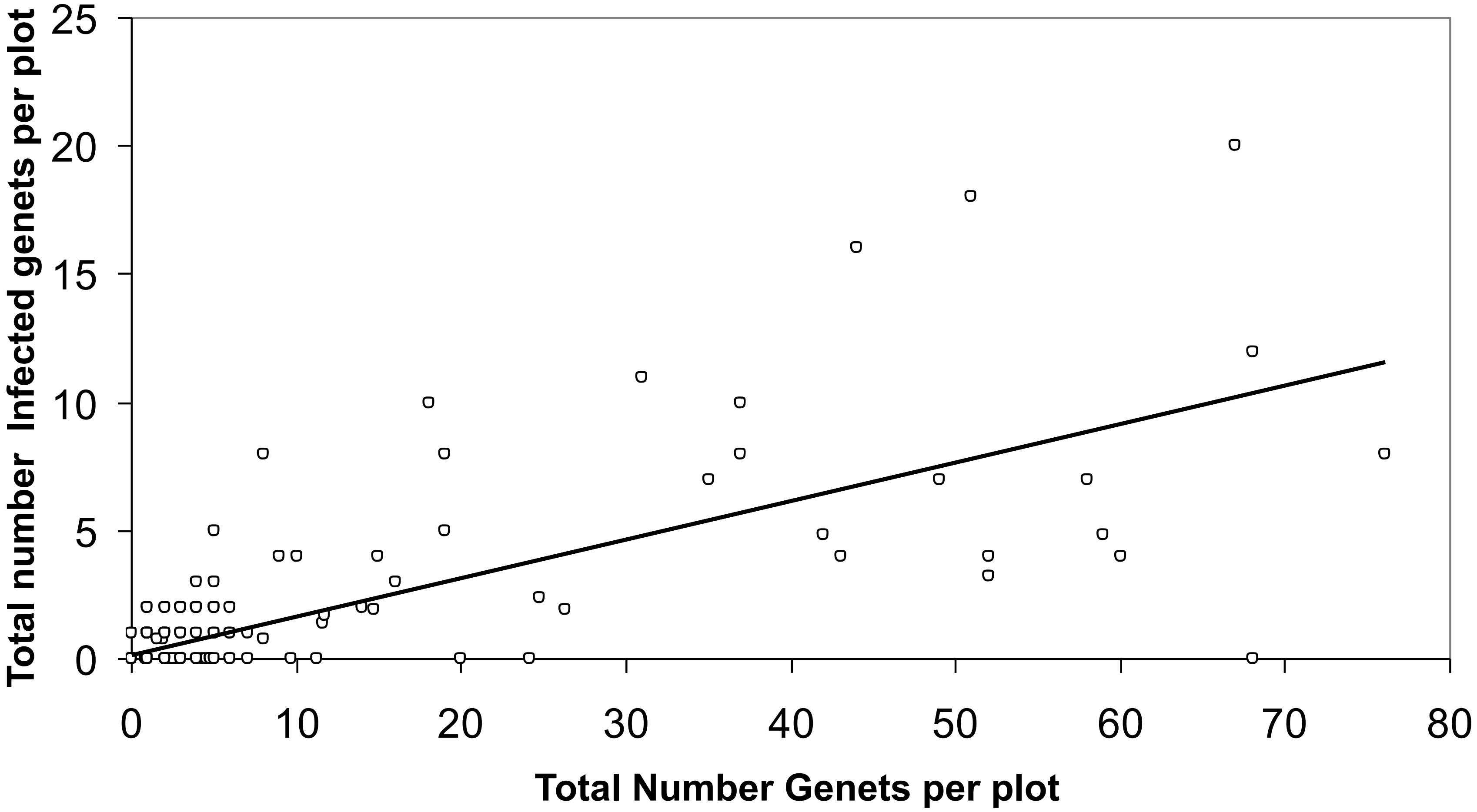
Figure 2. Elevation Predicted Chestnut Presence by Logistic Regression. Average elevation of sites with chestnut present compared to average elevation of sites without chestnut. Elevation was the only significant predictor of chestnut presence in a logistic regression of environmental variables with chestnut presence. Error bars are 95% Confidence Intervals.



Chestnut Abundance (# in 1/25 ha plot)
76.00
67.56
59.11
50.67
42.22
33.78
25.33
16.89
8.44
0.00
5.55
4.80
4.04
3.29
Soil pH
637
854
1070
1287
Elevation (m)

Figure 3

Figure 3. Soil pH and Elevation plotted against chestnut abundance. Soil pH and Elevation were the only environmental variables found to be strongly correlated with chestnut abundance (Standardized canonical correlations were 0.60 and 0.96, respectively; N = 140).



Total number Infected genets per plot
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
Total Number Genets per plot

Figure 4

Figure 4. Number of infected genets versus total number of chestnut genets. A stepwise multiple regression testing a linear (density independent) or quadratic (density dependent) relationship, found the quadratic model was not a significantly better fit than the linear model. Thus, chestnut blight infection is independent of chestnut density at the scale of this study, with 15.1% of the total genets infected.

CHAPTER 2

Niche contraction and long-term decline of American chestnut in response to chestnut blight

ABSTRACT

Invasive pathogens can cause native population declines and change native species distributions. This study explored spatiotemporal variation in American chestnut (*Castanea dentata*) survival over an eighty-year period in response to the introduction of an invasive pathogen, chestnut blight (*Cryphonectria parasitica*), and identified changes by comparing its current realized niche with its original niche. Two study areas sampled for chestnut volume and abundance before blight invasion in southwestern Virginia, U.S.A., were re-sampled, and measures of topography, soil chemistry, and forest composition were taken. Pre-blight chestnut abundance was not significantly correlated to current chestnut abundance, suggesting that chestnut survival rate was not constant across stands. A principal components analysis was used to represent the variation in environment with fewer variables. Multiple regressions of principal components representing environmental variation with pre-blight chestnut abundance and with current chestnut abundance were analyzed. Principal components that were significantly related to pre-blight chestnut abundance were not the same principal components significantly related to current chestnut abundance. Further, significant slope differences were found between linear models of pre-blight and current chestnut abundance with two principal components that were highly related to a gradient in solar insolation, and in mesic to xeric species, indicating a shift in chestnut's niche toward dry sites on southern to western facing slopes. Post-blight chestnut abundance was most related to principal components representing habitats with high *Quercus montana* basal area. If survival rates remain constant, 53% of all sampled stands are expected to be extinct in 224 years, and 95% extinct in 1103 years. This study provides evidence that chestnut is being constrained to a portion of its former niche following chestnut blight introduction because of spatial heterogeneity in survival rate.

INTRODUCTION

Invasive pathogens are known to cause population declines (de Castro and Bolker 2005, Smith et al. 2006, Antonovics 2009, Smith et al. 2009). Range limitation or niche contraction, even to the point of extinction, can result from invasive pathogen introduction (deCastro and Bolker 2005). While studies have explored the niche shift of introduced, invading species from their original native niche to a new niche (Broennimann et al. 2007, Pearman et al. 2008, Steiner et al. 2008, Treier et al. 2009, Medley 2010), few studies have explored long-term niche contraction of a native species after the introduction of an invasive disease. The patterns of niche shift and range limitation imposed by novel diseases are not well-studied (Kauffman and Jules 2006, Antonovics 2009). This study explores spatiotemporal variation in tree host decline over an eighty-year period in response to an invasive pathogen and identifies changes in current realized niche compared to the original niche.

Chestnut blight (*Cryphonectria parasitica* (Murril.) Barr.) is an invasive fungal disease native to Asia that infects trees in the genus *Castanea* (Fairchild 1913, Shear and Stevens 1916). The American chestnut (*Castanea dentata* (Marsh.) Borkh.), which was a canopy-dominant tree in eastern deciduous forests of North America before the early to mid-twentieth century, has been declining since the introduction of the chestnut blight in 1904. The century-long decline of chestnut provides a unique opportunity to study niche contraction and population decline in response to a pathogen invasion. Chestnut blight prevents nearly all modern-day chestnut plants from reaching reproductive age. The pathogen cannot infect belowground tissues, so a tree can continue to produce new sprouts from its root collar following infection. Chestnut rarely reproduces in the wild and does not disperse. Thus, populations are restricted to the portions of the original niche at the time of initial blight infection.

Over the past century, the status of chestnut has changed from a dominant or co-dominant, nut-bearing, canopy tree to a small, understory tree that survives through re-sprouting from the roots and is essentially sterilized in that it rarely reaches a size that produces viable fruit. Many studies have assessed chestnut community change over time (Nelson 1955, Woods and Shanks 1959, Day and Monk 1974, Lorimer 1976, McCormick and Platt 1980, Stephenson 1986, Agrawal and Stephenson 1995, Elliott and Swank 2008). However, no studies have considered environmental interactions with chestnut population decline over large spatial and temporal scales because historical datasets that include chestnut abundance are rare. Many previous studies confirm that chestnut populations are declining (Braun 1950, McCormick and Platt 1980, Stephenson 1986, Parker et al. 1993, Agrawal and Stephenson 1995, Elliott and Swank 2008). Fifty-three percent of trees were lost on a site in southwestern Virginia, USA, from 1982 to 1988 (Parker et al. 1993). However, chestnut sprouts can advance to older age classes and larger size classes (Stephens and Waggoner 1980, Paillet 1982, Davelos and Jarosz 2004), so over short term periods of monitoring chestnut sprouts, one may see population or biomass increases even though the population has likely declined from pre-blight numbers due to lack of reproduction by seed. Now that blight is endemic in populations across the original range of chestnut, mortality occurs without replacement in the overall population, and local or range-wide extinction of the chestnut is possible. Exploring the variation in probability of local extinction across a landscape would inform conservation efforts as well as provide currently unknown information about the spatiotemporal effects of chestnut blight.

The areas where chestnut is most abundant today as an understory tree may not be where chestnut was once most abundant as a canopy tree, because of its restriction to the understory and because of variance in probability and effect of chestnut blight infection across space and time. Although chestnut is classified as moderately shade-tolerant (Joesting et al. 2007, Joesting et al. 2009), in its new position as an understory tree, shade has a major effect on chestnut's competitive ability. Studies have suggested that current chestnut growth and abundance are greater on sites with higher light availability (Paillet 1988, Griffin 1989, Griffin 1992). Whittaker (1956) and Braun (1950) showed that pre-blight chestnut was a generalist that could grow in a wide variety of environments, but that it grew best on mid- to high- elevation, xeric sites, that often had higher light than lower elevation stands. Chestnut's ability to re-sprout following blight infection is likely to also vary with nutrient dynamics and light availability, resulting in chestnut becoming restricted to a portion of its former realized niche.

Before the introduction of the blight, chestnut accounted for a large portion of the biomass and primary production of southern Appalachian deciduous forests, and it provided fall mast for primary consumers (Braun 1950, Ellison et al. 2005, Freinkel 2007). Understanding the variation in survival rate across the environment will better inform chestnut conservation efforts, the reduction of chestnut's realized niche, and spatial variation in decline and local extinction. The questions answered in this study are: 1) Is chestnut abundance before the blight correlated with chestnut abundance after the blight, indicating a similarity in pre-blight and post-blight niche space and constant population decline across all sites? 2) How do chestnut's pre- and post-blight niches compare? Was there a niche shift? 3) What environmental conditions favor chestnut survival? 4) When is chestnut predicted to become locally extinct in southwestern Virginia?

METHODS

Study Site

This study was conducted in Giles and Craig Counties, VA, in the Ridge and Valley Physiographic Province of the southern Appalachians of the eastern United States (N 37° 12' 38" to N 37° 22' 5"; W 80° 26' 1" to W 80° 39' 2"). Average annual temperature is 10.8°C, and average annual precipitation is 101.6 cm (Swecker et al. 1985). Bedrock geology in this region varies between limestone in the valleys, sandstone on the ridges, and shale on steep slopes. Elevation of the study area was between 544 and 1302 m. Most of the study area was within the Jefferson National Forest (JNF), but sections were on private lands.

Field Methods

Two areas surveyed before chestnut blight's appearance in the region were re-sampled: (1) Forest communities at 22 sites near Mountain Lake Biological Station (MLBS), originally sampled by station students during the years 1934-1941; and (2) Timber surveys of 17 tracts owned by the Craig-Giles Iron Company (CGIC) carried out in 1918. The original MLBS studies were conducted on land that had been cut for timber and, in most cases, the residueal logging slash burned after timber harvesting. The timber survey was conducted on land that was a mix of virgin timber and previously cleared land. Most of the land included in the CGIC timber survey was also burned in the 1920s or 1930s (USDA 1937). The MLBS studies gave detailed descriptions or maps of the original site, but only one site was permanently marked and thus re-located exactly. For the other 21 locations, precision varied but only areas that were in the same stand and on the same slope as the original sampling site were used. The CGIC timber survey included a topographical plat map that allowed exact re-locations of the original tracts. These areas were near (some plots < 1 km) two seminal studies of forest ecology in oak-chestnut forests, Braun (1950) and McCormick and Platt (1980). Braun (1950) found 80% chestnuts in the canopy on a slope near Mountain Lake, but this study could not be included in the re-sampling because she measured frequency (number of stems of species per total stems of all species) rather than density (number of stems of a species per unit area) of tree species. Frequency can change drastically over succession, and decline cannot be calculated without knowing the size of Braun's sampling area. The exact location of the original sampling area for McCormick and Platt (1980) is no longer documented (McCormick, *pers. comm.*).

Each original site of the Craig-Giles Iron Company timber survey and of the MLBS studies was re-sampled as follows. In 2008 and 2009, chestnut density and environmental variables were measured on three to ten non-overlapping 0.04 ha circular plots at each site. Plots were usually 150 m apart within a site. In cases where the original sampling site was so small that <3 plots fit into the sampling area at 150 m spacing, spacing between plots was reduced to 50 m. In large sampling areas where >10 plots were to be sampled at 150 m spacing, the spacing between plots was increased to 300 m. The CGIC tracts ranged from 8.2 to 1121 ha, in contrast to MLBS sites ranging from 0.1 to 7 ha. In especially large CGIC tracts, all of which occurred in JNF, a sub-sample of management units (5-81 ha) were surveyed within each tract. Selection of these stands was based on their canopy composition category, the stand age in the USFS JNF information, and their accessibility by USFS road. All categories of canopy composition were sampled once in each tract, unless the canopy composition was unlikely to have ever harbored chestnut (e.g., stands dominated by *Tsuga* *canadensis or, Pinus pungens*). Stands that were established between 1900 and 1918 (using JNF Blacksburg Ranger District Stand Information, *unpublished data*) were considered unlikely to have been forested when the timber survey was conducted and thus were discarded as potential sample sites. In the MLBS area, 121 plots were sampled on 22 sites. In the CGIC area, 257 plots were sampled on 17 tracts.

In each plot, all chestnut stems above breast height were measured for diameter at breast height (DBH) and height, measured from the ground to the highest living meristem. If a clump of chestnuts sharing a root collar (i.e., a genet) did not contain a stem above breast height, the tallest stem of the clump was measured (this was uncommon on most sites). Stems within 1 m of each other were counted as being part of the same genet from the same original root following the findings of a genetic study of chestnuts at MLBS (Stilwell et al. 2003).

The center of each 0.04 ha plot was used as the center for variable radius sampling of canopy composition. A 4.59 m^2/ha (20 ft^2/acre) basal area factor (BAF) wedge prism, which is generally used to measure basal area in mixed hardwood forests of the Appalachians (Zeide and Troxell 1979, Wiant et al. 1984, Packard and Radtke 2007), was used to measure and record forest species composition. On especially steep slopes (>15% grade), the Cruiser's Crutch (Forestry Suppliers, English Model) at 4.59 m^2/ha BAF was used instead of the wedge prism because it accounts for error due to slope. The distances to borderline trees, meaning trees that were difficult to determine using the wedge prism if they were within the variable sampling radius, were measured to ascertain if they should be included in the sample. Only very large trees (>48.4 cm dbh) fell outside of the 0.04 ha plot boundaries used to measure number of chestnuts. Trees <10 cm DBH were measured but were not used in data analysis for calculation of basal area per hectare because the wedge prism method is known at low DBH to inflate the density of small trees (Packard and Radtke 2007). Trees that were within the sampling radius of the wedge prism were identified to species, and their DBH was recorded.

In each 0.04 ha plot, four soil samples were taken to 10 cm depth, each 5.5 m from the plot center in the four cardinal directions, and combined into one plot sample to measure soil pH and soil C:N. Slope was measured with an Abney level, and aspect was measured with a compass. Solar insolation was calculated from slope and aspect following Equation 3 in McCune and Keon (2002). Elevation, latitude, and longitude were measured with a handheld Global Positioning System (GPS) allowed to average fixes for at least 10 minutes. In each plot, two randomly-selected canopy trees of any species that could be sampled (not hollow, rotten, diseased, or excessively crooked) were cored with an increment borer to calculate year of establishment of the stand. Cores were taken at stump height (60 cm above the ground) rather than breast height to more accurately estimate the age of the tree.

Laboratory Analysis

Soil samples were frozen until analysis. Soils were air-dried for 24 hours and sifted through a 2 mm mesh sieve. To measure soil pH, a 2:1 (by mass) water to soil slurry was prepared, and pH was measured with a calibrated pH meter (Thermo Orion Model 420A) (Watson and Brown 1998). Total N and C were measured in sub-samples that were dried (105 C for 24 hours) and ground (<149µm) by dry combustion with an elemental analyzer (Carlo Erba, Model NA 2500; Milan, Italy). Carbon:nutrient ratios are reported on a molar basis.

All tree cores were mounted and then sanded with increasingly finer grit sandpaper to 600 grit. Only complete cores that had a clear inner ring, defined as a clear semi-circle that showed that the borer had reached the center (though not necessarily the pith) of the tree, were used. The establishment number of rings was averaged across the two cores in each plot to compute what will be referred to as year of establishment.

Data Analysis

The two pre-blight datasets differed in the units used to measure chestnut, and thus chestnut decline was analyzed separately for MLBS and CGIC. The MLBS studies provided the number of individuals of each tree species in a sample unit. The CGIC timber survey provided volume of chestnut per acre.

Pre-blight chestnut abundance (individuals per hectare) in the MLBS study area, pre-blight chestnut volume per hectare in the CGIC study area, and CGIC and MLBS post-blight chestnut abundance (individuals per hectare) were all square-root transformed to meet assumptions of normality. Pearson's correlations between pre-blight and post-blight abundances, in the case of MLBS, and between pre-blight volume per hectare and post-blight abundance, in the case of CGIC, were calculated and tested for significance (PROC CORR, SAS 9.1.3, SAS Institute 2002). Since these analyses were not easily compared because of the difference in units, each site was ranked from lowest to highest for pre-blight chestnut volume or abundance and for post-blight abundance. The Spearman's rank correlations between pre-blight and post-blight rankings were calculated and tested for significance in the MLBS and CGIC study areas, respectively. To determine if chestnut's decline was density dependent, the linear regression between pre-blight and post-blight chestnut abundance was compared with the addition of post-blight chestnut abundance squared to the linear model. If the decline were density dependent, the better regression would be quadratic, so that more chestnuts died with increasing chestnut density, rather than a constant, density independent decline depicted in the linear regression.

A principal components analysis (PCA) was performed on the correlation matrix of environmental and species composition variables using PC-ORD 5.0 (McCune and Mefford 1999). Only tree species occurring in >5% of sites were included in the analysis. In the CGIC PCA analysis, the input variables were elevation, solar insolation, soil pH, soil C:N ratio, canopy year of establishment, and basal area per hectare of *Acer rubrum, Betula lenta, Carya glabra, Carya alba, Nyssa sylvatica, Oxydendrum arboreum, Pinus pungens, P. rigida, P. virginiana, Quercus alba, Q. coccinea, Q. montana, Q. rubrum,* and *Q. velutina.* In the MLBS PCA analysis, the input variables were elevation, solar insolation, soil pH, soil C:N, canopy year of establishment, and basal area per hectare of *A. rubrum, Amelanchier arboreum, B. lenta, C. glabra, C. alba, N. sylvatica, P. rigida, P. strobus, Q. alba, Q. montana, Q. rubrum,* and *Q. velutina.*

Multiple regressions using stepwise selection were used to analyze the ability of the environmental principal components to predict the response variables, pre-blight volume or abundance and post-blight abundance, using PROC GLM in SAS 9.1.3. One pre-blight multiple regression analysis and one post-blight analysis were analyzed separately for data from the CGIC and MLBS study sites. Pre-blight volume per hectare in CGIC, pre-blight abundance per hectare in MLBS, and post-blight abundance per hectare in CGIC and in MLBS were each square-root transformed.

To test whether there was a niche shift, or differences in slopes of linear relationships between a component of the environment and chestnut abundance, a multiple regression was used to test the effects of the interaction between sampling time and the principal components on pre-blight and current chestnut abundance. This test was only performed in the MLBS area, where chestnut abundance could be compared (rather than volume and abundance, as in the CGIC area). The effects of the interaction were then compared to the model without the interactions (assuming slopes of the relationship between principal components and chestnut abundance were equal between the pre-blight and current models).

The survival rate of chestnut was calculated for each site in the MLBS study area, assuming a constant negative exponential decline from the pre-blight sampling to the post-blight sampling. Then, assuming that each site's survival rate continued to be constant in the future and that chestnut root sprouting ability did not decline with age, the time to extinction of each sample stand was predicted using equation (1).

(1),

$$T = \frac{\ell n\,(N_t)}{\ell n\,(s)}$$

where T is the time to extinction, N_t is chestnut abundance (number individuals per hectare) at the current sampling date (t), s is the survival rate, and the quasi-extinction threshold is one remaining individual. In order to understand variation in probability of local extinction (at the scale of one hectare) over space and time, the cumulative probability distribution for probability of local population extinction (<1 genet per hectare) over time following the last sampling date (2007-2009) was calculated by dividing the number of stands expected to be extinct at time t by the number of stands in the sample. The cumulative probability distribution, which gives the probability that a population will have hit the quasi-extinction threshold at or before a given future time, is considered a valuable method of understanding extinction risk because one can visualize the rate of increase of overall risk of extinction through time (Morris and Doak 2002).

RESULTS

Pearson's correlation between pre-blight and current chestnut abundance in the MLBS study area was not significant ($R = 0.21$; $p = 0.34$, $N = 22$; Fig 1a). Similarly, pre-blight chestnut volume was not significantly correlated with current abundance in the CGIC study area ($R = -0.16$, $p = 0.54$, $N = 17$; Fig 1b). Further, after pre-blight and post-blight chestnut volumes or abundances were ranked from lowest to highest starting with 1 at the lowest, pre-blight and post-blight ranks were uncorrelated in both study sites ($p >> 0.05$; Fig 1c and 1d). Current chestnut density was not predicted by initial chestnut density in the MLBS study area (regression $R^2 = 0.05$, $F_{1, 20} = 0.95$, $p = 0.342$). Current chestnut density was independent of initial chestnut density in the MLBS study area (regression $R^2 = 0.003$, $F_{1,\,20} = 0.07$, $p = 0.799$). A quadratic model was also not significant. The lack of correlation between pre-blight chestnut abundance or volume and current chestnut abundance suggested that spatial variation in chestnut decline was high.

The principal components of environmental space were tested for their ability to explain the differences between pre-blight and current chestnut abundance. In the CGIC study area, the first four principal components of the environment and species variables accounted for 61.2% of the variation among the samples (Table 1; also see Table 1A in Appendix A for coefficients of the principal components by site). Principal component 1 represented 25.1%, principal component 2 represented 14.9%, principal component 3 represented 12.2%, and principal component 4 represented 9.1% of the variation among the samples. Positive values of principal component 1 represented low elevation, neutral soil sites harboring more mesic species such as *Carya sp., P. virginiana,* and *Q. alba.* Positive values of principal component 2 represented low elevation sites with acidic soil and high basal areas of *C. alba, P. pungens,* and *P. virginiana.* Positive values of principal component 3 represented young forests on low fertility soils receiving high solar insolation with high basal area of *Q. coccinea* and *Q. velutina.* Positive values of principal component 4 represented young forests at high elevations with high basal area of *P. pungens.*

In the MLBS study area, the first four principal components of the environment and species variables accounted for 63.8% of the variation (Table 2, also see Table 2A in Appendix A for coefficients of the principal components by site). Principal component 1 accounted for 19.4%, principal component 2 accounted for 18.8%, principal component 3 accounted for 15.4%, and principal component 4 accounted for 10.2% of the variation in the sampled environment and canopy species composition. Positive values of principal component 1 represented young forests on low fertility soils receiving high solar insolation with high basal area of *A. rubrum, N. sylvatica, P. rigida, P. strobus,* and *Q. alba.* Positive values of principal component 2 represented older forests with high soil fertility on acidic soils with high basal area of *P. strobus* and *Q. montana.* Positive values of principal component 3 represented forests with more neutral pH with high basal area of *Carya sp., Q. alba,* and *Q. velutina.* Positive values of principal component 4 represented forests with mesic species *A. arboreum, B. lenta, P. strobus,* and *Q. alba* receiving low solar insolation.

The principal component most highly related to pre-blight chestnut abundance or volume was not the same principal component most highly related to post-blight chestnut abundance in either study area. In the CGIC multiple regression analysis, principal components 3 and 4 were significantly related to the response variables pre-blight chestnut volume ($R^2 = 0.35$; $F_{2, 14} = 3.76$; $p = 0.049$), and principal component 1 was significantly related to post-blight chestnut abundance ($R^2 = 0.64$; $F_{1, 15} = 26.69$; $p = 0.0001$). The positive relationship between principal component 3 and pre-blight chestnut volume (Coefficient = 0.182; $F_{2, 14} = 4.43$; $p = 0.054$) and the negative relationship between principal component 4 and pre-blight chestnut volume (Coefficient = -0.188; $F_{2,14} = 4.86$; $p = 0.045$) indicated that pre-blight chestnut volume was higher on low elevation sites receiving high solar insolation. The positive relationship between principal component 1 and post-blight chestnut abundance (Coefficient = -0.199) indicated that current chestnut abundance is higher on sites harboring xeric species (e.g., *N. sylvatica, O. arboreum, P. rigida,* and *Q. montana*) at higher elevations with more acidic soils.

In the MLBS multiple regression analyses, principal component 1 was related to pre-blight chestnut abundance ($R^2 = 0.34$; $F_{1, 20} = 10.52$; $p = 0.0041$), and principal component 4 was related to post-blight chestnut abundance ($R^2 = 0.43$; $F_{1, 20} = 15.16$; $p = 0.0009$). The negative relationship between principal component 1 and pre-blight chestnut abundance (Coefficient = -7.72) indicated that pre-blight chestnut was more abundant on sites with low solar insolation and high soil fertility. The negative relationship between principal component 4 with post-blight chestnut abundance (Coefficient = -6.80) indicated that current chestnut abundance is highest on sites with more neutral pH receiving high solar insolation with more xeric species such as *Q. montana* and *Q. rubra*.

Overall, the principal components significantly related to current chestnut abundance in both study areas represented sites with high basal area of xeric species, most saliently chestnut oak (*Q. montana*) (Table 1, Table 2).

The multiple regression testing for a shift in chestnut's realized niche since blight introduction was significant ($R^2 = 0.63$; $F_{9, 34} = 6.51$; $p < 0.0001$), and the most significant independent variables in the model were sampling time ($F_{1, 34} = 34.35$; $p < 0.0001$), principal component 1 by sampling time ($F_{2, 34} = 7.58$; $p = 0.0019$), and principal component 4 by sampling time ($F_{2, 34} = 3.10$; $p = 0.058$). When the interactions between sampling time and each of the environmental principal components were not considered, and the slopes of the relationships between the principal components and chestnut abundance were assumed not to change with time, the model was also significant ($R^2 = 0.52$; $F_{5, 38} = 8.14$; $p < 0.0001$), with the effects of principal component 1 significant ($F_{1, 38} = 6.83$; $p = 0.0128$), of principal component 4 nearly significant ($F_{1, 38} = 3.04$; $p = 0.089$), and of sampling time significant ($F_{1, 38} = 29.20$; $p < 0.0001$). The first regression model with interaction terms was not significantly better than the model without the interactions (a comparison of the two mean square errors yields $F_{38, 34} = 1.18$; $p = 0.31$), however the first model accounted for more of the variation ($R^2 = 0.63$ versus $R^2 = 0.52$) and also emphasized that the relationship of chestnut abundance to these environments had changed between the two sampling times. Returning to the regressions of the principal components' effect on chestnut abundance for each separate sampling time, the model for pre-blight chestnut, including only principal components 1 and 4, was: [43.90 – 7.72 x PC1 – 0.52 x PC4], whereas the model for current chestnut abundance was: [13.99 – 0.23 x PC1 – 6.80 x PC4] (Figure 2).

Proportional chestnut loss varied between 25 and 100% across the MLBS study area (Table 3). In three of the 22 sites, 100% of chestnuts were lost. The remaining 19 were used to estimate survival rate, time to extinction, and cumulative probability of local extinction over time. Annual survival rate could not be calculated on the CGIC site because the pre-blight unit was volume per hectare.

Annual survival rate in the MLBS sites varied between 0.904 and 0.996 per year, with an average among plots of 0.963 (Table 3). Assuming this survival rate remains constant, predicted time to one-hectare stand extinction ranged between 81 and 1153 years, with a mean of 451 years (Table 3; Figure 3a). The cumulative probability distribution showed that 53% of stands are likely to be extinct in 224 years and that 95% are likely to be extinct in 1103 years (Figure 3b).

DISCUSSION

Across both study areas, pre-blight chestnut abundance or volume was not correlated with post-blight chestnut abundance. Ranks from lowest to highest chestnut abundance or volume before and ~80 years after blight introduction were not correlated. This result indicates that chestnut's survival rate was both highly variable and unrelated to original density. This was also confirmed by comparison of the linear and quadratic regressions of post-blight chestnut abundance on pre-blight abundance in the MLBS study area; the quadratic effect was not significant, indicating that chestnut survival rate was independent of initial chestnut density, at least at the scale of this study. Chestnut blight prevalence has also been shown to be density independent at a landscape scale (see Chapter 1). Further, in one stand at MLBS monitored for two years, likelihood of blight infection was unrelated to the distance to the nearest infected neighbor, which ranged from 5 m to 27.6 m (Milo 2009). Thus, chestnut density does not appear to be driving decline or probability of infection. Hebard (1982) hypothesized that probability of infection was related to size of the chestnut plant. In a two-year study of 80 cankers on 70 chestnut stems, Milo (2009) found that the probability of chestnut infection on a twelve-hectare site at MLBS was positively related to chestnut sprout diameter at breast height. Thus, although chestnut density may not affect chestnut blight infection, the size of chestnut stems on a site may affect probability of infection. An association between tree size and probability of infection has also been reported in Port Orford cedar (*Chamaecyparis lawsoniana*) susceptibility to *Phytophthora lateralis* infection (Kauffman and Jules 2006). In fact, this relationship between plant size and probability of infection has been noted in a number of plant-fungal pathogen systems (Morrison 1996, Lopez-Villavicencio et al. 2007), and, theoretically, plant size is more likely to affect probability of infection when a disease is more uniformly distributed than when disease foci are widely separated (Mundt and Leonard 1986).

Spatial heterogeneity can affect probability of infection, genetic variation in disease resistance, and hence influence the design of suitable management policies (Real and Biek 2007). Few studies have demonstrated the influence of spatial heterogeneity in population decline due to pathogen introduction (Kauffman and Jules 2006), although this phenomenon has been demonstrated in theoretical modeling (Antonovics 2009). Chestnut decline was not constant, so areas that had high chestnut abundance before do not necessarily have high chestnut abundance today relative to other sites, indicating that spatial heterogeneity in chestnut blight infection and spread exists. Recent spatially explicit models of pathogen prevalence and host abundance in the case of a sterilizing disease (like chestnut blight) showed that, regardless of density or frequency dependence in the model, disease could limit the host to regions where the host would otherwise be most abundant in a disease free state (Antonovics 2009). However, such effects are dependent on differences in tree longevity, assuming longevity (and therefore disease persistence) is greatest in areas of greatest tree abundance. The spatiotemporal patterns of chestnut blight in a landscape are complex, and blight's ability to limit the range of the chestnut merits further modeling and empirical study.

Environmental principal components associated with chestnut abundance or volume before the blight were not significantly related to chestnut abundance after the blight, indicating that the optimal environment for chestnut has changed. The environment and especially the species in these areas likely have changed non-linearly since blight introduction, which may have added to the variation in the relationship between principal components representing the environment and pre-blight chestnut volume or abundance. For example, pre-blight volume in the CGIC area was most related to principal component values associated with high solar insolation, while pre-blight chestnut abundance in the MLBS area was most related to principal component values associated with low solar insolation. These results indicate that pre-blight chestnut was affected by solar insolation (slope and aspect) differently at low elevations than at high elevations, since the CGIC study area was lower in elevation than the MLBS study area. However, significant results with such small sample sizes ($n < 25$ in both cases) demonstrate rather substantial effect sizes suggesting that more stable features of these environments (e.g., slope, aspect, soil moisture, bedrock geology, elevation) do help to explain variation in pre-blight chestnut. Pre-blight chestnut was a generalist that could grow in a wide variety of environments (Zon 1904, Braun 1950, Whittaker 1956). Since the CGIC and MLBS study areas were at different elevations (CGIC elevation ranged between 500 and 900 m, while MLBS ranged between 900 and 1300 m), it is not surprising that pre-blight chestnut was abundant in different environments in these two areas. Further, areas with high chestnut abundance were not necessarily areas with high chestnut volume.

All current chestnuts occur within the original realized niche of pre-blight chestnut because chestnut populations essentially do not reproduce new individuals in the wild. Biotic restraints imposed by the chestnut blight introduction are certainly affecting both the realized niche through resource limitations and through mortality imposed by multiple chestnut blight infections in a genet over time, each followed by recovery through re-sprouting. Negative interactions between native and invasive species, though considered highly important in invasion dynamics, are generally poorly understood (Thomson 2004). Niche shifts in native species in response to competitive exclusion by an invasive have been seen in a wide variety of systems (Douglas et al. 1994, Mooney and Cleland 2001, Thomson 2004). However, niche shifts or range limitation following the introduction of an invasive disease that has become endemic are not well-documented (Antonovics 2009, Holt 2009). Although it is widely accepted that invasive species negatively impact native species that host an invasive pathogen, the ecology of such negative impacts and subsequent patterns of coexistence or decline generally remain unknown, except in the case of either small population size before pathogen introduction or in the case of a pathogen with a reservoir host that also infects a more susceptible host (de Castro and Bolker 2005).

In both study areas, despite variation in elevation and species associations, post-blight chestnut abundance was related to the principal component values associated with xeric species and, most notably, *Q. montana*, a xerophilous species that occurs at a wide range of elevations. Braun (1950), Whittaker (1956), and McCormick and Platt (1980) showed that chestnut and *Q. montana* were correlated in their distribution before the blight. Elliott and Swank (2008) showed that *Q. montana* and chestnut were correlated in their distribution before and seventy years after the blight, but whether this association became stronger cannot be inferred from their analysis. My results indicate that chestnut abundance is higher in areas currently dominated by *Q. montana.* Using cores taken for the year of establishment that was used in the PCA analysis, the cores from *Q. montana* trees in the MLBS study area ranged in age between 69 and 126 years, with an average of 86 years. Because these sites were beginning to experience chestnut blight infection 70 to 80 years ago, it is difficult to determine whether areas where chestnut is highest in abundance today are also areas where *Q. montana* benefited most from chestnut loss, or whether there is a mechanistic relationship between chestnut survival and *Q. montana* presence. Since *Q. montana* is known to be dominant on rocky ridges with xeric, poor soils (Burns and Honkala 1990), two hypotheses are generated from my results showing that *Q. montana* is related to a higher abundance: (1) Chestnut is currently more abundant on dry, poor soils because chestnut blight did not infect chestnut in these areas as often as in more mesic, fertile sites, if higher probability of multiple genet infections per unit time affects the genet's probability of mortality; (2) chestnut is currently more abundant on dry, poor soils because it is not as light limited and is more likely to re-sprout following blight infection in these areas than on sites with moister, more fertile soil that presumably have more closed canopies.

This study indicated that chestnut's niche shifted with chestnut blight introduction by demonstrating a change in the relationship of chestnut abundance to two principal components representing aspects of the environment. Pre-blight chestnut was more limited in values of principal component 1 than post-blight chestnut, which showed that post-blight chestnut is not as restricted in abundance by high solar insolation, low elevation, low soil fertility, and pine-dominated sites as pre-blight chestnut but is more restricted in older forests with higher amounts of the shade-tolerant *B. lenta*. Post-blight chestnut was more limited in values of principal component 4 than pre-blight chestnut, which showed that post-blight chestnut is more restricted to areas with higher solar insolation and higher basal area of *Q. montana*, showing reduced relative abundance in areas with mesic species, such as *P. strobus, Q. alba, A. arboretum,* and *B. lenta.*

These results suggest that solar insolation may have a striking effect on current chestnut abundance, with post-blight chestnut's niche space shifting towards an optimum in areas that have southern to western facing slopes receiving high amounts of solar insolation and also toward areas with high basal area of xeric species. Although no studies have tested for a shift in chestnut's niche, multiple studies indicate that chestnuts are more abundant in xeric or high-light environments. Stephenson et al. (1991) found that chestnuts were more abundant in areas with low overstory basal area and diversity, high shrub density, and high number of xeric species, including *Q. montana.* The correlations between chestnut abundance and overstory basal area, overstory diversity, or shrub density indicate that chestnuts are more abundant on sites receiving more light through the canopy. These effects were stronger for study areas at higher elevations, although the effect of elevation on chestnut abundance among plots within these study areas was not significant. In another study, chestnut survival was negatively related to overstory hardwood basal area, again emphasizing the effects of light penetrating the canopy, and sites with higher overstory basal area were composed of more mesic species than sites with lower hardwood basal area (Griffin et al. 1991). Chestnut survival was also higher for sprouts receiving higher levels of solar irradiance (Griffin

1992). Using ordination techniques, Elliott and Swank (2008) assessed the changes in forest composition and environmental characteristics in oak-chestnut forests in western North Carolina, USA. Their ordination axes show that chestnut basal area in the 1930's was negatively related to current solar radiation (calculated using slope and aspect), but that current chestnut basal area was weakly positively correlated with solar radiation. In general, environmental conditions associated with high chestnut abundance before the blight are different than conditions found to harbor high abundance today (Burke 2007).

Whether chestnut's niche shift toward dry, high light environments is due to a negative effect on chestnut blight, a positive effect on chestnut's ability to re-sprout, or some combination thereof, is unclear. Dry conditions do not appear to inhibit chestnut blight's growth rate nor affect chestnut susceptibility (Stevens 1917). However, the sexual stage of chestnut blight is affected by moisture, with wind-dispersed ascospores more likely to be produced following months with higher rainfall (Stevens 1917). Asexual reproduction of chestnut blight is affected by light, with animal-dispersed conidia formed when exposed to an alternating light/dark cycle, but pynidial formation much lower when subjected to continuous light or to continuous darkness (Anagnostakis 1987). Chestnut blight's ability to grow is affected by temperature, and the fungus will grow above a threshold temperature of 8-9°C, regardless of how long the blight has experienced temperatures below this threshold

(Stevens 1917). Chestnut blight can grow at an optimum rate at a wide range of temperatures, and light does not affect the rate of growth (Anagnostakis 1987). In Chapter One, note that chestnut blight prevalence was not correlated with solar insolation across the CGIC and MLBS study areas, which cover a larger range of elevations than MLBS alone. Pre-blight volume in the CGIC area was most related to principal component values associated with low elevation and high solar insolation, while pre-blight chestnut abundance in the MLBS area was most related to the principal component associated with low solar insolation and high soil fertility. The effect of solar insolation on current chestnut abundance may be stronger at high elevations, may be confounded with elevation, and may vary considerably across the original range of the chestnut.

Much less is known about the effect of the environment on chestnut's ability to re-sprout. Woody species that re-sprout, such as chestnut, tend to be more abundant on less productive sites (Midgley 1996, Ojeda 1998, Bellingham and Sparrow 2000, Bond and Midgley 2001). In productive sites, vigorous sprouters would be out-competed by seedlings, but in unproductive sites with slower growth, seedlings are more likely to be killed by disturbance or resource limitation without re-sprouting (Midgley 1996, Ojeda 1998). Since chestnut must rely solely on re-sprouting to escape disease, poor sites with high turnover from disturbance, such as those occupied by *Q. montana,* may be best for chestnut survival through re-sprouting. Re-sprouting is generally considered an adaptation to sites with higher frequency and severity of disturbance (Bellingham and Sparrow 2000, Bond and Midgley 2001).

The result that chestnut may continue re-sprouting for centuries to millennia is interesting and raises many questions about changes in survival rate. As these forests undergo succession, canopy closure and understory thinning could ensue, which would accelerate chestnut's mortality. It is unclear how climate change could affect chestnut mortality by changing the temperature or precipitation regime. However, elevated CO_2 will likely increase carbon storage and carbon allocation to stem sprouting (Hoffmann et al. 2000, Bond and Midgley 2001), thus increasing sprouting ability of remaining chestnuts. In general, climate warming can increase pathogen survival and reproduction when winters are milder, decrease plant resistance to fungi, and affect fungal infection and sporulation by interacting with humidity and temperature (Harvell et al. 2002). The biggest risk may be factors such as deer overpopulation and climate change, because chestnut cannot disperse as climate changes and because intense deer herbivory restricts sprouting (see Chapter 3).

In the prediction of chestnut's decline, re-sprouting ability of a root collar was assumed to be constant across root collar ages. Very little information exists on the variation in sprouting ability in most tree species across life history stages, root collar ages, environments, and disturbance severities (Bond and Midgley 2001, Tredici 2001, Clarke et al. 2010). Some trees that sprout following disturbance have come close to immortality, most notably *Tilia cordata* in Great Britain, populations of which have survived since climates cooled and their reproduction ceased 5000 years ago (Pigott and Huntley 1980). Re-sprouting ability has been postulated as the reason *Ginkgo biloba* was able to avoid extinction in China (Tredici 1992). Rackham (2003) mentions the ability of European chestnuts (*Castanea sativa*) in Europe to have survived coppicing for centuries. It is thus quite possible that this assumption of continuous re-sprouting ability is true – and quite possible it is not, given that stands have gone extinct or been reduced in size. More research on re-sprouting in chestnut, and other trees, would increase our understanding of forest response to disturbances.

According to this study, 50% of one-hectare stands in this area would be extinct in about 200 years; 80% would be extinct in about 600 years. Chestnuts have survived with blight for over a century, and, unless survival rate decreases substantially over time, chestnuts may continue to be common understory trees for another century or more. Very few studies causally link extinction with disease, and the simplest disease ecology models generally do not predict host extinction due to disease alone (de Castro and Bolker 2005). However, there are multiple attributes of chestnut blight that are associated with host population extinction in modeling scenarios (de Castro and Bolker 2005, Antonovics

2009). Firstly, chestnut blight can continue to grow saprophytically on dead host stems for two years (Prospero et al. 2006), and has been observed with pycnidia on reservoir hosts such as *Q. coccinea* (Torsello et al. 1994). However, chestnut blight reproductive structures were never observed in this study's area on hosts other than those in the genus *Castanea*. Secondly, chestnut blight prevents chestnut reproduction and immigration. The potential for reservoir hosts and the lack of reproduction are disease attributes associated with population extinction in models of disease-host dynamics. More studies of decline across chestnut's range with more samples across time are needed.

CONCLUSION

This study provides evidence that chestnut is being constrained to a portion of its former niche because of spatial heterogeneity in survival rate. First of all, pre-blight and post-blight chestnut abundances were not correlated. Secondly, principal components that predict pre-blight chestnut abundance or volume are not the same as those that predict post-blight chestnut abundance. And, finally, chestnut abundance showed significant changes in its relationship to principal components that indicated that current chestnut is restricted more by low solar insolation and mesic conditions than previous to blight introduction. This study also highlights the potential for chestnut to continue to re-sprout for centuries in this region, but it would be important to look at the pattern of chestnut decline with more samples in time. It is unlikely that survival rate will remain constant, as assumed in this study, because of forest succession, climate change, and changes in deer densities. This study opens new questions requiring further research regarding: (1) the spatiotemporal dynamics of chestnut blight, which could provide input parameters for epidemiological models, (2) the mechanisms of chestnut survival and chestnut blight infection that make sites with high solar insolation and xeric tree species present especially favorable to chestnuts (3) integration of this knowledge with restoration efforts based on breeding resistant chestnut trees. Disease introductions are becoming more frequent and can cause local extinctions and major niche shifts. Studying these shifts over long-term periods informs our understanding of the effects of spatial heterogeneity on disease invasions.

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TABLES

Table 1. Eigenvectors of the environmental variables of the CGIC study area for each principal component. Eigenvectors with a magnitude >0.3 are bold-faced.

Variable	**Principal Component**			
	1	**2**	**3**	**4**
Solar	**0.375**	**-0.309**	**0.548**	0.062
Elevation	**-0.476**	**-0.480**	-0.077	**0.523**
Stand year	0.195	-0.057	**0.313**	**0.770**
Soil pH	**0.314**	**-0.728**	-0.267	-0.033
Soil C:N	**-0.687**	0.152	**0.541**	-0.152
Acer rubrum	0.061	**-0.665**	0.099	-0.040
Betula lenta	**-0.562**	-0.076	-0.268	0.164
Carya glabra	**0.378**	-0.231	-0.234	0.177
Carya alba	**0.432**	**0.306**	**-0.512**	**-0.380**
Nyssa sylvatica	**-0.699**	0.031	0.239	-0.235
Oxydendrum arboreum	**-0.607**	-0.188	0.093	-0.298
Pinus pungens	0.111	**0.729**	0.181	**0.381**
Pinus rigida	**-0.862**	0.145	0.266	-0.038
Pinus virginiana	**0.510**	**0.443**	0.012	0.057
Quercus alba	**0.777**	-0.187	0.206	**-0.446**
Quercus coccinea	0.237	0.060	**0.781**	-0.252
Quercus montana	**-0.703**	-0.175	**-0.351**	-0.238
Quercus rubra	-0.244	-0.295	-0.167	0.107
Quercus velutina	0.240	**-0.640**	**0.412**	-0.049

Table 2. Eigenvectors of the environmental variables of the MLBS study area for each principal component. Eigenvectors with a magnitude >0.3 are bold-faced.

	Principal Component			
Variable	**1**	**2**	**3**	**4**
Solar	**0.406**	**0.479**	-0.150	**-0.560**
Elevation	**-0.608**	**-0.619**	-0.295	-0.094
Stand year	**0.338**	**-0.501**	0.079	-0.272
Soil pH	0.290	**-0.620**	**0.479**	-0.164
Soil C:N	**0.583**	**-0.652**	-0.090	0.180
Acer rubrum	**0.665**	-0.148	**-0.552**	-0.121
Amelanchier arborea	-0.196	**-0.572**	0.195	**0.346**
Betula lenta	**-0.705**	-0.063	-0.068	**0.374**
Carya glabra	0.178	0.008	**0.512**	0.036
Carya alba	-0.004	**-0.317**	**0.515**	-0.228
Nyssa sylvatic	**0.479**	-0.170	**-0.510**	0.270
Pinus rigida	**0.557**	-0.300	**-0.611**	0.075
Pinus strobus	**0.364**	**0.656**	0.049	**0.513**
Quercus alba	**0.555**	-0.021	**0.464**	**0.354**
Quercus montana	0.131	**0.348**	0.255	**-0.602**
Quercus rubra	**-0.410**	**-0.440**	**-0.455**	**-0.350**
Quercus velutina	0.242	**-0.443**	**0.516**	-0.033

Table 3. Past and projected chestnut decline across the MLBS study area. Proportional per cent loss of chestnut from pre-blight sampling to post-blight, survival rate *per annum*, current number of chestnut genets per hectare, and time in years to quasi-extinction of <1 chestnut per hectare are shown in the table columns.

Site	Proportional % loss	Survival rate	Current No. Genets/ha	Time to extinction (y)
1	100.0	--	0	--
2	100.0	--	0	--
3	96.6	0.950	59	122.0
4	44.4	0.991	470	757.6
5	91.8	0.963	149	198.4
6	99.2	0.937	15	115.5
7	26.7	0.996	1467	1153.0
8	91.7	0.966	192	224.3
9	100.0	--	0	--
10	25.0	0.996	75	1764.0
11	99.5	0.928	42	109.2
12	40.0	0.993	1500	1103.0
13	62.2	0.987	1058	586.9
14	69.8	0.983	1357	505.2
15	73.9	0.982	783	328.7
16	62.6	0.986	1083	583.0
17	99.5	0.930	19	114.6
18	99.9	0.905	5	90.2
19	94.5	0.957	7	145.5
20	66.8	0.983	80	429.3
21	92.2	0.962	38	159.9
22	99.9	0.904	4	81.6

FIGURES

Figure 1

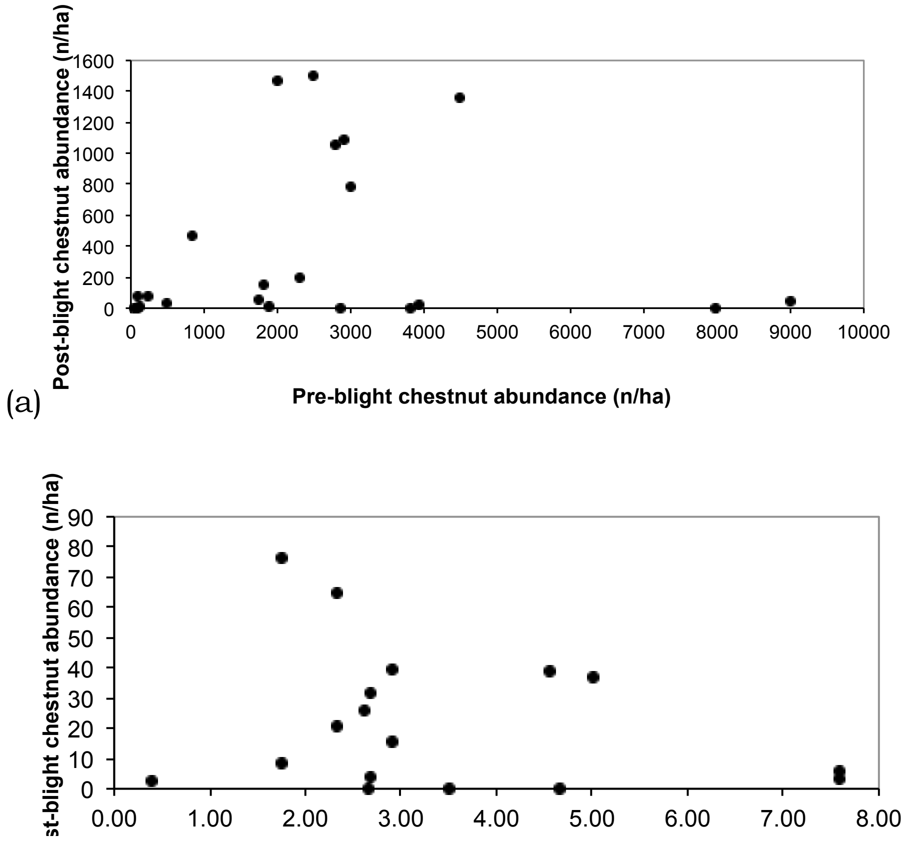
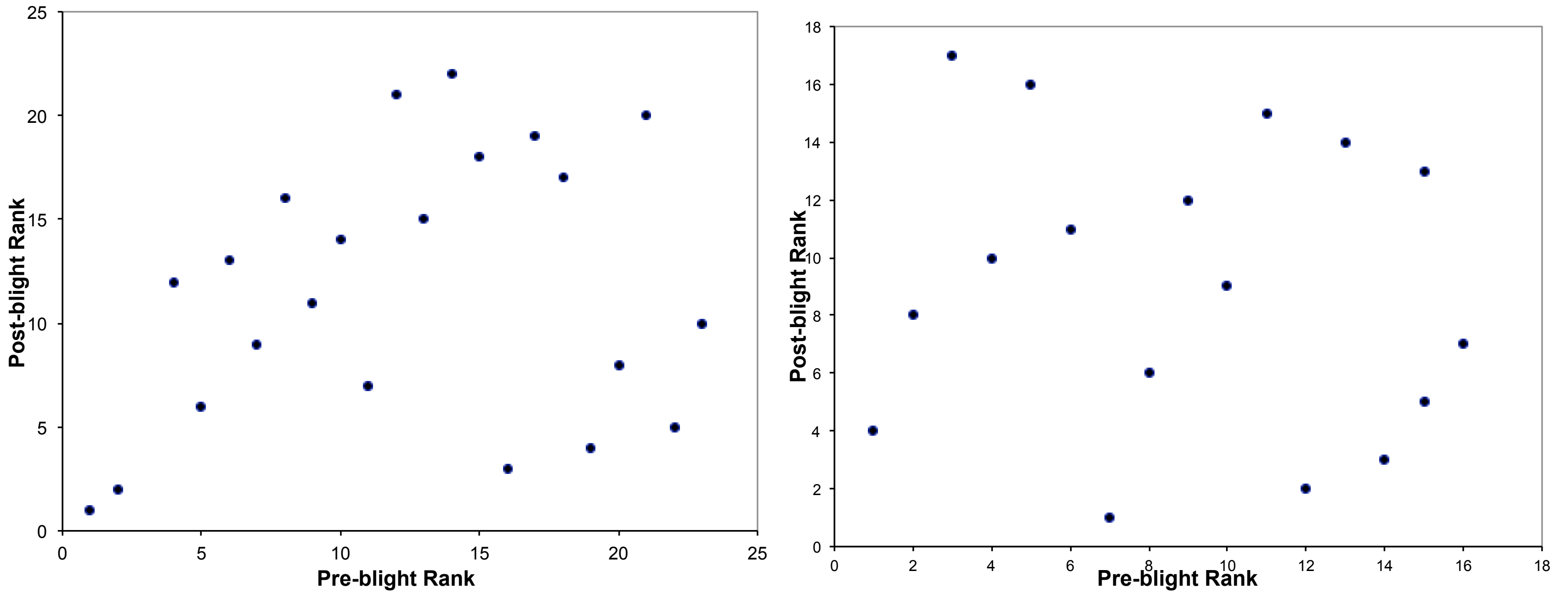


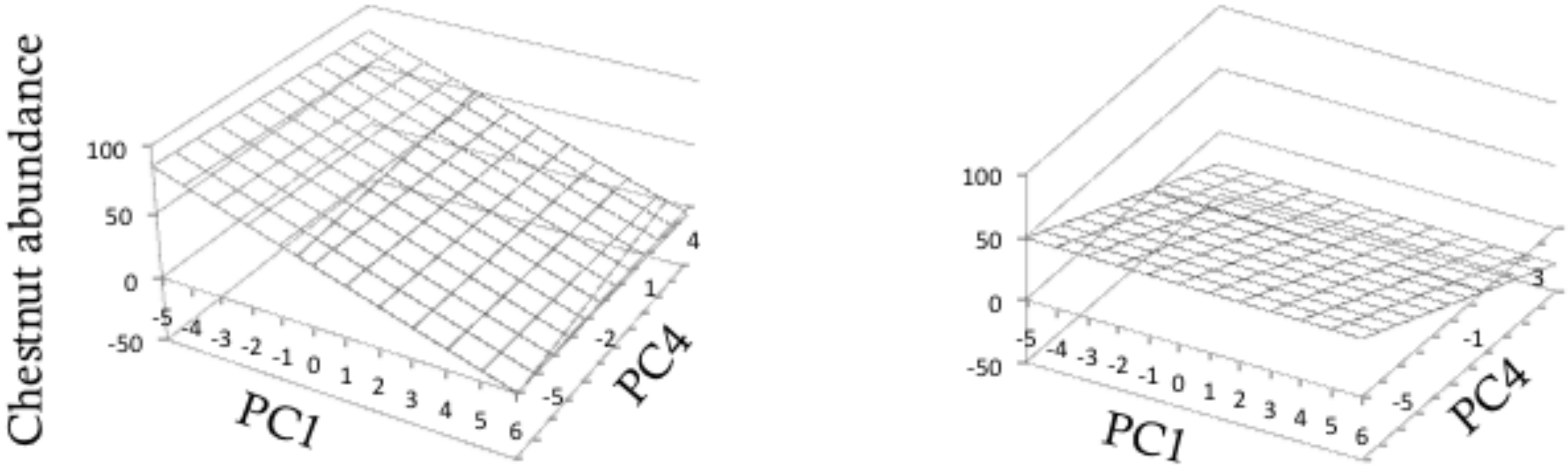
Figure 1 (*cont.*)



(c) (d)

Figure 1. Comparison of pre-blight and current chestnut abundance in (a) the MLBS study area, (b) the CGIC study area, and pre-blight and current abundance ranks in (c) the MLBS study area, and (d) the CGIC study area.

Figure 2

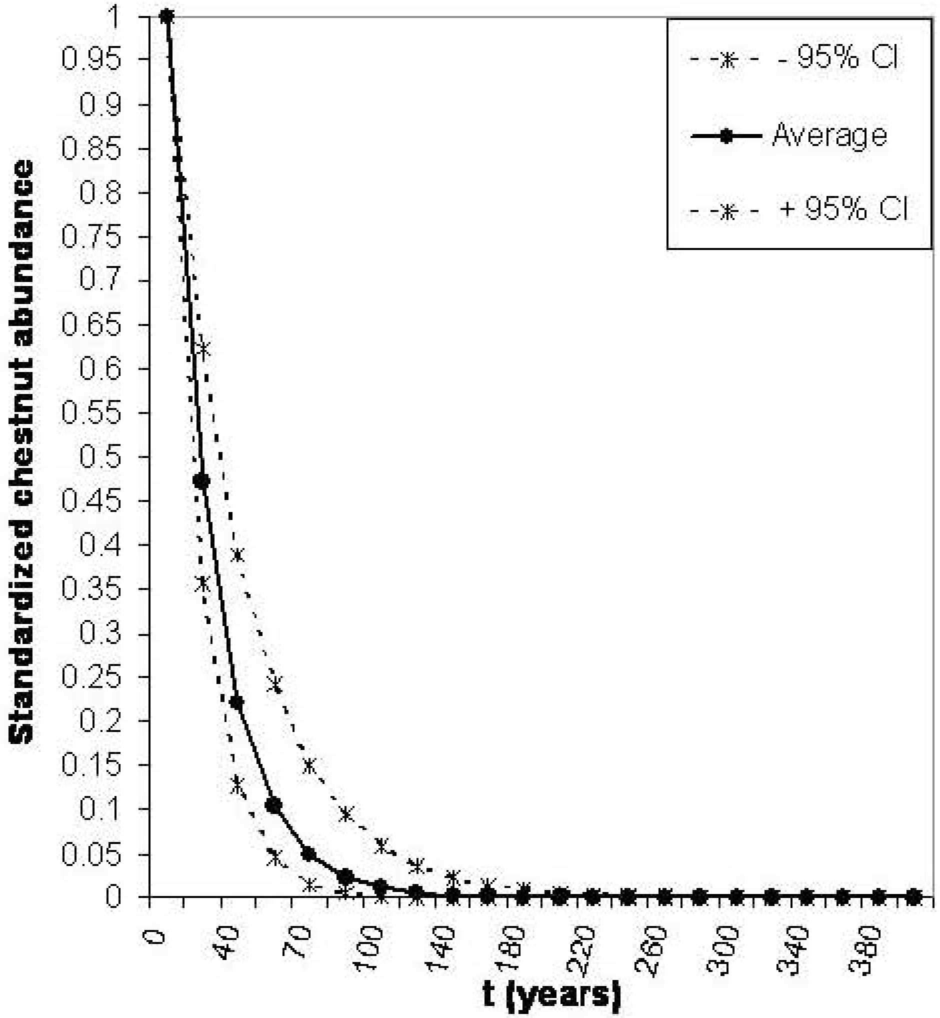


(a)

(b)

Figure 2. Niche shift of chestnut. (a) Pre-blight relationship in the 1930's between chestnut abundance and principal components 1 and 4 [Chestnut abundance = 43.90 –7.72 x PC1 – 0.52 x PC4], and (b) current relationship between chestnut abundance and principal components 1 and 4 [Chestnut abundance = 13.99 – 0.23 x PC1 – 6.80 x PC4].

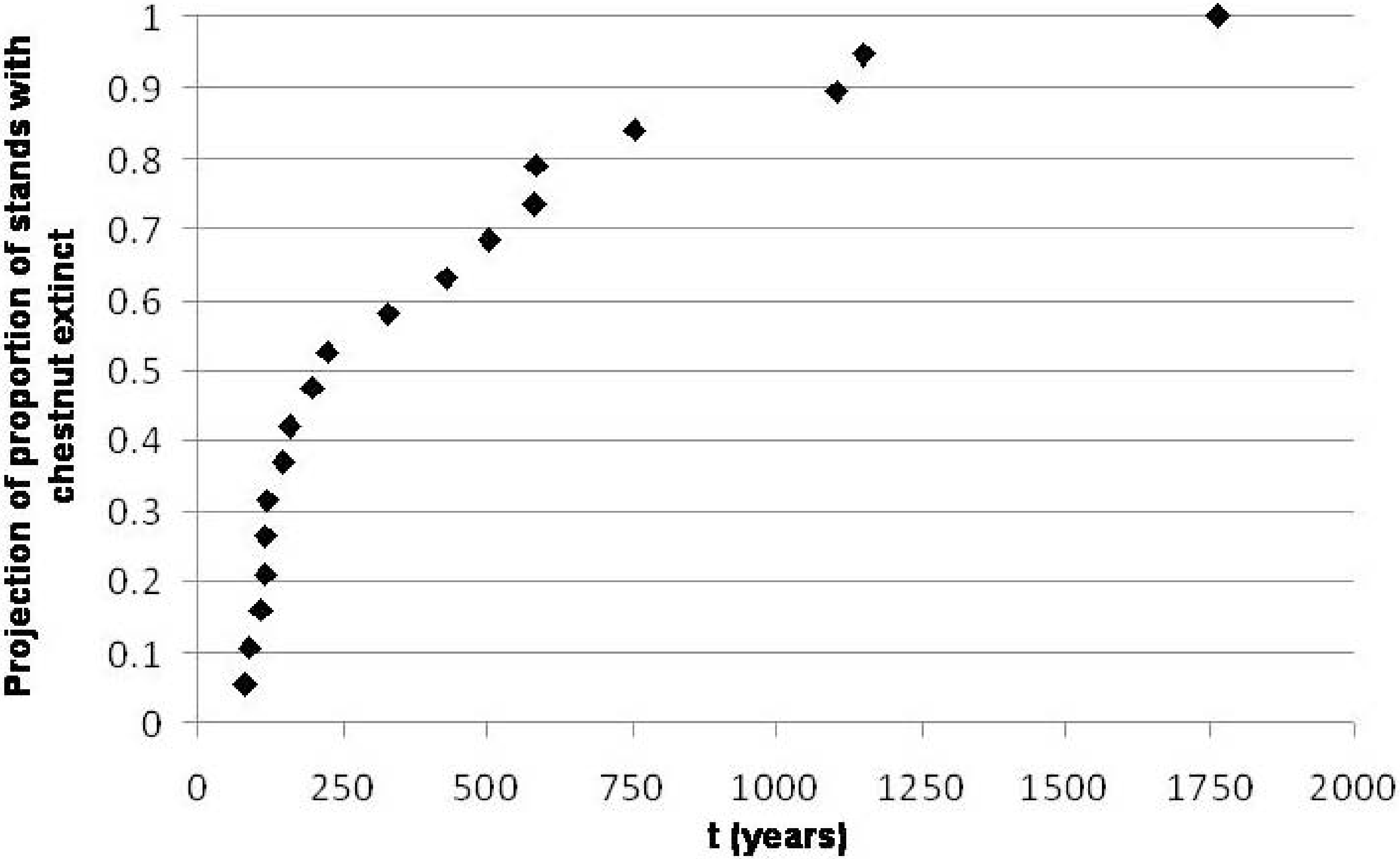
Figure 3



- -95% CI
Average
+ 95% CI
Standardized chestnut abundance
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
40
70
100
140
180
220
260
300
340
380
t (years)

(a)

Figure 3 (*cont.*)



(b)

Figure 3. Decline of chestnut abundance based on the survival rate calculated from stands at the MLBS study area. (a) Negative exponential decline of chestnut based on the average survival rate calculated at each MLBS site from the pre-blight sampling (1934-1950) and the post-blight sampling (2007-2009). The y-axis represents the proportion of the initial chestnut abundance. Dotted lines represent the 95% confidence intervals around the average survival rate. (b) Cumulative probability distribution function for the 19 MLBS sites, showing proportion of one-hectare sites projected to have chestnut extinct over time, based on the survival rates calculated for each stand.

APPENDIX A

Table 1A. Correlation coefficients of each principal component of environmental space with each tract of the CGIC study area.

Site	Principal Component 1	2	3	4
1	-1.776	-0.874	1.297	0.550
2	-2.982	0.276	-0.148	-0.573
3	-2.651	-0.810	0.143	-0.132
4	-3.419	-0.344	-1.004	0.568
5	-0.650	-0.703	0.846	0.354
6	2.014	-3.457	-1.144	1.095
7	0.621	-0.083	1.478	-0.193
8	2.545	3.049	0.579	0.316
9	1.241	1.107	-2.424	-1.575
10	2.423	1.965	-1.893	-1.903
11	2.901	-0.222	-1.454	1.072
12	0.767	-0.279	-2.176	-0.286
13	0.002	3.743	1.646	2.694
14	-2.516	0.053	-1.738	0.645
15	1.323	-1.527	-0.332	2.779
16	0.002	-1.536	0.588	-1.789
17	-3.741	0.722	0.649	-1.261

Table 2A. Correlation coefficients of each principal component of environmental space with each site of the MLBS study area.

	Principal Component			
Site	**1**	**2**	**3**	**4**
1	0.458	0.600	-2.104	-0.319
2	4.121	-1.811	-2.707	2.021
3	0.216	-2.941	2.983	0.400
4	-0.190	-3.262	2.565	2.261
5	0.882	-0.378	0.800	0.180
6	-2.091	0.616	-0.136	0.707
7	0.307	1.720	0.678	-2.010
8	0.739	1.337	1.599	-0.623
9	1.563	4.240	0.586	2.253
10	0.827	2.995	-0.232	-0.184
11	-4.478	-0.105	-1.004	1.639
12	-0.475	-0.423	1.476	-1.048
13	-0.352	-0.312	-0.429	-1.045
14	0.119	0.250	-0.100	-1.689
15	0.204	0.434	0.259	-1.368
16	0.253	-0.665	1.783	-2.100
17	-2.625	-0.371	-1.422	0.134
18	-3.587	0.246	-1.733	0.057
19	2.124	-1.910	-3.307	-1.253
20	0.232	-0.811	-1.274	0.535
21	0.612	-1.890	0.317	-0.202
22	1.141	2.440	1.402	1.655

CHAPTER 3

The effects of white-tailed deer on growth and mortality of two understory dominants, American chestnut (*Castanea dentata*) and striped maple (*Acer pensylvanicum*)

ABSTRACT

White-tailed deer (*Odocoileus virginiana*) are selective browsers that have increased across eastern North America, and their effects on forest ecosystems were studied in fenced exclosures monitored for four years from 2006-2009 and compared to unfenced plots. Effects of white-tailed deer browsing on the growth and mortality of two co-dominant understory trees are reported: American chestnut (*Castanea dentata*), a palatable species of conservation concern due to decline caused by an invasive pathogen chestnut blight (*Cryphonectria parasitica*); and striped maple (*Acer pensylvanicum*), a less palatable, browse-resilient species. Diameter, height, number of stems, mortality rate, and blight prevalence were measured annually over the four-year period. Results showed that in chestnut, stem number and survival rate increased significantly in the fencing treatment, while in striped maple stem number decreased slightly and mortality rates were not different between fenced and control plots. Proportional change in basal area and mean height over the four-year period were not significantly affected by fencing treatment for either

species. While it was surprising that change in chestnut mean height was not different between fencing treatments, this result is due to large stems dying similarly across all plots, but small chestnut sprouts increasing in number in fenced plots only. This study suggests that deer exacerbate decline in chestnut populations through preferential browsing, facilitating an increase in striped maple. Deer are a major concern for chestnut conservation and restoration.

INTRODUCTION

High densities of cervids can change an ecosystem's plant composition, structure, and function through preferential browsing on palatable species (McInnes et al. 1992, Manseau et al. 1996, McShea et al. 1997, Olofsson et al. 2001, De Jager and Pastor 2009, Takatsuki 2009). Cervid population densities have increased in a variety of ecosystems across the world due to the elimination or decline of predator populations, decreases in hunting, changes in climate and land use, or limitation of large mammals to small areas. Examples include roe deer (*Capreolus capreolus*) in western Europe; mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) in western North America; white-tailed deer (*Odocoileus virginiana*) in eastern North America; and Sika deer (*Cervus nippon*) in Japan. Intense herbivory due to these high cervid densities has major impacts on plant community structure and function (Motta 1996, McShea et al. 1997, Cote et al. 2004, Ripple and

Beschta 2006, Bradford and Hobbs 2008, Takatsuki 2009). Herbivores can suppress more palatable species, allowing less palatable species to increase in abundance (McInnes et al. 1992, Ripple and Beschta 2006). Intense herbivory by large mammals also can have major effects on the management or restoration of plant populations and communities of conservation concern (Barnes 1983, Frelich and Lorimer 1985, Lewis 1985, Hatch et al. 2002, McGraw and Ferudi 2005, Martin and Wilsey 2006).

White-tailed deer (*Odocoileus virginianus*) selectively browse certain plant species more than others (Verme and Ullrey 1984, Johnson et al. 1995). Overpopulation of white-tailed deer has altered the structure and function of many North American ecosystems because of browsing pressure on preferred species (Johnson et al. 1995, McGraw and Ferudi 2005, Eschtruth and Battles 2008, Heckel et al. 2010). For example, deer overpopulation may be one reason for the decrease in regeneration of oaks (*Quercus spp.*) and the increase in prevalence of maple species (*Acer spp.*) in eastern deciduous forests (Abrams 1998, Rooney and Waller 1998). In general, deer prefer species with higher nitrogen content and lower tannin content (Cates and Orians 1975, Tripler et al. 2002, Spiller and Agrawal 2003). Deer herbivory can act to either enhance or counteract the effects of other agents of mortality, such as disease or land use change. For example, decline of hemlock (*Tsuga canadensis*) in eastern North American forests as a result of infestation with hemlock woolly adelgid (*Adelges tsugae*) has been exacerbated by the suppression of regeneration that is associated with over-browsing by white-tailed deer (Rooney 2001, Eschtruth and Battles 2008, Witt 2010). The effects of deer on forest regeneration and composition in southeastern United States is less studied than other parts of white-tailed deer range in North America (Russell et al. 2001). The purpose of this study was to investigate if selective deer browsing affects growth and mortality of two dominant understory trees in a high elevation southern Appalachian oak forest: American chestnut (*Castanea dentata*), a palatable species of conservation concern due to disease-related decline, and striped maple (*Acer pensylvanicum*), a less palatable, browse-resilient species.

The American chestnut was once a canopy dominant in deciduous forests throughout eastern North America. This species has been slowly declining in much of the eastern United States since the introduction from Asia of an invasive disease, the chestnut blight (*Cryphonectria parasitica*), and is now a species of conservation concern. Chestnut blight prevents nearly all afflicted chestnuts from reaching reproductive age by causing dieback of aboveground tissues, which in turn keeps most chestnuts from reaching the subcanopy or canopy. The pathogen cannot infect belowground tissues, so a tree can produce new sprouts from its root collar following infection. Deer herbivory is likely to have a major impact on chestnut mortality due to the tree's dependence on re-sprouting for survival.

Striped maple and chestnut are both shade-tolerant trees that grow best in temporary canopy gaps (Hibbs et al. 1980, Wang et al. 2006), and are both restricted to the understory, striped maple by its growth form and chestnut by blight infections. Striped maples are less palatable and more browse-resilient than chestnuts (DeCalesta 1997, Latham et al. 2005). Thus, deer browsing may have interesting effects on the performance of these two species when both are dominant in the understory, either through direct competition or deer-mediated indirect effects between these two species.

There is evidence that cervid browsing can lead to changes in the composition of the forest understory. In a low-diversity boreal forest, moose browsing has been shown to shift understory dominance from balsam fir saplings (*Abies balsamea*) to white spruce saplings (*Picea glauca*). In Michigan, Frelich and Lorimer (1985) documented a change in dominance from eastern hemlock (*Tsuga canadensis*) to sugar maple (*Acer saccharum*) due to increased deer browsing.

In this study, experiments based on fences used to exclude deer ask if growth and mortality of these two understory tree species differ between plots accessible to deer and those fenced to exclude deer.

METHODS

Study Area

This study was located in a 0.98 ha area of deciduous oak-dominated forest at Mountain Lake Biological Station (MLBS) in Giles County, Virginia, USA (37°22’32”N, 80°31’20”W) at an elevation of 1160 m. The dominant species in the canopy were *Quercus rubra* and *Q. alba.* The dominant understory species were *C. dentata* (29% ± 8% of individuals >25 cm in height) and *A. pensylvanicum* (33% ± 11% [mean±2SE] of individuals >25 cm in height). Slope of the site was 2-15%, with a northeastern aspect. The soils in this area are stony, consisting of sandy to very cobbly silt loam, and are classified as the Lily-Bailegap complex (Swecker et al. 1985). Bedrock geology is typically fractured sandstone, and the soil is very acidic, with poor natural fertility (Swecker et al. 1985). The site has not been burned since the 1920s (USDA 1937), and some canopy trees date as far back as the early-1800s (H.M. Wilbur, *pers. comm.*).

White-tailed deer were nearly extirpated in Virginia by the turn of the 20th century (McShea et al. 1997, Davis 2000). Changes in forest and wildlife management in the 1920s and 1930s, which encouraged deer population growth, as well as a decline in native top-predator populations, led to great increases in deer abundance over the following half-century (Shrauder 1984, McShea et al. 1997). Downing (1987) speculated that deer abundance did not begin increasing in Virginia until the 1930s, soon after restoration efforts by the newly established Virginia Department of Game and Inland Fisheries began in 1926 (Knox 1997). In 1988, a Southwestern Cooperative Wildlife Disease Study showed that Giles County had one of the highest deer densities (>12 deer/km^2) among all Virginia counties (Knox 1997). This estimated deer density is far above estimates of Virginia's pre-colonial deer density (3-4 deer/km^2; Knox 1997). Rearick et al. (*in review*) estimated that deer density in the same stand as this study's field experiment was as high as 90.2 deer/km^2 ± 12 during the summer, so this area is ideal for studies of the effects of high deer densities on the composition of the forest understory. In forests surrounding MLBS, chestnut is known to be declining, while striped maple has been increasing (Parker et al. 1993), H.M. Wilbur *pers. comm.*).

Field Experiment

In April 2006, twelve 10 x 10 m plots were established across the study area. Plots were randomly assigned one of two treatments, fenced deer exclosures and unfenced control plots (n = 6 for each). Each plot was divided into nine 3 x 3 m subplots, leaving about 0.5 m inside the fence as an edge to allow for disturbance associated with fence construction and a path around the inside perimeter of the plot. Fences were 2.44 m high, constructed using 5.1 x 5.1 cm plastic mesh.

All American chestnuts and striped maples that were >25 cm in height were tagged with individual aluminum tags. Striped maples <25 cm in height but >2 mm in basal diameter and American chestnuts <25 cm in height but >3 mm in basal diameter were also tagged. A slightly larger basal diameter criterion for tagging of the chestnuts was chosen because first-year chestnut sprouts tend to be larger than first-year striped maple seedlings. First-year sprouts (chestnut and maple) and seedlings (maple) have very high turnover, so tagging all of them would be inefficient. Each tagged tree was measured annually for DBH (or basal diameter if below breast height) and height of the highest living meristem. The presence of blight was recorded when chestnut blight conidia or perithecia were found on a stem. American chestnuts within 1 m of each other were considered the same genet, or genotype of the original tree, according to findings of a genetic study by Stilwell et al. (2003). Sites were sampled in June-August 2006, July-August 2007, July-August 2008, and June-August 2009.

Data Analysis

Since more stems were measured at basal diameter than at breast height, DBH was converted to basal diameter using a conversion equation from a separate linear regression for each species, so that all stem diameter measurements were on the same scale. These regressions were derived from 102 striped maples and from 17 chestnuts that were measured for both basal diameter and DBH in the same stand as the field experiment plots. The intercept for each regression was set to 0. The conversion for striped maple, with $R^2 = 0.91$, was: Basal diameter = 1.346 x DBH. The conversion for chestnut, with $R^2 = 0.57$, was: Basal diameter = 1.352 x DBH. Basal area of each stem was then calculated from the basal diameter measurements or estimates. Basal area of each species respectively was then summed in each plot for each year, and the proportional change in basal area of each species was calculated as $[(BA_{2009} - BA_{2006}) / BA_{2006}]$. For each species, height of stems was averaged within each plot for each year. Proportional change in mean height was then calculated as $[(H_{2009} - H_{2006}) / H_{2006}]$.

Pearson's correlations between the two species' proportional changes in basal area and between the two species' proportional changes in height were not significant (respectively, $r = 0.06$; $p = 0.85$; $N = 12$; and $r = -0.21$; $p = 0.52$; $N = 12$). This indicates that striped maple basal area growth and chestnut basal area growth were independent of one another. Proportional change in basal area and proportional change in average height were analyzed in a two-way MANOVA assessing the effects of treatment, of species, and of treatment by species interaction. All analyses were performed using SAS 9.1.3 (SAS Institute 2002, Cary, NC).

Proportional change in number of stems from 2006 to 2009 was calculated for both species in each plot: $[(N_{2009} - N_{2006}) / N_{2006}]$. Pearson's correlation between the two species' proportional changes in number of stems was not significant (r = -0.09; p = 0.78; N = 12). Proportional change in total stems was arcsine square-root transformed to meet the assumption of ANOVA of normality of residuals. The effects of treatment, species, and treatment by species interaction on proportional change in number of stems were analyzed with a two-way ANOVA.

Mean annual mortality rate was also calculated for both species in each plot by averaging the annual mortality rate (number of genets that died in a year / total number of genets monitored in a year) across years. Pearson's correlation between the two species' average annual mortality rate was not significant (r = -0.13; p = 0.68; N = 12). Mean annual mortality rate was arcsine square-root transformed to meet the assumption of normality of residuals. The effects of treatment, species, and treatment by species interaction on average annual mortality rate were analyzed with a two-way ANOVA, with observations weighted by number of genets in the initial year 2006.

Blight prevalence (number infected genets / total number genets) was calculated for each year in each plot, and the mean annual blight prevalence was calculated by taking the average across years for each plot. Mean annual blight prevalence was arcsine square-root transformed to meet the assumption of normality of residuals. Mean annual chestnut blight prevalence was compared between treatments using a t-test.

RESULTS

Plot-level averages for each independent variable assessed in this study (mean annual mortality rate, blight prevalence, and proportional changes in basal area, height, and number of stems) are reported in Appendix A, Table 1A.

A significant species effect was found in the MANOVA assessing the effects of treatment and species on proportional change in mean height and in total basal area (Table 1), which demonstrates that chestnut declined significantly in basal area and height across all plots regardless of treatment, while striped maple increased in basal area and height in all plots except one (Figure 1; Appendix A, Table 1A). No significant treatment by species or treatment effects were found (Table 1). The two ANOVA's assessing the effects of treatment and species on each dependent variable individually showed that the model of proportional change in total basal area alone was significant and the model of proportional change in mean height alone was not (Table 2). The effect of species on proportional change in basal area was significant, but there was not a significant treatment by species interaction effect (Table 2; Figure 1b). Mean height of chestnuts declined across all plots, but declined slightly more in control plots than in fenced plots (Figure 1a). Mean height of striped maples increased across all plots (Figure 1a). Mean basal area of chestnuts decreased across all plots, but decreased more in control plots than in fenced plots (Figure 1b). Mean basal area of striped maples increased across all plots, but increased slightly more in control plots than in fenced plots (Figure 1b).

The ANOVA assessing the effects of treatment and species on proportional change in number of stems was significant ($R^2 = 0.49$; $F_{3, 20} = 6.52$, $p = 0.0030$). Proportional change in number of stems was not significantly affected by treatment ($F_{1, 20} = 3.13$; $p = 0.092$) nor species ($F_{1, 20} = 3.08$; $p = 0.094$). However, the effect of the treatment by species interaction was significant ($F_{1, 20} = 13.34$; $p = 0.0016$), showing that treatments affected the two species differently. Fencing treatment increased number of chestnut stems but slightly decreased number of striped maple stems (Figure 2). On average, number of chestnut stems declined in control plots but increased in fenced plots, while number of striped maple stems increased in control plots and decreased in fenced plots (Figure 2).

The ANOVA assessing the effects of the treatment mean annual mortality rate was significant ($R^2 = 0.64$; $F_{3, 20} = 11.97$, $p = 0.0001$). The effect of the treatment on number of stems of all species was not significant ($F_{1, 20} = 2.56$; $p = 0.13$), and the change in number of stems was significantly different between species ($F_{1, 20} = 23.79$; $p < 0.0001$). The effect of the treatment by species interaction was significant ($F_{1, 20} = 9.56$; $p = 0.0058$), highlighting the fact that chestnuts had a much higher mortality rate in control plots than in fenced plots, while striped maple mortality rate was not greatly affected by the fencing treatment (Figure

3). Mean annual mortality rate of chestnuts was higher in control plots than in fenced plots, while mean annual mortality rate of striped maples was low across both treatments (Figure 3).

Mean annual blight prevalence was lower in fenced plots than in control plots, but this difference was not significant, though the p-value was notably low (Student's t = 1.84, df = 10, p = 0.095; Figure 4).

DISCUSSION

The fence treatment had little effect on striped maple survival, while it had a large positive effect on chestnut survival. Chestnuts in fenced plots experienced an increase in number of stems, while striped maple stem number decreased in fenced plots. These discrepancies in effects of fencing treatment on growth and survival of these two species suggest that striped maple is either browsed less often (and thus is less palatable) than chestnut, more resilient to browsing, or both. The increased chestnut stem number in fenced plots presumably allowed for higher genet survival. These results provide evidence that deer could be a driver in the replacement of chestnut by striped maples in the understory of the forest at the study site.

Results suggest that the main effect of the fencing treatment was exclusion of deer browsing, and thus it can be inferred that differences between treatments were caused by differences in deer browsing and presence. Browsed stems lacking terminal buds were observed on both species on all unfenced control plots but not on fenced plots (*pers. obs.*). Plants experiencing browsing would be expected to be shorter in height and have fewer living stems than those that were not browsed. In both species, there was a trend of lower change in mean height in control plots than in fenced. Total number of chestnut stems per plot was much lower in control plots than in fenced plots, but the opposite effect was found in striped maples.

In chestnut, the fencing treatment resulted in more stems and lower mortality, but did not significantly affect change in basal area or height. Although it was surprising that change in chestnut stem height was not significantly lower in control plots, these results show that tall chestnut stems died in all plots regardless of treatment, but that more small stems grew in the fenced treatments.

Because deer affected striped maple and chestnut differently, deer may also affect their competitive interactions. Convincing evidence that chestnut and striped maple were directly competing was not found, because neither change in basal area, change in height, change in number of stems, nor mortality rate was negatively correlated between the two species. Nevertheless, the trends in change in basal area, change in number of stems, and mean annual mortality rate indicate that when chestnut grew and survived better, striped maple did not, and vice versa. Competition may be difficult to pick up at the plot level without understanding more about how performance changes with distance between plants. Conversely, it may be the case that striped maple does not cause increased mortality in chestnut directly, but rather, deer cause increased mortality of chestnuts, which facilitates an increase in striped maple. Indirect amensalisms, where one species is unaffected by the presence of a preferred alternative prey, have been found in a variety of plant systems (Chaneton and Bonsall 2000).

The higher chestnut mortality in control plots compared to fenced plots could be because browsed sprouts lack sufficient photosynthate production to continue re-sprouting or because browsed sprouts are more susceptible to blight prevalence. Blight prevalence was lower in fenced plots than in unfenced plots, and this difference approached significance ($p = 0.095$). Since blight spores enter through breaks in the cortex of the tree (Bramble 1936), browsing may facilitate spore entrance by creating wounds in the bark. Deer are a major conservation concern for the American chestnut because of the high palatability of chestnut sprouts combined with chestnut's inability to escape the understory due to chestnut blight infections.

Shifts in tree species dominance driven by herbivory can have widespread repercussions on the abiotic function of an ecosystem. For example, Pastor et al. (1993) found that selective foraging decreased leaf litter quality, resulting in lower N mineralization and net primary production. Harrison and Bardgett (2004) also found that soils from areas browsed by red deer in the Scottish Highlands had lower dissolved organic carbon, nitrate, ammonium, and nitrogen mineralization rates and higher microbial C:N ratio than unbrowsed exclosures. Such changes in nitrogen cycling can reduce ecosystem productivity and feedback to further change vegetation composition. The effects of deer on chestnut and striped maple may also be indirect through fecal and urine inputs to the soil that change the performance of these two species. However, recent research on the same site as this study showed no significant differences between fencing treatments for soil pH, K+, Mg2+, Ca2+, P, H+, organic matter, and cation exchange capacity, although deer fecal pellet abundance was negatively related to soil organic matter (Rearick et al. *in review*).

These results were consistent with conclusions from two previously published studies. In northwestern Pennsylvania, striped maple was one of two species that increased at high deer densities (>7.9 deer/km^2; Tilghman 1989). In a study of oak forest regeneration in thinned and unthinned stands at high and low deer densities in central Massachusetts, the American chestnut was a dominant understory species in all stands at low deer densities, but at high deer densities was only dominant in the thinned stands (Healy 1997).

This study emphasizes that herbivory associated with high deer densities can lead to changes in tree species dominance, and can exacerbate declines in plant populations of conservation concern. Deer density is thus an important factor to consider in future studies of chestnut decline, and of changes in species composition in eastern North American forests. Efforts to restore resistant, backcrossed American chestnuts to eastern forests may be hindered considerably in areas with high deer densities. This study also highlights the strong interaction between wildlife management decisions and the structure of forest ecosystems.

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TABLES

Table 1. Results from MANOVA analyzing the effects of treatment and species on proportional change in height and basal area.

Independent Variable	Wilk's Lambda	$F_{2, 19}$	p
Fence treatment	0.84	1.81	0.1906
Species	0.49	9.82	0.0012
Treatment x Species Interaction	0.88	1.31	0.2922

Table 2. ANOVA's of the effects of treatment and species on proportional change in height and on proportional change in basal area. The model testing the effects of proportional change in total basal area was significant ($R^2 = 0.55$; $F_{3, 20} = 8.16$; $p = 0.0010$), but the model testing the effects of proportional change in mean height was not ($R^2 = 0.21$; $F_{3, 20} = 1.79$; $p = 0.181$).

Independent Variable	Proportional Change in Basal Area $F_{1, 20}$	 p	Proportional Change in Mean Height $F_{1, 20}$	 p
Fence Treatment	0.66	0.4268	0.87	0.36
Species	22.63	0.0001	6.58	0.02
Treatment x Speacies Interaction	3.72	0.0681	0.05	0.83

FIGURES

Figure 1

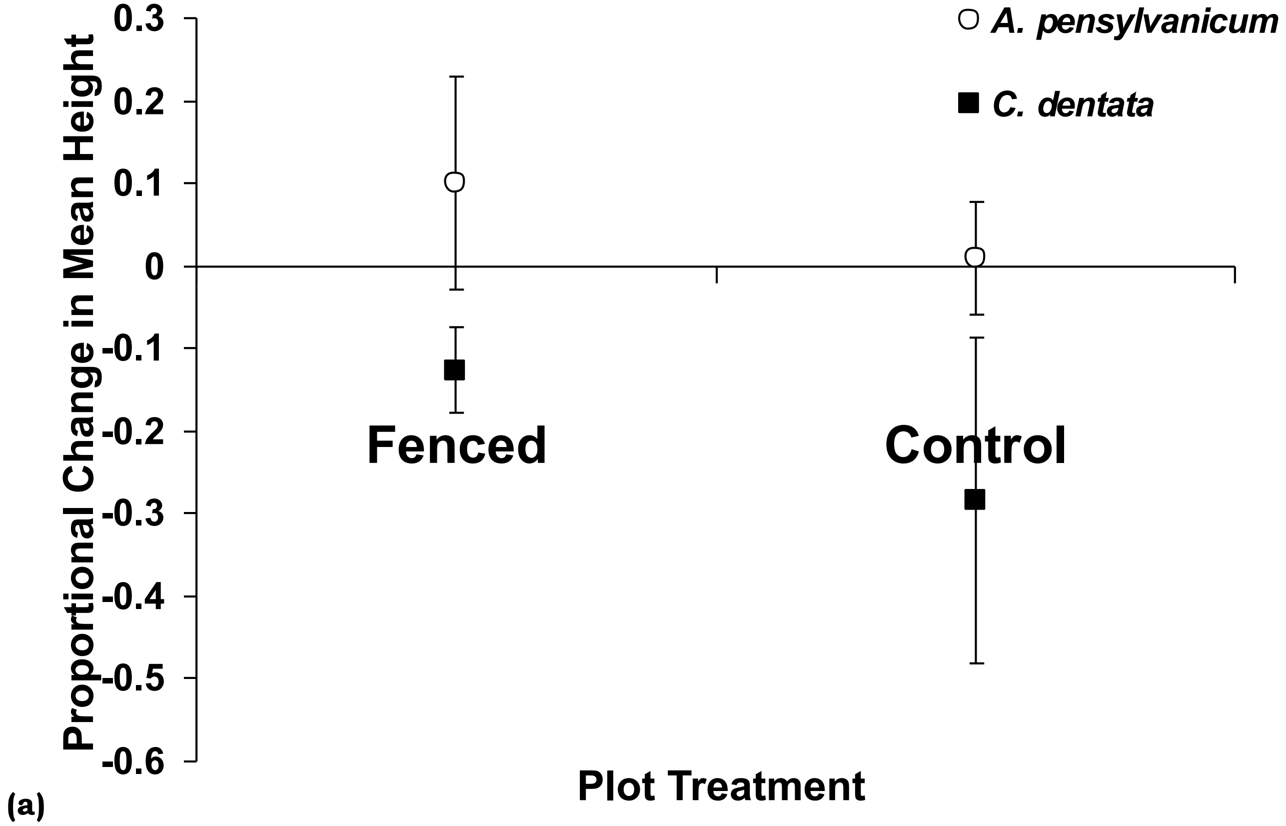

Figure 1 (*cont.*)

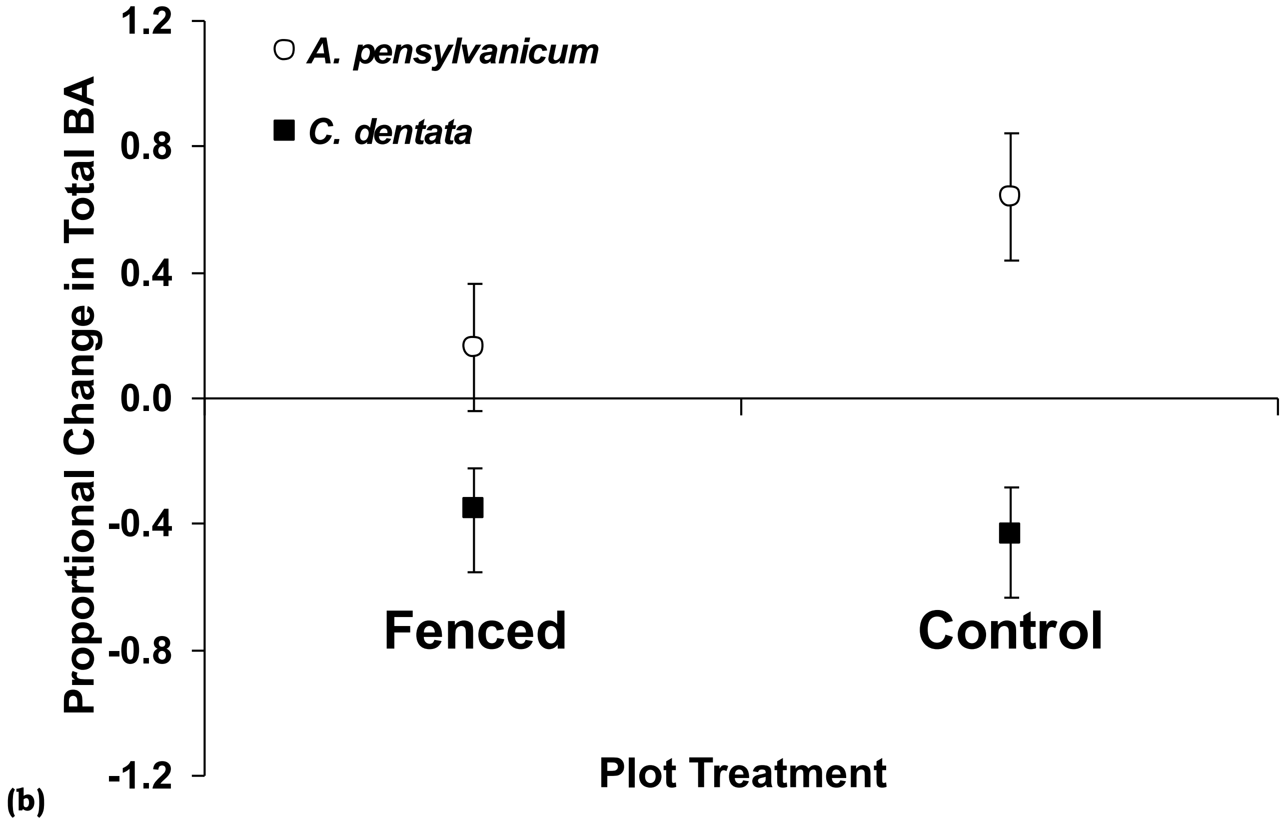

Figure 1. (a) Proportional change in mean height from 2006 to 2009 by treatment and species, and (b) Proportional change in total basal area from 2006 to 2009 by treatment and species. Error bars are 1 standard error.

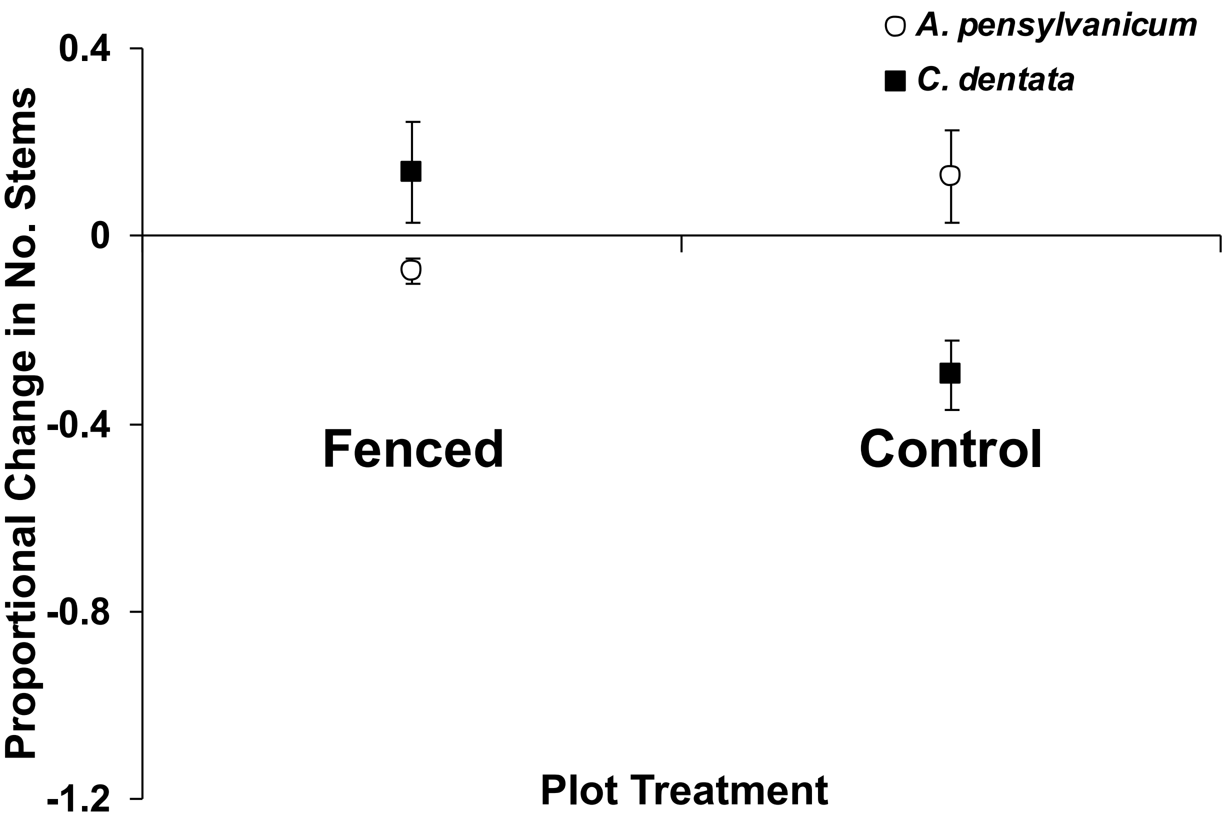

Figure 2. Proportional change in number stems from 2006 to 2009 by fencing treatment and species. Error bars are 1 standard error.

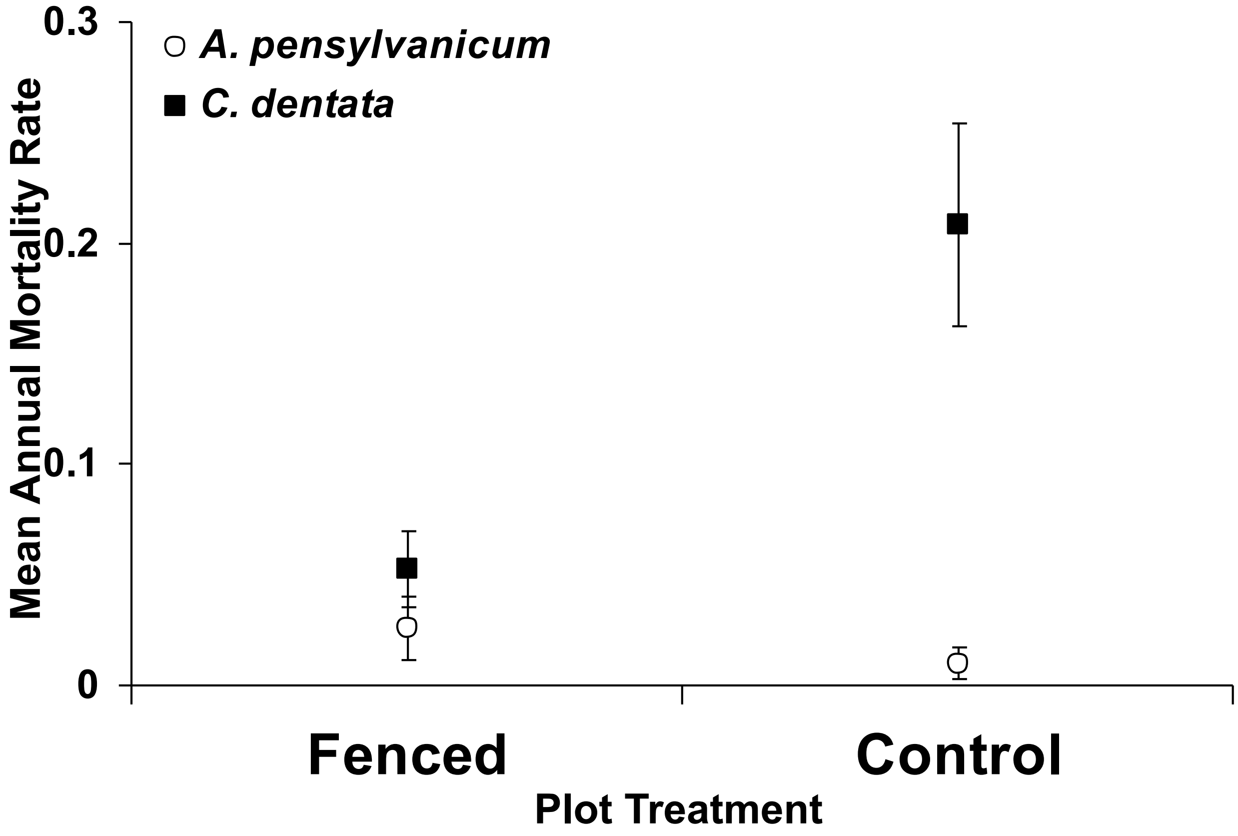

Figure 3. Average annual mortality rate of genets from 2006 to 2009 by fence treatment and species. Error bars are 1 standard error.

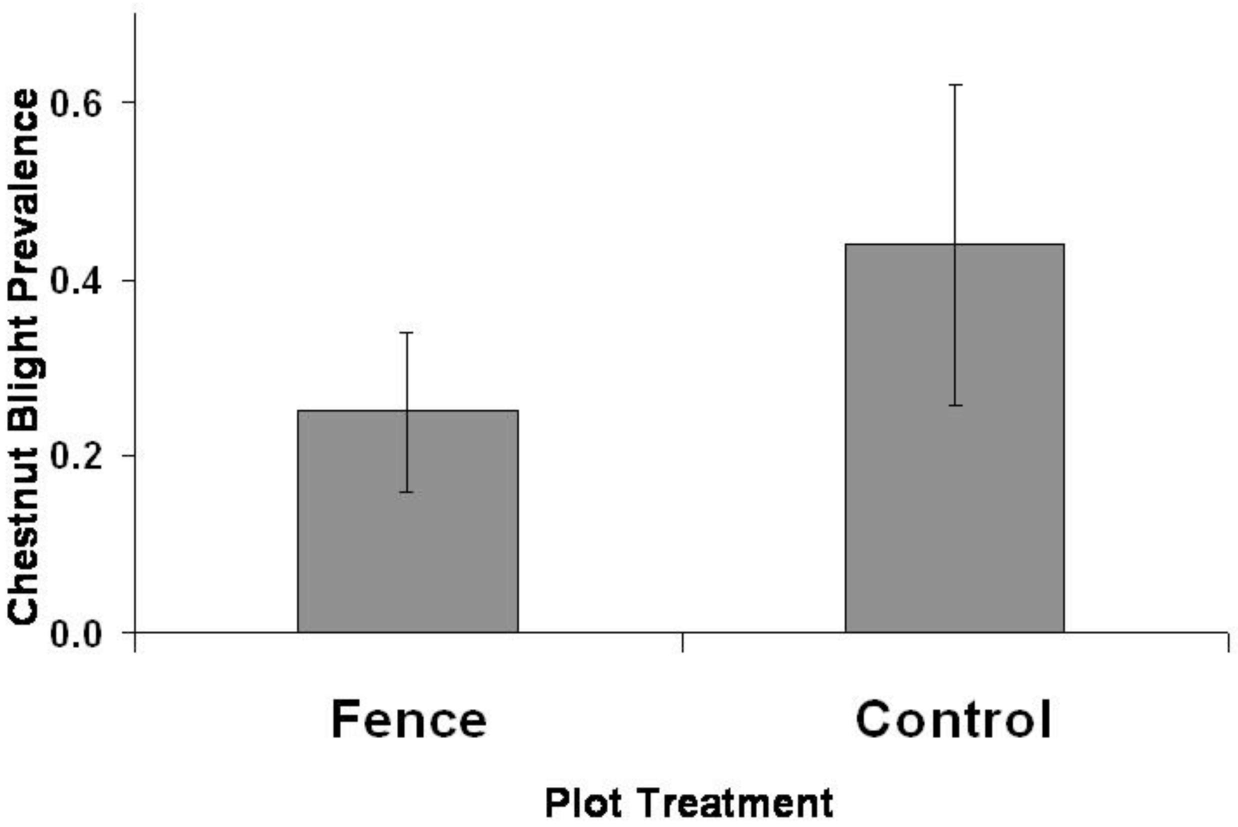

Figure 4. Mean annual blight prevalence (number blighted chestnut genets / total chestnut genets) in fenced and control plots. Error bars are 95% confidence intervals.

APPENDIX A

Table 1A. Averages by plot of independent variables in the study.

		Proprotional change in basal area		Proportional change in mean height		Proportional change in stem number	
Plot	Treatment	*A. pensylvanicum*	*C. dentata*	*A. pensylvanicum*	*C. dentata*	*A. pensylvanicum*	*C. dentata*
1	Control	0.59	-0.99	0.20	-0.96	0.00	-0.43
2		0.49	-0.14	0.08	-0.12	0.00	-0.22
3		1.62	-0.28	-0.30	-0.18	0.62	-0.07
4		0.33	-0.28	-0.01	-0.54	0.07	-0.14
5		0.26	-0.81	0.09	-0.40	0.08	-0.38
6		0.53	-0.10	-0.01	0.48	0.00	-0.55
7	Fenced	0.53	0.02	0.16	-0.03	-0.09	0.45
8		0.59	-0.88	0.15	-0.30	0.00	0.44
9		0.25	-0.35	0.06	-0.23	0.00	0.05
10		0.12	-0.23	0.13	-0.13	-0.06	-0.09
11		-0.78	-0.48	-0.44	0.03	-0.14	0.14
12		0.26	-0.18	0.54	-0.10	-0.15	-0.18

Table 1A (*cont.*)

Plot	Treatment	Mean annual mortality rate		Initial number of genets in 2006		Blight prevalence
		A. pensylvanicum	*C. dentata*	*A. pensylvanicum*	*C. dentata*	
1	Control	0.000	0.395	9	6	0.79
2		0.000	0.083	8	4	0.58
3		0.017	0.182	13	9	0.29
4		0.000	0.226	27	14	0.29
5		0.043	0.251	35	9	0.49
6		0.000	0.111	6	6	0.19
7	Fenced	0.000	0.000	11	8	0.38
8		0.000	0.103	8	7	0.41
9		0.017	0.098	20	11	0.21
10		0.000	0.049	16	15	0.20
11		0.056	0.015	7	19	0.15
12		0.083	0.048	10	7	0.16