Email Correspondence

zhihong.zhang@mail.mcgill.ca

Zhihong Zhang[1], Ema Casandra Varela Perez[1], Anna Chinn[2], Johnathan Davies[1]

Tree Diversity has Limited Effects on Beech Bark Disease Incidence in American Beech Population of Mont St-Hilaire

Abstract

Background: American beech trees (Fagus gandifolia) exist in many areas in northeastern North America. Beech bark disease (BBD) is caused by a scale insect and bark-killing fungus (Cryptococcus fagisuga and Nectria spp.). We aim to study the correlation between diversity and the presence of BBD, and predict that tree diversity in Gault's Nature Reserve in Mont St-Hilaire (MSH), Québec decreases the presence of BBD and that F. grandifolia density would increase the presence of this disease.

Methods: We randomly chose 15 sites for sampling of individual tree species. F. grandifolia trees were identified as "healthy" or "infected". Simple regressions, ANOVA, two and three-way interaction, linear mix effect model, and paired t-test were performed using R and Excel.

Results: Our results show no significant correlation of infected individuals and total number of either A. saccharum or A. pensylvanica, unless analyzed with a linear mixed effect model (p=0.0256). However, there was a strong, positive correlation between the number of infected trees and the density of F. grandifolia (R2=0.6712), and this relationship was stronger in disturbed areas compared to undisturbed areas in the reserve (t=2.0492, p=0.047, $t_{critical}$=2.0211).

Conclusion: We found beech tree density and habitat disturbance, but not community diversity, to have a significant positive effect on Beech Bark Disease infection rates.

Introduction

The American beech (Fagus grandifolia) is a shade tolerant, long-lived canopy tree species that is the only species of the genus known to exist in North America. (1-3) The American beech is considered to be a foundation species that influences the ecosystems in which it grows by providing different resources such as understory shade, leaf litter, and food for the wildlife. (1-6) Thus, it is an ecologically important species that coexists with other dominant canopy species such as Sugar maple (Acer saccharum) in Northern hardwood, mixed deciduous, and temperate forests in northeastern North America. (2, 3, 6, 7)

The American beech tree is a monoecious species that can reproduce clonally by root sprouts under situations of stress. (1, 8) After a disturbance resulting from tree injury or disease, this vegetative reproduction leads to dense thickets of clonal beech sprouts. (9, 10) This phenomenon makes clonal beech thickets an important determinant of local biodiversity as sprouts can readily come to dominate a disturbed area. (4)

Towards the end of the 19th century, when nursery stocks of ornamental European beech (F. sylvatica) were brought to Halifax, Beech Bark Disease was introduced to North American forests from Europe. (11, 12) Since its appearance in Nova Scotia in 1911, the disease has spread outwards within the American beech's range. (11, 13, 14) Today, the disease can be found throughout northern hardwood forests from the Canadian Maritimes to southern Quebec and Ontario. (15, 16)

Beech Bark Disease is an insect and fungus complex that begins with injury to the tree's bark by an alien scale insect, Cryptococcus fagisuga, followed by the more deadly infiltration of bark killing pathogens in the Ascomycetes family of the genus Neonectria whose spores are propagated by wind and water. (11, 17) As larvae, the scale insects pierce the beech's bark to feed on the tree's phloem throughout the late summer. (17) Crawlers develop between June and September, and are easily dispersed by wind, wildlife, and even humans. (6, 11, 18, 19) The insects overwinter until they can molt during the spring into wingless adults. (11, 17, 20) Insect feeding causes tree cells to desiccate locally and becomes clearly visible on the trunk as clusters of small white spots of dried sugary sap. (11) Once the bark has been penetrated, fungal species Neonectria faginata and Neonectria ditissima infiltrate and cause severe cankering and formation of callus tissues that cause the tree to be girdled and eventually killed. (13, 21) The presence of the scale alone is not fatal to beech trees, though it highly predisposes the bark to infection from Nectria. (4, 11)

Of all the Monteregian Hills, Mont Saint-Hilaire (south of Montreal, Quebec) is least disturbed by human activity and the richest in terms of natural history and cultural interest. It is also the location where Beech Bark Disease was first observed in the late 1980s. (22) Its northern hardwood community is an appropriate study area because its forests contain many diverse microhabitats that could potentially foster different levels of tree diversity. The variation in diversity could correlate with the presence of Beech Bark Disease. In the years ahead, forest communities found at Mont Saint-Hilaire are expected to undergo significant changes in species composition, some of which can be attributed to the impacts of Beech Bark Disease. (22)

The objective of this study was to investigate the relationship between forest diversity and the presence of Beech Bark Disease in Mont Saint-Hilaire Recent studies have linked biodiversity loss with increased rates of disease and parasite severity in both animal and plant systems. (23, 24) With this in mind, we predicted that increased tree diversity in the reserve will correlate negatively with the presence of Beech Bark Disease, because

we expected community diversity to slow down disease spread. (25, 26)

Methods and Materials

Data was gathered from the 26th to 28th of August 2014. We randomly selected 15 sites on the reserve with a random generator (www.random.org) from an alphanumeric gridded map of Mont Saint-Hilaire (Fig. 1). Each site measured 500 m by 500 m. Eight sites fell in disturbed areas, and seven in undisturbed areas. Disturbed areas were defined as areas where the public has access to trails which are wide and frequently visited by the public or the reserve's staff. Undisturbed areas were defined as areas where the public does not have access, with narrow or nonexistent trails.

Each site contained at least three circular 100 m2 quadrats. Each quadrat was between 20 m and 40 m away from the closest trail. Using a compass and key landmarks, such as trails and streams, to reach the approximate centre of each site, the "ignorant man" technique was then used to select the three separate sample quadrats. (27) We counted the number of trees of each different species in each quadrat. We considered only mature individuals having a breast height diameter larger than 8 cm, measured with a 25 cm long string. We noted whether each individual beech tree was infested using the presence of white traces of scale insect penetration as a proxy for Beech Bark Disease. We also made notes on subjective observations regarding the disease's severity.

For every statistic test performed, we assumed that trees, quadrats, and sites are independent data points and that there is no overlap between plots and sites (random sampling). All levels of significance were set at $p < 0.05$.

Diversity index and correlation analysis

We used Shannon's and Simpson's indices as measures of diversity as they are direct measures of ecological diversity and account for the community weight and the species abundance. (18, 29) We calculated these indices on Microsoft Excel (2007) for every site.

As many of the data sets were not normally distributed and were therefore analyzed non-parametrically, we used Kendall's tau rank to determine whether the number of infected individuals was correlated with Shannon's index of diversity, Simpson's index, number of American beech, number of sugar maple, or number of striped maple.

T-test

We performed t-tests in R (version 3.1.1 2014) to identify differences in infection frequencies between the categorical split between sites (disturbed and undisturbed).

Results

A total of 49 plots were recorded, accounting for 560 trees sampled. From this data, 39% were American beech (F. grandifolia), 38% were Sugar maple (A. Saccharum), and 7% were Striped maple (A. pensylvanicum); the remaining 16% accounts for different species of trees that we did not consider in our calculation as they occurred in very reduced numbers across plots. From the proportion of American beech counted in this experiment, 69% showed signs of C. fagisuga invasion via the presence of dried sugary sap and were therefore assumed to be infected with Beech Bark Disease.

Correlation Analysis (Kendall's Tau Hypothesis)

When performing the Kendall's tau calculations where $\tau_{crit}=0.163$ for all cases, we found that diversity indices were not correlated to the presence of infection in any way ($\tau_{Shannon}=0,061$; $\tau_{Simpson}=0,140$). However, the density of number of American beech is correlated to the number of infected trees ($\tau_{beech}=0,752$). Furthermore, the number of species and the number of trees per site are also correlated ($\tau_{\#species}=0,316$; $\tau_{\#trees}=0,434$). The presence of red

maple ($\tau_{r. maple}=0,621$) also showed correlation, and the presence of sugar maple showed no correlation ($\tau_{s. maple}=0,07$)

T-test

When the data were separated categorically by habitat type (disturbed vs undisturbed), a t-test revealed that the mean number of infected beeches in each plot in undisturbed areas (mean = 1.77, sd = 2.14) was significantly lower than the mean number of infected beeches in disturbed areas (mean = 3.67, sd = 4.18, t = 2.0492, df = 40.233, p = 0.047), though the mean number of beeches between the two habitat types did not differ significantly (mean$_{disturbed}$ = 3.636 , sd$_{disturbed}$ = 4.20, mean$_{undisturbed}$ = 5.259, sd$_{undisturbed}$ = 3.1403, t = 1.4224, df = 45.085, p = 0.1618). Furthermore, the interaction between beech density and habitat type on number of infected beeches was also significant (t = -2.516, p = 0.0155) (Fig. 2). This fact directed our attention to a relationship that we did not consider at the beginning of our experiment. The correlation between the number of infected individual by Beech Bark Disease not only increases as the density or number of American beech increases, but has a noticeable and much stronger effect in disturbed areas ($R2 = 0.7824$) than in undisturbed areas ($R2 = 0.3158$). This indicated that disturbance could be a major factor driving the prevalence of Beech Bark Disease in Mont Saint-Hilaire (Fig. 3).

Discussions

The objective of this study was to explore the relationship of tree diversity and density on the presence of Beech Bark Disease in Mont Saint-Hilaire. Our analysis indicate that though community diversity has no significant effect on Beech Bark Disease infection rates on Mont Saint-Hilaire, American beech tree density does correlate significantly with disease incidence. In addition to tree density, the impact of habitat disturbance on infection incidence is positive and interacts with density effects on the Beech Bark Disease.

Our data showed no significant correlation between tree diversity and Beech Bark Disease frequency. It is possible that other trees influence the incidence of Beech Bark Disease, for example, by facilitating niches for animals that have been shown to transport the scale insect, but this is beyond the breadth of our study. (28) Although communities of greater Shannon's and Simpson's diversity indices contain greater diversity, it is possible that the areas on Mont Saint-Hilaire we assessed contain habitats that are not different enough from one another to be called different "communities", and that therefore diversity does not play a role. (29) In addition, many past studies that link diversity and infection have measured disease severity rather than disease frequency. Mitchell et al. (2002) also suggested that the effect of diversity on disease might be stronger in natural systems than in their laboratory experiments because differences in diversity would occur at a larger scale. (23) This may well be the case for Beech Bark Disease and Mont Saint-Hilaire's American beech trees. Therefore, an objective and quantifiable measure of disease severity should be recorded in further research.

Although it is difficult to understand the precise community composition effect from the data recovered from this study, the relationship between beech population density and Beech Bark Disease frequency is clear. Though it cannot be said that increased diversity slows down the spread of the infection as initially hypothesized, the number of beech trees in each quadrat, i.e. beech tree density, is highly correlated with the infection density in the quadrats. The trend of increasing disease frequency with increasing beech numbers suggests a density-dependent relationship between Beech Bark Disease and the American beech. Density dependence is a common theme in disease ecology, characterized by increased infection rate with increased host density; that is to say, as more individuals are present in a given area and come into contact with one another, the probability of the disease spreading between individuals increases as well. (30) Density dependence cannot be directly observed by this study, as this would require an analysis of contact rate between infected and non-infected individuals over time. (30) It is therefore possible that our findings are simply a product of the probability of encountering an infected individual

increasing with the total number of individuals encountered. Nevertheless, density dependence is supported by one of the three main factors outlined in early literature regarding the spread of Beech Bark Disease; the density of the stand highly influences the development of the disease. (11) Density dependence is known to affect plant demography from growth to production and mortality. (31) As beech trees lack mobility, the rate at which potential hosts become exposed to the disease (contact rate) is a function of the ability of both the insect and the fungus to contact the tree. The scale's chance of encountering a beech tree increases with the density of beech trees around the point source of infection. (13) Houston (1994) also added that at least 80% of American beech mortality happens where the density of this tree is high, which can support the explanation of density dependency. (13) Other fungal infections similar to Beech Bark Disease have overwhelmingly been found to be density dependent, despite being vector borne, possibly due to the lack of vector (fungal) behavioural variation with increased host density. (2, 31-33)

Alternately, because of the American beech's tendency to produce clonal sprouts via their root system, large, densely-populated patches observed in the field may have been made up of one single individual with many clonal sprouts. (9, 10, 34) This possibility of genetic relatedness was not accounted for in our survey, as each trunk above ground was sampled as a genetically distinct individual. The clonal sprouting capacity of the American beech is likely to influence the overall susceptibility of a so-called "population" of beech trees in an area, as it is known that genetic uniformity in clonal plant populations renders them more susceptible to infection. (35) Past genetic variability in Mont Saint-Hilaire's American beech population has no doubt impacted today's community, considering Beech Bark Disease has been observed on Mont Saint-Hilaire since the 1980s. (22) Nonetheless, selective pressure for disease resistance in trees on the mountain, as well as the root sprouting and as full- or half-sib seedlings cluster due to the species' limited seed dispersal radius may have led to the existence of more or less tolerant individuals and sub-populations on the mountain. This could in turn impact the diversity and composition of the forest. It is for these reasons that genetic analysis of relatedness is sub-populations should be addressed when investigating Beech Bark Disease on Mont Saint-Hilaire. It is necessary to investigate whether the healthy beeches growing around a surviving American beech individual are closely related, or whether the trees growing around a survivor are clones of the same tree, which indicates that a new individual with resistant genes does not exist. This might suggest whether there is inheritance of a resistant phenotype in Mont Saint-Hilaire, and will show whether the spread of disease has already slowed and entered aftermath phase.

Habitat disturbance was also found to significantly correlate with Beech Bark Disease incidence. In addition to density mediated disease transmission, habitat disturbance may facilitate the propagation of Beech Bark Disease. Even though Mont Saint-Hilaire's reserve area is rather small (10 km2), the mountain can be characterized as being highly fragmented, particularly in the disturbed publicly accessible areas. The edge of a habitat is often cited as the area at which abiotic factors, such as wind and temperature changes, act most harshly, and effect which may be amplified if the edge is expanded by fragmentation, a phenomenon that may be especially harmful in small communities such as Mont Saint-Hilaire. (36) The large-scale alteration of the natural forest to accommodate leisure activities on Mont Saint-Hilaire contributes to habitat fragmentation within the forest by breaking up contiguous forested area for trails and roads, generating corridors for Beech Bark Disease to be spread between patches while isolating stands of American beech from dispersal and migration between sub-populations. It is possible that by opening spaces in the forest for pedestrians and cars, the increased wind flow through these corridors could aid the spread of scale insect and fungus, as wind flow speed is known to be a limiting factor to the spread of the disease. (4, 13) Furthermore, C. fagisuga crawlers are transported by animals – including humans (11). First insights into Beech Bark Disease spread was the transport of infested logs or firewood by humans. (11, 13, 22) The enormous number of people visiting Mont Saint-Hilaire on a daily basis may serve as vectors transmitting scale larvae and fungal spores around the mountain.

Beyond accelerating the rate of disease transmission, human activity may also increase the severity of the disease. The fungus infects the American beech individuals by penetrating into the compromised cells via the cracks in the bark. (11) Therefore, it is possible that disturbances by human activities lead to more injuries on the American beech bark, enabling Nectria to penetrate the bark tissue and causing more severe Beech Bark Disease.

In further research, it would be important to consider the idea that disturbance and beech density might not be independent factors. It could be possible that density of American beech could increase as a result of disturbance, given its capability to form clonal thickets under stress. (1) Assuming that each susceptible American beech tree has an identical possibility of the scale insect introduction, this result suggests that beech trees within areas containing more disturbances are more severely affected by Beech Bark Disease than those in areas with less human activity. Scale feeding wounds are not a necessary precursor of infection, and the pathogen can even penetrate healthy, previously unwounded tissues, though to a limited extent. (37) Further research should be carried out and take the infection rank of Nectria colonies into the consideration. No matter the mechanism, it is clear that disturbance and human interaction with the habitat is related to the propagation of Beech Bark Disease through Mont Saint-Hilaire's forest and has most likely also played a role in its spread throughout North America.

Anthropogenic changes to habitat affecting American beech populations are not limited to direct changes to the physical environment. Climate change due to ever-increasing human consumption of fossil fuel and carbon dioxide emissions and other greenhouse gases will certainly have an impact on the range of both the beech and its parasitic detractors. The successful survival of the beech scale, and thus the disease, from one year to the next is heavily determined by environmental factors. (13) If the environment were to become more hospitable to the insect, it is probable that the disease's range would subsequently expand. (20) Heavy rains that wash larval insects to the ground and cold temperatures inhibit the severity and spread of the disease. (13) During the colder months, as the beech scale overwinters, temperatures of -34°C or lower cause reductions of scale populations found in the following growing seasons. (13, 17) Strong warming has been observed in southern Quebec since 1950; continual warming and mild winters could have disastrous consequences in terms of both disease spread and severity due failed dieback and higher recruitment rates. (20, 38) This pattern has been observed in other bark pests, such as the mountain pine beetle of British Columbia. (39) Though the scale is limited in its spread northward by range of the American Beech itself, incidents of colonization will likely be more persistent and successful as daily low temperatures increase.

Conclusion

It is important to continue to study the stage of Beech Bark Disease in Mont St-Hilaire, as this research provides powerful insights that could be extrapolated to a larger scale to understand the function of forest communities related to the spread of other diseases, as well as other environment-altering forces. Changes in forest composition and diversity may well play a role in Beech Bark Disease's spread and severity in North America. However, these are but mechanisms of an overlying, human-driven issue. Limited, short-term solutions such as pesticide application are unlikely to provide respite from the advancing front that is Beech Bark Disease. As we advance to the future, human activity will dictate the spread of Beech Bark Disease through North America in the same way human activity initially introduced it to the continent. Unfortunately, the solution will prove to be far more complex than the problem's initial nautical delivery.
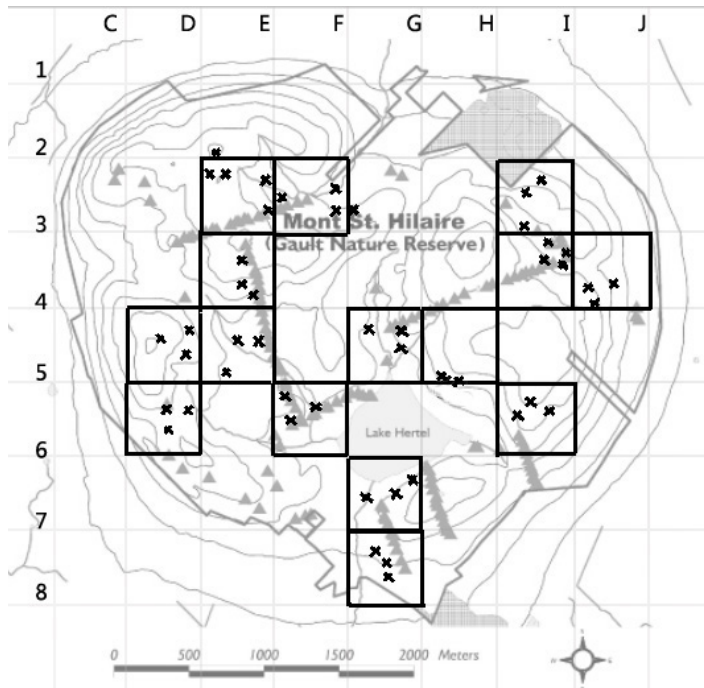
Figure 1. Map of Mont Saint–Hilaire. Sample sites are represented by darkened squares and approximate quadrat locations are represented by 'x's. Figure modified from Arii et al. (2005).
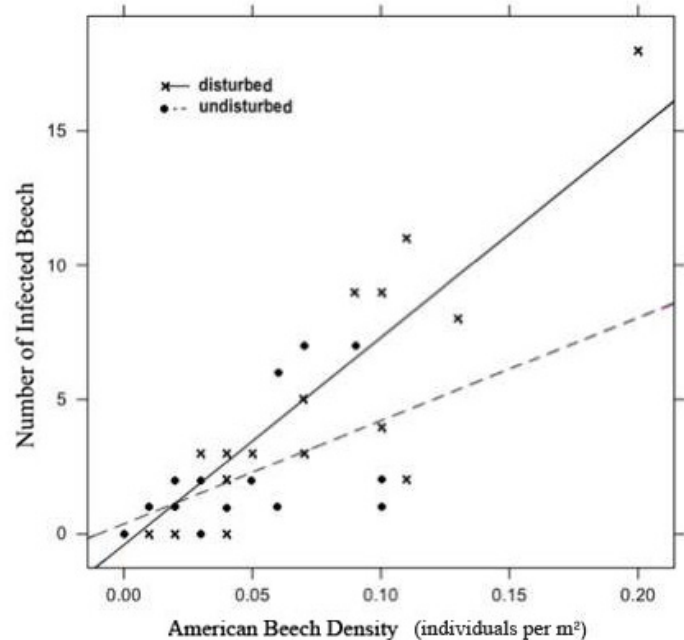

Figure 3. Figure shows the interaction between the number of infected individuals by BBD in disturbed and undisturbed areas with respect to the number of F.grandifolia. In disturbed areas, R2 = 0.7824, and in undisturbed areas, R2 = 0.3158.
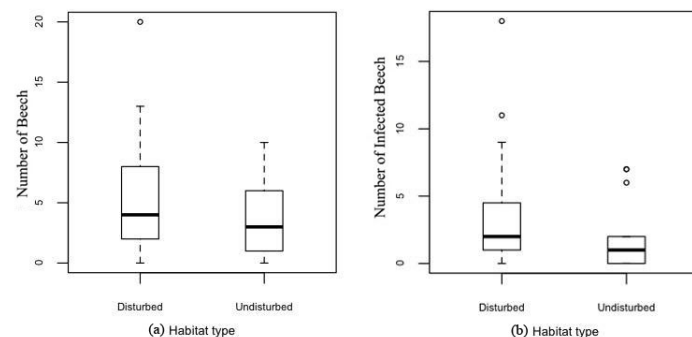

Figure 2. Figure shows the results of T–test performed on the correlation of disturbed and undisturbed habitats on (a) number of American beech; (b) number of infected American beech.

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