

1 The Effects of Logging and Disease on American Chestnut

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17 **ABSTRACT**

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

42

43 **Keywords:**

44 Appalachian forests, *Castanea dentata*, chestnut blight, *Cryphonectria parasitica*,
45 disturbance ecology, land-use history, long-term forest change

46

47 **1. Introduction**

48 Forests are characterized by complex disturbance histories that drive
49 spatiotemporal patterns of species distributions and functional processes. Traditionally,
50 plant ecologists have viewed climate and topography as the major variables that limit
51 plant species distributions (Curtis and McIntosh, 1951; Whittaker, 1956; Bray and
52 Curtis, 1957). It is now clear that anthropogenic and natural disturbance history must
53 also be considered before forest spatiotemporal patterns and processes can be clearly
54 understood (Shugart and West, 1977; Pickett and White, 1985). For example, logging
55 is known to affect species composition and forest nutrient cycling (Chapin *et al.*, 2002).
56 The effects of multiple disturbances can result in forest spatiotemporal patterns that are
57 different than any single disturbance alone (Veblen *et al.*, 1994; Busby *et al.*, 2008;
58 Garbarino *et al.*, 2009). Specifically, land-use and disease can result in divergent
59 outcomes in population responses and in the re-growth of individuals (Veblen *et al.*,
60 1994; Kizlinski *et al.*, 2002; Latty *et al.*, 2004; Vepakomma *et al.*, 2010). A disease
61 epidemic causing large-scale tree mortality results in the removal of or change in a
62 species' function within the ecosystem, in the addition of large amounts of coarse
63 woody debris through tree-fall, and in increased light due to opening of canopy gaps
64 (Franklin *et al.*, 1987). These environmental changes affect inter-specific interactions
65 and may also feedback to affect the disease and the host species.

66 The chestnut blight (*Cryphonectria parasitica* (Murril.) Barr.) was the first invasive
67 tree disease to capture national attention in the United States because it affected a
68 valuable and ubiquitous lumber species, the American chestnut (*Castanea dentata*
69 (Marsh.) Borkh.) (Freinkel, 2007). The chestnut blight, introduced from Asia, was
70 identified in 1904 in New York City, and spread throughout the range of the American
71 chestnut during subsequent decades. The spread of chestnut blight occurred during a
72 period of increased timber harvesting in the eastern United States. In the 1920s and
73 1930s, when the front of the blight pandemic was sweeping across Virginia (Clapper
74 and Gravatt, 1943), demand for chestnut lumber also increased. Landowners were
75 strongly encouraged to cut any chestnuts on their land, first in an attempt to halt disease
76 spread, and later to profit from chestnut lumber before the opportunity was lost (Murrill,
77 1908; Carleton, 1913; Gravatt, 1914; Kelley, 1924; Gravatt, 1925; White, 1930; Baxter

78 and Gill, 1931). Today, the chestnut blight is endemic, with surviving chestnuts re-
79 sprouting from pre-blight root stocks until re-infection with the blight, after which all
80 above-ground parts of the stem eventually die. The blight does not directly infect and
81 kill roots of the chestnut, although the root system can decline and die following blight
82 infection as a result of inadequate photosynthate production. Almost a century after the
83 blight invaded, chestnuts are declining but not extinct, and their persistence varies
84 across sites of different topographies, soils, and disturbance histories. This scenario is
85 ideal for a study of the long-term effects of logging and disease on host-pathogen
86 interactions, differential tree mortality, and population decline.

87 Both logging and tree disease remove trees from the canopy and cause dieback
88 via different mechanisms having distinct effects on the environment and inter-specific
89 interactions. Logging can influence pathogen infection rates and thus host species
90 mortality, resulting in complex effects on forest processes such as nutrient cycling,
91 decomposition, and interspecific competition (Lewis and Lindgren, 2000; Kizlinski *et al.*,
92 2002; Latty *et al.*, 2004). Furthermore, timber harvesting can lead to the
93 homogenization of stand age or species composition, and a decrease in structural
94 diversity may facilitate disease spread (Hebard, 1982; Smallidge *et al.*, 1991). Young
95 trees often have different disease susceptibility than older trees, and thus a younger
96 stand can harbor different rates and patterns of disease spread (Veblen *et al.*, 1994). A
97 relationship between land use and chestnut decline has been indicated in previous
98 studies, but results on the magnitude and direction of the effect differ between studies
99 (Hebard, 1982; Schwadron, 1995; Paillet, 2002; Fei *et al.*, 2007; Elliott and Swank,
100 2008). Interestingly, with the exception of Hebard (1982), none of these studies
101 measured chestnut blight prevalence, which has a major influence on chestnut decline.
102 It is clear that land use impacts chestnut survival, but the effects of different land use
103 types and their varied timing and intensity are still unclear in the literature.

104 In addition to an increase in forest disease in North America, cleared land has
105 been returning to forest over the past half-century (Foster *et al.*, 1997). Understanding
106 the individual and combined effects of tree disease and logging will inform forest
107 management and will improve conservation of species declining because of disease,
108 such as the American chestnut. Most studies in disturbance ecology emphasize the

109 effect of one disturbance event rather than characterizing the effect of multiple
110 disturbances. This study will assess the long-term effects of multiple disturbances on
111 host population dynamics and pathogen prevalence. Specifically, the questions
112 addressed in this study were: (1) Do areas selectively logged for chestnut have different
113 present-day chestnut abundance than areas not logged for chestnut? (2) Does timing
114 of logging (stand age) have long-term effects on chestnut abundance? (3) How does
115 chestnut blight prevalence vary across sites of differing chestnut densities, environment,
116 and history?

117

118 **2. Methods**

119

120 *2.1 Study Area*

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

129

130 *2.2 Field Methods*

131 Two historical datasets, pre-dating chestnut blight infection in the region, were
132 used to choose sites to re-sample where chestnuts were known to have occurred before
133 the blight: (1) Forest communities covering 22 sites near Mountain Lake Biological
134 Station (MLBS) sampled by station students during the years 1934-1941; (2) Timber
135 cruises of 21 tracts owned by the Craig-Giles Iron Company (CGIC) in 1918. Areas re-
136 visited were in the Jefferson National Forest (JNF), on MLBS land, or on private lands
137 adjacent to JNF or MLBS. The original MLBS studies were conducted on land that had
138 been timbered and, in most cases, burned, while the timber cruise was conducted on
139 land that was a mix of virgin timber and previously cleared land, according to notes in

140 the survey. Most of the land included in the CGIC timber cruise was also burned in the
141 1920s or 1930s, according to 1937 USFS aerial photographs. Only 15 plots (<4%) were
142 located on land that was being used for agriculture in 1937. Thus, agriculture was not
143 an important aspect of land clearing across the study area. Rather, most land clearing
144 was a result of a combination of timbering and burning.

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

150 Each original sampling area was re-sampled. In 2008 and 2009, chestnut
151 density and site environment were measured on three to ten non-overlapping 0.04 ha
152 circular plots. Plots were usually 150 m apart within a site. In cases where the original
153 sampling site was so small that <3 plots fit into the sampling area at 150 m spacing,
154 spacing between plots was reduced to 50 m. In large sampling areas where >10 plots
155 were to be sampled at 150 m spacing, the spacing between plots was increased to 300
156 m. The CGIC sampling areas ranged from 8.2 to 1121 ha, in contrast to MLBS areas
157 ranging from 0.1 to 7 ha. In especially large CGIC sampling areas (>55 ha), all of which
158 occurred in JNF, stands designated as the USFS management units (5-81 ha) were
159 selected as a sub-sample within each sampling area. Selection of these stands was
160 based on their canopy composition, the stand age in the USFS Jefferson National
161 Forest Stand Information database, and their accessibility by USFS road. All categories
162 of canopy composition were sampled once in each tract, unless the canopy composition
163 was unlikely to have ever harbored chestnut (e.g., *Tsuga canadensis*, *Pinus pungens*).
164 Stands that were established between 1900 and 1918 were considered unlikely to have
165 been forested when the timber cruise was conducted and thus were discarded as
166 potential sample sites. In 2007, 11 MLBS study sites were sampled with a different re-
167 sampling method than 2008 and 2009. Four randomly selected transects (500 m²) were
168 sampled for chestnut abundance throughout the original study area that was re-located,
169 as well as sampling the original 100 m² quadrat as closely as possible. After the 2007
170 field season, this sampling method was replaced with the more efficient regularly-

171 spaced circular plot sampling method used in the rest of the MLBS study sites and all of
172 the CGIC tracts. In the MLBS area, 121 plots were sampled on 22 sites. In the CGIC
173 area, 289 plots were sampled on 21 tracts.

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

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

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

198 The center of each 0.04 ha plot was used as the center for variable radius
199 sampling of canopy basal area. A 4.59 basal area factor (BAF) wedge prism, which is
200 generally used in mixed hardwood forests of the Appalachians (Zeide and Troxell, 1979;
201 Wiant *et al.*, 1984; Packard and Radtke, 2007), was used to select overstory trees to

202 measure and record forest species composition. On especially steep slopes (>15%
203 grade), the Cruiser's Crutch (Forestry Suppliers, English Model) at 4.59 BAF was used
204 instead of the wedge prism because it accounts for error due to slope. The distance to
205 borderline trees, meaning trees that were difficult to determine using the wedge prism if
206 they were within the variable sampling radius, was measured in order to ascertain if
207 they should be included in the sample. Only very large trees (>48.4 cm dbh) fell outside
208 of the 0.04 ha plot boundaries. Trees <10 cm DBH were not used in data analysis for
209 calculation of basal area per hectare because the wedge prism method is known to
210 have increased error at low DBH by inflating the density of small trees (Packard and
211 Radtke, 2007). The DBH of trees that were within the sampling radius of the wedge
212 prism was recorded.

213

214 *2.3 Laboratory Methods*

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

219 All cores were mounted and then sanded with increasingly finer grit sandpaper to
220 600 grit. Only complete cores that had a clear inner ring, defined as a clear semi-circle
221 that showed that cores had reached the center (though not necessarily the pith) of the
222 tree, were used. This year of tree establishment was averaged across the two cores in
223 each plot, and from here on will be referred to as year of establishment.

224

225 *2.4 Data Analysis*

226 In all analyses, slope and aspect were converted to a measure of solar insolation
227 following McCune and Keon (2002). This transformation puts aspect on an ordinal
228 rather than a cardinal scale and incorporates steepness of slope in the calculation of
229 solar radiation, unlike the similar conversion for heat load index. Spatial autocorrelation
230 of variance in number of chestnuts between plots was tested with a Mantel test using
231 the function `mantel.rtest` in the "ade4" package in R, across all plots visited in 2007,
232 2008, and 2009 (Crawley, 2007). A variogram was created using the "variog" function

233 in the spatial library in R to plot variance in number of chestnuts per plot with spatial
234 distance between plots.

235 A generalized linear model of number of chestnut genets with chestnut logging
236 as a two-state class variable, in addition to continuous independent variables solar
237 insolation, soil pH, elevation, canopy basal area per hectare, and year of establishment,
238 was analyzed using PROC GENMOD in SAS v. 9.1 (SAS Institute, Cary, NC). Errors
239 were assumed to be Poisson distributed, and the model was corrected for
240 overdispersion by dividing the deviance by the degrees of freedom using the SCALE =
241 DEVIANCE option in the MODEL statement. Three plots with extremely high z-scores
242 (4.32, 5.03, and 7.71) for number of chestnut genets were deleted as outliers, leaving a
243 total of 130 plots for analysis. Four additional missing values due to poor quality cores
244 left a total of 126 plots in the analysis (83 not logged and 43 logged).

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

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

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

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

271

272 **3. Results**

273 405 plots were sampled. They ranged in elevation 544-1302 m, in solar
274 insolation 0.50-1.07 MJ cm⁻² yr⁻¹, in year of establishment from 1778 to 1999, and in soil
275 pH 3.00-5.98. Number of chestnut stems per hectare varied from 0 to 3775, and number
276 of chestnut genets per hectare varied from 0 to 1900. Chestnut tree remains, indicating
277 whether or not chestnuts had been selectively logged, were found at 129 of the 405
278 sites. Spatial autocorrelation between variance in number of chestnut genets per plot
279 and spatial distance between plots was weak but significant ($r = 0.049$, $p = 0.024$, $n =$
280 405). The variogram showed a peak in autocorrelation at 4000 m, which is close to the
281 average distance between stands of 3013 m. The variogram showed another peak at
282 17.5 km, which is close to the distance between the MLBS study area and the centroid
283 of the CGIC study area. The MLBS study area is higher in elevation than the CGIC
284 study area, which accounts for the second peak seen in the variogram.

285 In a generalized linear model of the dependence of chestnut abundance (number
286 of chestnut genets per 0.04 ha) on the continuous environmental variables (elevation,
287 solar insolation, soil pH, canopy basal area per hectare, and average year of
288 establishment) and on the binary variable chestnut logging history, chestnut logging
289 history was the only significant independent variable ($X^2 = 5.32$, $p = 0.021$, $df = 119$)
290 (Fig 1). There was no significant difference between year of establishment in chestnut
291 logged or unlogged sites. Mean year of establishment dated to 1916 in the chestnut
292 logged sites (median = 1930, ranging 1807-1982). Mean year of establishment dated to
293 1919 in the unlogged sites (median = 1931, ranging 1778-1974).

294 In the logistic regression of chestnut presence or absence, the only significant
295 environmental variable among elevation, solar insolation, soil pH, and average year of
296 establishment was elevation ($\chi^2 = 9.76$, $df = 1$, $p = 0.0018$; Fig 2). There was good
297 model fit using elevation as the sole predictor ($\chi^2 = 3.84$, $p = 0.43$, $df = 4$). Elevation
298 was not significantly correlated with any other environmental variable using Pearson's
299 correlation, although solar insolation and soil pH were almost significant (respectively, r
300 $= 0.099$, $p = 0.055$; and $r = 0.097$, $p = 0.063$). In the model without the environmental
301 predictors, the model was not a good predictor because the null model of the logistic
302 curve fitting the data was rejected ($\chi^2 = 13.50$, $p = 0.019$, $df = 5$). The full model
303 including elevation found 62.0 % of predictions of chestnut presence were concordant
304 with the observed data. The odds ratio estimate was 1.002, indicating that for every 1
305 m increase in elevation, the odds of chestnut being present are 1.002 times greater
306 (Tabachnick and Fidell, 2007).

307 On sites where chestnut was present, the canonical correlation between chestnut
308 abundance and the same five environmental variables was 0.53 and was significant ($F_{5,}$
309 $_{130} = 10.16$; $p < 0.0001$; Table 1). The environmental variables with highest canonical
310 coefficients on the first canonical variate with chestnut abundance in the analysis were
311 elevation (0.909), soil pH (0.601), and canopy basal area (0.322) (Table 1 and Fig 3).
312 The assumption of linearity between the independent variables and the response
313 variables was tested by comparing a linear regression of each independent variable
314 with the dependent variable (chestnut genet abundance) to the quadratic regression. In
315 no case was the quadratic regression a better fit to the data.

316 The canonical correlation of the same environmental variables with chestnut
317 blight prevalence was 0.25 and was not significant, although the p-value was low ($F_{5, 130}$
318 $= 1.73$; $p = 0.132$; Table 1). Canopy basal area per hectare was very strongly
319 correlated to blight prevalence in this analysis ($r = -0.992$). The assumption of linearity
320 in this canonical correlation was also tested in the same way as described in the
321 previous paragraph. In the multiple regression analysis, only the linear relationship
322 between number of blighted genets and total number of genets was significant ($F =$
323 568.41 , $df = 1$, $p < 0.0001$; Fig 4). The mean square error for the linear model was
324 2.053, and the mean square error for the quadratic model was 1.930. Dividing the

325 linear model's mean square error by the quadratic model's mean square error yields an
326 F statistic of 1.064, showing that the quadratic model was not significantly better than
327 the linear model. Overall, 15.1% of the total genets were infected with chestnut blight.

328

329 **4. Discussion**

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

343 Selective logging of the chestnut during the blight pandemic has often been
344 suggested as the reason why so few trees free of blight are found today (Kelley, 1924;
345 White, 1930; Clapper and Gravatt, 1943), but my data do not support this contention.
346 This study indicates that chestnut abundance was significantly lower on sites that had
347 been selectively logged for chestnut than on sites that had not been logged for chestnut,
348 which suggests that selective logging of healthy chestnuts removed resistant trees from
349 the population. This result is consistent with a study by Elliott and Swank (2008), whose
350 data suggest lower chestnut abundance was found in areas where a higher basal area
351 was removed in a selective logging event of oak and chestnut in the 1930s. The lack of
352 difference in stand age (as indicated by year of establishment) between chestnut logged
353 and unlogged sites could be for three reasons: (1) Selective logging events were not
354 detected by the stand age because old and young trees are more likely to co-occur on a
355 site than after a more extensive cut (Oliver and Larson, 1996); (2) Most of these sites

356 were burned in the 1920s or 1930s, according to USDA 1937 aerial photographs, notes
357 in the MLBS studies, and communication with local residents in the area; and (3) If the
358 oldest stems in forests dominated by chestnut were chestnut stems, then the trees
359 cored in this study would have been those that were released by the chestnut death
360 rather than regeneration that occurred as a result of the logging event.

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

387 frequency of these fires are generally not recorded. Thus, the effects of logging and
388 land clearing on chestnut persistence may be site-specific and highly complex, which
389 could obscure any relationship between timing of last logging event and chestnut
390 abundance.

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

403 Elevation was found to be an important predictor of chestnut presence and also
404 strongly correlated with chestnut abundance, and soil pH was also found to be strongly
405 correlated with chestnut abundance. Other studies of chestnut abundance have not
406 found elevation to be a significantly correlated variable but also did not compare
407 chestnut abundance across sites of such a wide range of elevations (Stephenson *et al.*,
408 1991; Fei *et al.*, 2007). This increase in chestnut abundance with increasing elevation
409 would be reversed at some maximum elevation for chestnut. Chestnut's ideal elevation
410 is likely different across variation in latitude. Stephenson *et al.* (1991) and Fei *et al.*
411 (2007) did not measure soil pH, but Fei *et al.* (2007) did find that chestnut presence was
412 associated with local geology. In particular, presence differed between sandstone
413 ridges and limestone slopes, and these bedrock geologies are tightly coupled with soil
414 pH in this region. Chestnut does not grow as well on more basic, limestone soils
415 (Russell, 1987). All the soils sampled in this study were acidic, but chestnut showed a
416 preference for a higher soil pH (4 to 5) within this range (Fig 3).

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

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

448 inoculum in this area is other infected or recently dead chestnut stems, but the
449 epidemiological importance of blight's ability to grow on other species merits further
450 study.

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

471

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611

612

613 **TABLE AND FIGURE CAPTIONS**

614

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

621

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

627

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

632

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

637

638 **Figure 4. Number of infected genets versus total number of chestnut genets.** A
639 stepwise multiple regression testing a linear (density independent) or quadratic (density
640 dependent) relationship, found the linear model to be a significantly better fit ($F =$
641 568.41 , $df = 1$, $p < 0.0001$; $R^2 = 0.58$). Thus, chestnut blight infection is independent of
642 chestnut density, with 15.1% of the total genets infected.

Figure
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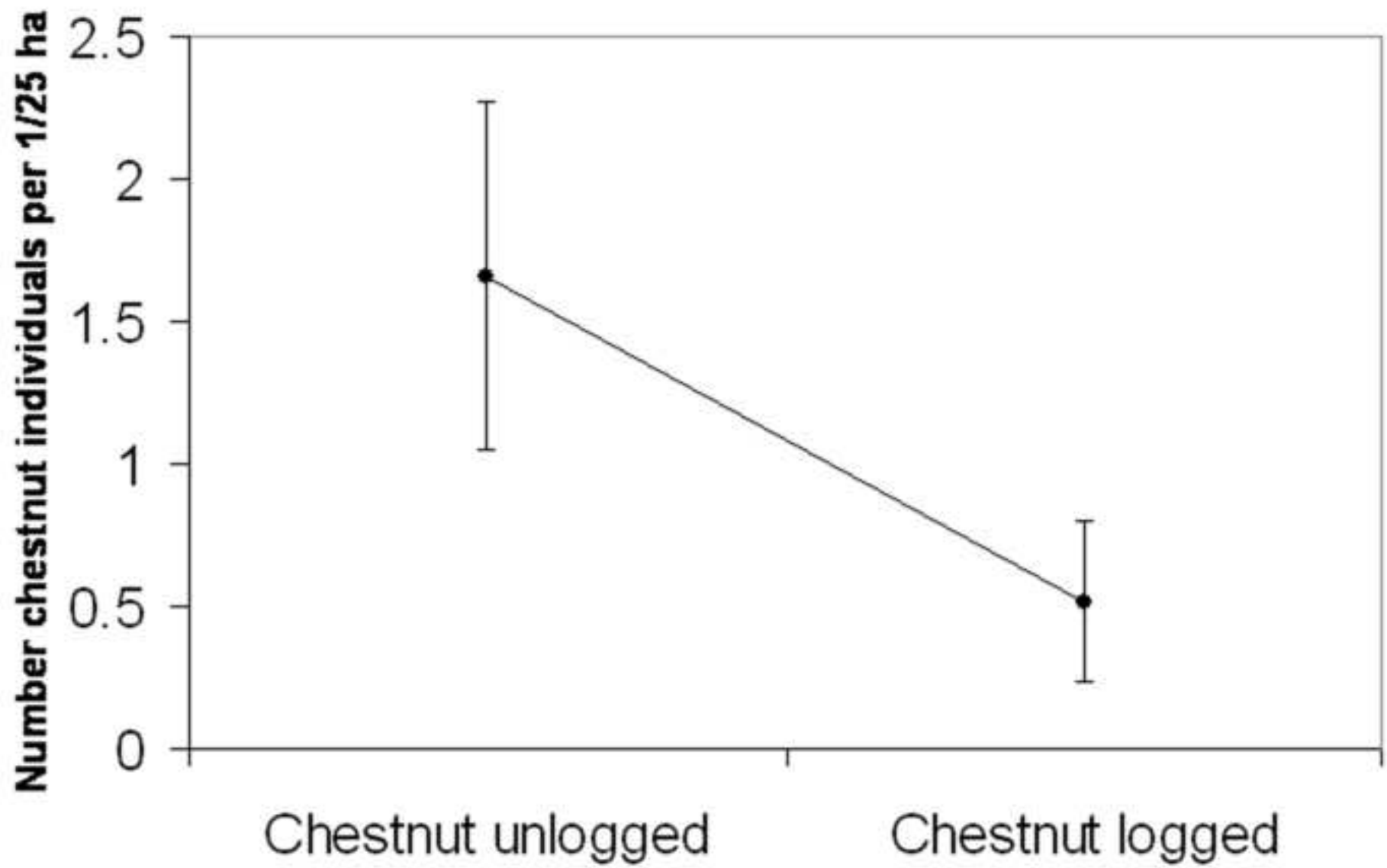


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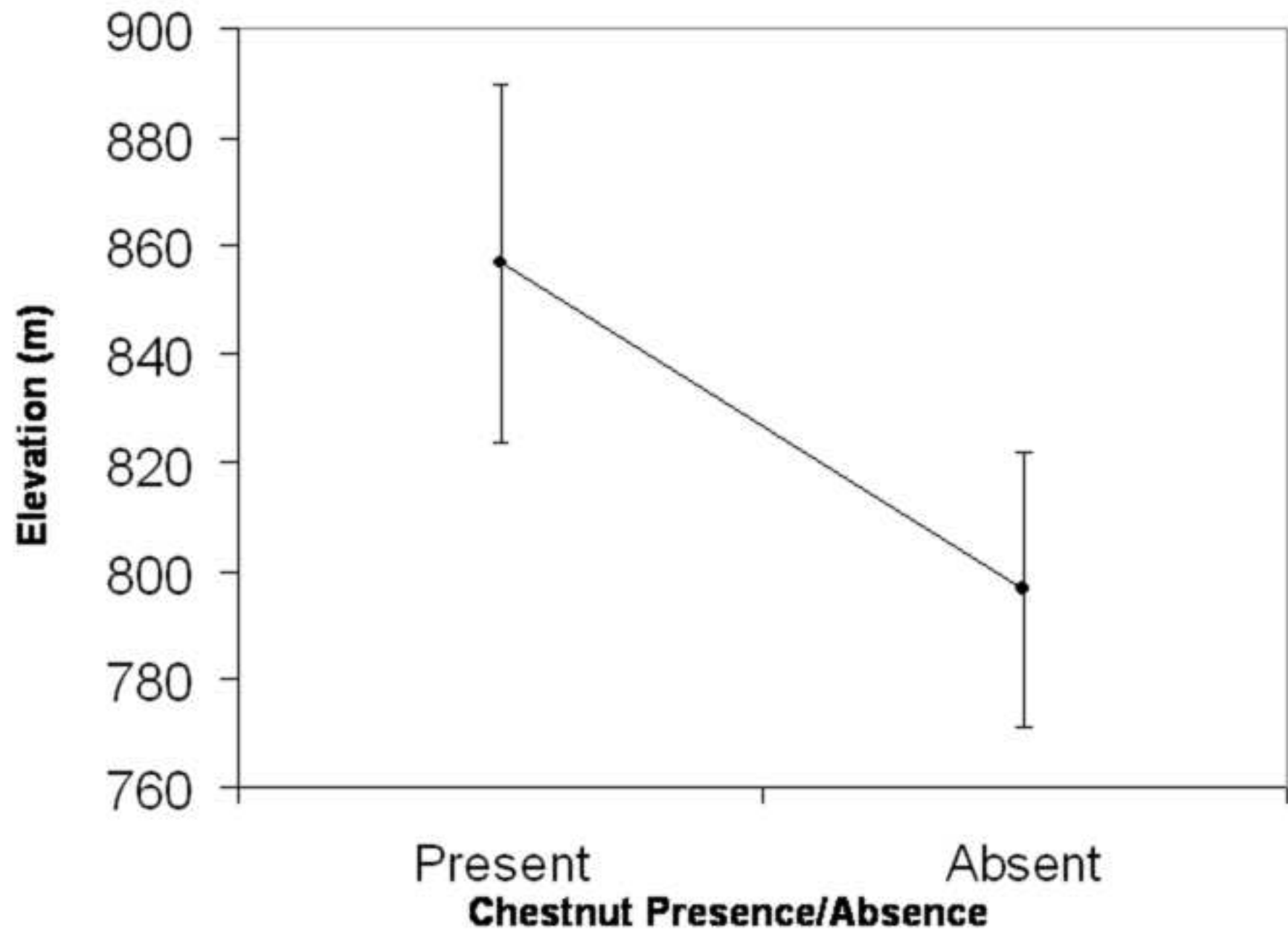


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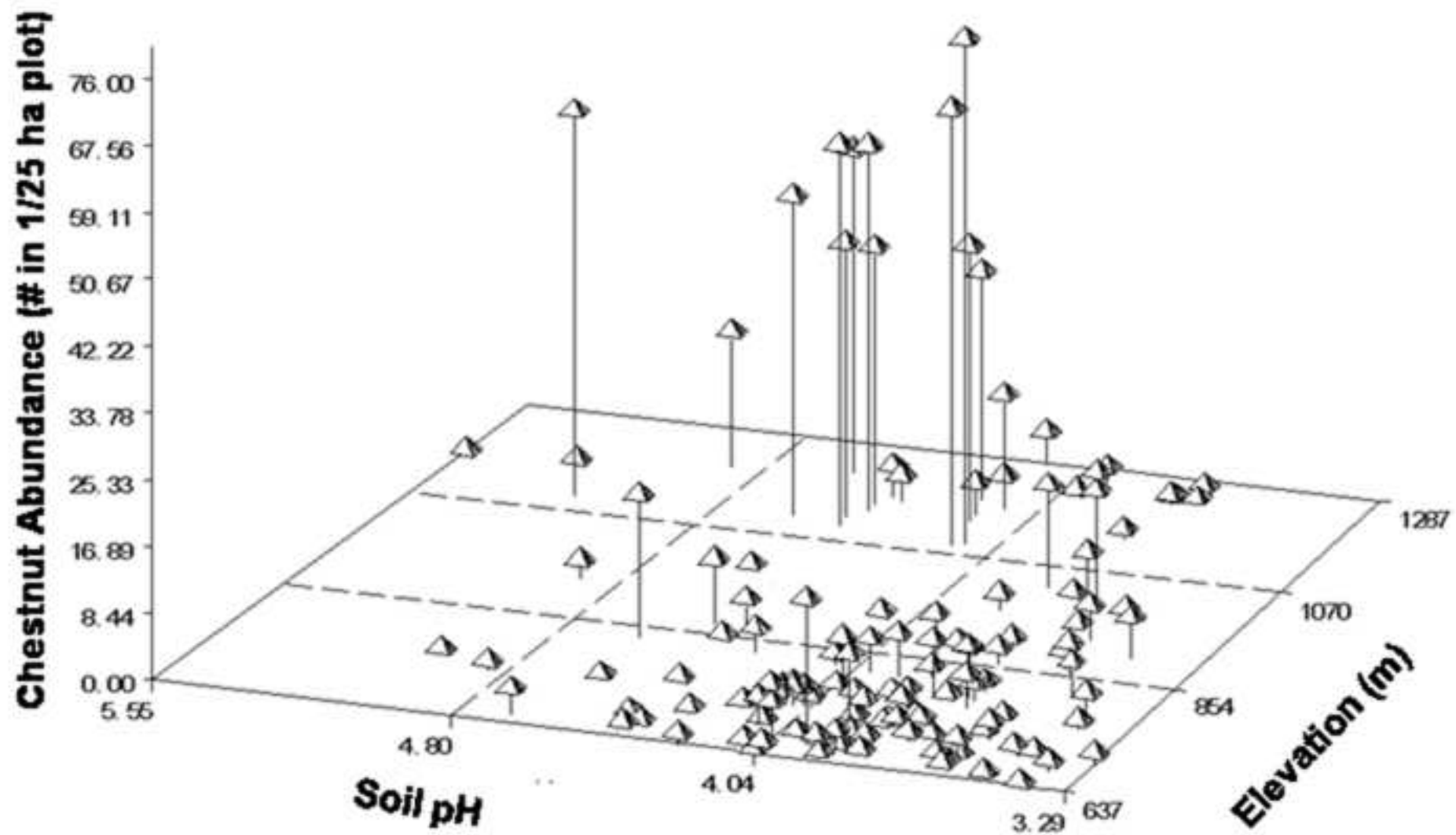
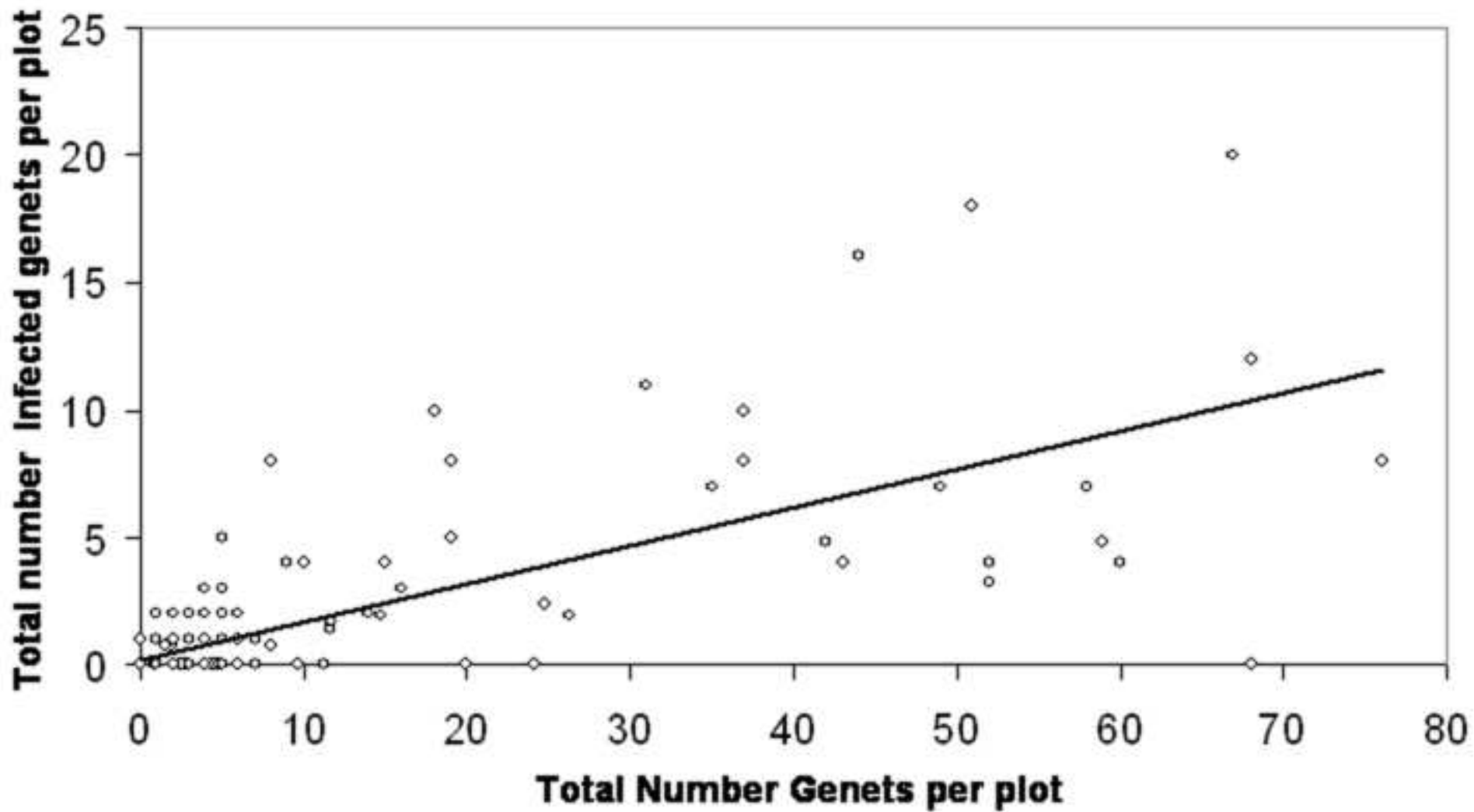


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Table

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| 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 |