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FRAGMENTATION INHIBITS PATHOGEN CONTROL OF OUTBREAK INSECT

Lymantria dispar (GYPSY MOTH)

by

Jessica Romero

A Thesis Submitted in Partial Fulfillment

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ABSTRACT

Fragmentation inhibits pathogen control of outbreak insect *Lymantria dispar*

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Lymantria dispar (Gypsy moths) are an invasive species in North America that devastate forests by causing mass defoliation. While *L. dispar* populations persist each year in an expanding range, defoliation events are most extreme during outbreak years. Two non-native pathogens are known to help control *L. dispar* populations in North America: the fungus *Entomophaga maimaiga*, and virus *Lymantria dispar* nucleopolyhedrovirus (*LdNPV*). Both pathogens and their host *L. dispar* are found in the heavily fragmented forests of eastern Connecticut, where this study was conducted. Because forest fragments of different sizes vary in microclimate and other attributes, control of *L. dispar* by these pathogens may also vary. For instance, as a fungus, *Entomophaga* may be more likely to spread in larger forest fragments that have higher moisture and vegetation density than smaller fragments. *LdNPV* spreads at a higher rate with increased population density, but the relationship between *L. dispar* population density and forest fragment size is not documented. I reared a sample of fifteen individuals of *L. dispar* from each of thirty-two forest fragments and found that mortality from both *Entomophaga* and *LdNPV* is higher in large forest fragments than small fragments ($X^2 = 12.64$, $df = 1$, $p < 0.0004$). This suggests that forest conditions that vary with fragment size may influence pathogen spread and inhibit control of *L. dispar* by these pathogens.

KEYWORDS: Invasive species, fragmentation, *Lymantria dispar*, gypsy moth

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CHAPTER ONE

History

Overview of invasive *Lymantria dispar* and their impact in North America

Lymantria dispar (Gypsy moth) is an invasive species and devastating forest pest in North America (USFS 2003). Native to Eurasia, *L. dispar* is a generalist herbivore with a broad and continuously expanding geographic range in North America. These generalist folivores overwinter as egg masses, spend most of their lives as caterpillars in spring, and reproduce once as non-feeding adults that live up to two weeks (Figure 1, Figure 2). Over 300 species of deciduous and coniferous host trees are exploited by these caterpillars across all instars (Liebhold et al. 1995). Since this species does not eat as adults, the period of forest devastation occurs during the larval stage. Adult females are unable to fly, but early instars may travel several kilometers by larval ballooning in short trips, which involves drifting through wind using silk as parachutes and bungee cords. Often, humans aid in the movement of this species by moving boats, trucks, and lumber with hidden egg masses (Hajek and Tobin 2009). The land area infested with *Lymantria dispar* in 2005 was around 25% of the area in North America that is considered to be susceptible to further invasion, and the species is likely to continue expanding to these habitats (Morin et al. 2005).



Figure 1: An example of a *Lymantria dispar* caterpillar. Credit: E. Bradford Walker, Vermont Department of Forests, Parks and Recreation, Bugwood.org



Figure 2: A mating pair of adult *Lymantria dispar*. The white female has wings, but is unable to fly.

In 1868, *Lymantria dispar* was brought to Boston, Massachusetts on a ship from France by Étienne Léopold Trouvelot with the hope of producing silk in the United States. Egg masses were stowed on the ship and further cultivated in the backyard of Trouvelot's new home. Once the species spread to surrounding forest, he informed the government about the impending invasion (USFS 2003). A decade after the initial introduction of *Lymantria dispar*, the first outbreaks began. Although this species causes forest damage each year, only some

years are considered outbreak years. In 1890, the Massachusetts state government and the United States federal government began attempting to stop these outbreaks and locally eradicate the species. These attempts included strategies like trapping devices with live females as bait, semi-controlled burning of forests to harm particular life stages and microhabitats, and insecticides that were often arsenic based (Forbush and Fernald 1896 cited in Tobin et al. 2012). In total, these initial efforts cost \$1.2 million, which is equivalent to \$28 million in 2010 United States dollars (Tobin et al. 2012). In 1906, the United States federal government tried a new strategy. Natural parasitoids of *Lymantria dispar*, largely consisting of several species from the family of true flies Tachinidae, were successfully imported and released in outbreak regions (Gould et al. 1990; Erb et al. 2001). Many of these parasites still act to control *L. dispar*, but some have also been found to harm some native Lepidopterans (Gray et al. 2008; Boettner et al. 2000). The 1950s saw another wave of efforts to control outbreaks, including the establishment of barrier zones on the East coast, aerial applications of DDT, and eradication programs using a several of these techniques together (McManus 2007). All efforts ultimately failed to stop the spread of *Lymantria dispar*, and the species' range in North America has continued to expand. It appears inevitable that this range will continue to spread throughout North America (USFS 2003) (Figure 3).

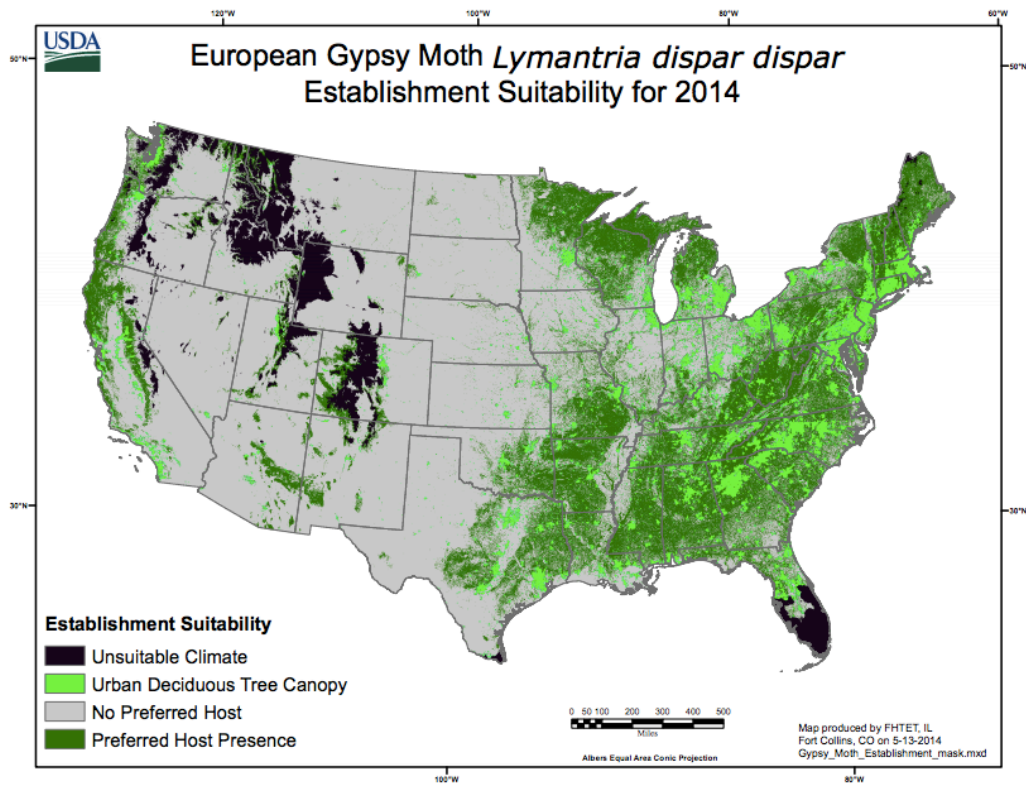


Figure 3: Map showing modeled suitable habitat for *Lymantria dispar* in the continental United States for 2014.

CHAPTER TWO

Introduction

Species interactions

As ranges expand largely as a result of anthropogenic factors, the consequences of *Lymantria dispar* spread are reaching farther than ever before. *Lymantria dispar* egg masses and larvae travel with trucks and cars across wide landscapes, escaping biocontrols and founding new populations. During outbreak years, this species is capable of defoliating large expanses of forest, which damages trees and shrubs and alters forest microclimates. Additionally, extreme defoliation removes food and shelter resources for a multitude of other species in forest communities.

The effects of the *Lymantria dispar* invasion are complex, far-reaching, and include novel interspecific interactions - including those with co-occurring invasive insects and plants, which are common in forest fragments and on edges (McEwan et al. 2008). Presence of *Lymantria dispar* may also influence patterns of bird migration and habitat shifts. Native cuckoo (*Coccyzus erythrophthalmus* and *Coccyzus americanus*) abundances have been found to be significantly above average during *L. dispar* outbreaks because of high food availability, while cuckoo abundance is average or below during subsequent years (Barber et al. 2008). This abnormal pattern of food availability causes cuckoos to alter typical migratory paths. Shifting the annual distribution of birds may also affect the native trophic system (Barber et al. 2008).

Red oaks (*Quercus rubra*), which are native to the same region in North America as the current *L. dispar* distribution, are affected by both *L. dispar* and *Phytophthora plurivora*, a fungus responsible for global declines and cascading ecological effects

(Milanović et al. 2015). Given the choice, *L. dispar* larvae are four times more likely to consume the leaves of *Phytophthora* infected red oak trees than the leaves of uninfected trees, likely as a result of an irregular increase in soluble protein and water content in infected leaves (Milanović et al. 2015). Since the fungus infected leaves are more likely to be predated on by *L. dispar*, this interaction may generate a positive feedback loop for oak decline (Milanović et al. 2015).

Lethal pathogens for *Lymantria dispar*

Species interactions include those between pathogens and hosts. Two major introduced pathogens are severely impacting *Lymantria dispar* populations in North America. The two lethal pathogens include the fungus *Entomophaga maimaiga* (hereafter *Entomophaga*) and virus *Lymantria dispar* nucleopolyhedrovirus (hereafter *LdNPV*) (Hajek 2014). The fungus has been found to disproportionately affect gypsy moths, rather than other Lepidoptera, as a result of their unusual larval behavior. Late instars of *Lymantria dispar* move to the bottom of trees and dark areas during the day, where fungi thrive (Hajek 2001). This differs from most Lepidoptera, who rarely descend from canopies onto low trunks. For *LdNPV*, the density of *L. dispar* was found to have an inverse relationship with disease resistance to *LdNPV*, meaning disease prevalence is likely density-dependent (Reilly 2007).

Both *Entomophaga* and *LdNPV* are native pathogens of *Lymantria dispar* in Eurasia, and arrived to North America unexpectedly (Bauer 1999). *LdNPV* was first discovered in 1907, and *Entomophaga* was first found in Connecticut in 1989 when an outbreak of *L. dispar* dissipated unexpectedly (Bauer 1999; Hajek et al. 1995). Although it is unclear how *Entomophaga* was brought to North America, a likely hypothesis ties it

to the intentional introduction to New England from Japan in 1909, which was considered a failure. *Entomophaga* appears to have no effect on non-target Lepidoptera (USDA 2004). As of 1999, the potential for the fungus to become a type of commercialized pesticide has not been realized (Hajek 1999). However, *LdNPV* has been used to create a biological control agent called “Gypchek,” which is currently being used in small amounts to suppress outbreaks.

Infection from *LdNPV* occurs when foliage infected with viral occlusion bodies are consumed by *Lymantria dispar*. However, the most common way for dispersal of *LdNPV* is from the carcasses of dead *L. dispar* individuals. The virus invades through the gut wall and reproduces in internal tissue, quickly causing the disintegration of internal organs and, ultimately, the death of the host larva. When the host ruptures, viral occlusion bodies are spread to infect other individuals on a density-dependent basis. In small populations, *LdNPV* is still able to persist in soil (Liebhold 2003).

The introductions of these lethal pathogens have apparently changed the intensity of *Lymantria dispar* outbreaks. Although not all outbreak dynamics are explicitly understood, life history traits of host *Lymantria dispar* likely contribute to outbreak patterns (Páez et al. 2015). Understanding how these pathogens interact with habitat type, life history, and human-assisted transportation should all influence management strategies to control *L. dispar* outbreaks.

Forest fragmentation

Habitat fragmentation is the division of natural land that is characterized by both a decrease in total area and an increase in the amount of edges. As individual forest fragments become isolated, resident species often face changes to microclimate,

competition with non-native species, habitat loss, and barriers to movement that limit mating opportunities and exploitation of available habitat among separated fragments (Oxford Reference 2017). In many places, including Connecticut, these fragments are primarily separated by roads and agricultural land.

Unlike in many other species, *L. dispar* may benefit from forest fragmentation and increased forest edge habitat through an increased ability to locate mates. Specifically, *L. dispar* is better at successfully locating mates on forest edges, suggesting that forest fragmentation and increased edges may contribute to species proliferation (Thompson et al. 2016). There is a positive relationship between success of *Lymantria dispar* and forest fragments. Identifying a relationship between *Lymantria dispar* pathogen interactions and forest fragment size could be vital for understanding how forest fragmentation influences *L. dispar* survival, reproduction, and dispersal.

Hypotheses & purpose

In the summer of 2017, an outbreak of *Lymantria dispar* occurred in the Northeastern United States, including in several fragmented forests of eastern Connecticut. During this outbreak, many *Lymantria dispar* mortality due to exposure to *Entomophaga* and *LdNPV* was evident (Figure 4). I hypothesized that the relative mortality caused by these pathogens was likely tied to habitat fragment size, due to differences in *L. dispar* population



Figure 4: An example of a tree covered in individuals of *Lymantria dispar*.

density across fragments of varying sizes and with variable microclimatic climatic, including moisture, relative pathogen exposure, and vegetation composition.

The purpose of this study was to investigate whether forest fragmentation influences the ability of *Lymantria dispar* to avoid pathogen exposure and survive. Understanding the relationship between *L. dispar* survival and fragment size can inform conservation plans and forestry practices to limit the spread of this species. Potential physical factors that are related to forest fragment size like moisture, soil composition, or temperature may influence the *L. dispar* survival. Clarifying the relationship between physical and biotic factors better also informs conservation of native species that are impacted by or are competing with *L. dispar* larvae. Creating a management strategy for such a challenging and devastating invasive species requires management tactics beyond what has already been tried; therefore, understanding interactions of *L. dispar* with physical and biological agents is essential for improved and effective management.

CHAPTER THREE

Methods

Collection in the field

To collect *Lymantria dispar* individuals for lab rearing, I used three points oriented in the shape of an equilateral triangle placed within each fragment using GPS technology (Figure 5). Within each fragment, I collected a total of 15 *L. dispar* caterpillars at intervals of approximately ten meters along two randomly selected 200 meter transects out of a possible three running between these three points. I collected individuals into vials capped and labeled with the fragment and transect in which they were collected, and an individual identification number (1-15), without allowing contact with skin or clothes. I kept vials in a cooler until brought to the lab, and within a period of 10 days after pathogen outbreak was evident by observation of extreme defoliation and tree trunks coated in *L. dispar* larvae. In total, I collected 480 *L. dispar* individuals from each of 32 forest fragments of different sizes (calculated using GIS) in eastern Connecticut.

Lab rearing

As samples of *Lymantria dispar* were brought into the lab, I immediately placed them in isolated cups under a fume hood. These cups contained premade food



Figure 6: Trays filled with cups containing individuals of *Lymantria dispar* from 32 forest fragments.

supplied by the University of Massachusetts with (Figure 6). I labeled cups with fragment, individual number, and date of collection. After the individuals were sealed inside, the lids to these cups remained closed until after individual death. I placed cups in trays labeled by fragment, totaling 32 trays, and monitored cups each day for mortality.

Death determination

I determined cause of death by symptoms exhibited by each sampled individual. These outcomes were typically determined within seven days. Possible outcomes included death by *Entomophaga* (fungal pathogen), *LdNPV* (virus), or parasitoids, and pupation. DeI determined death by parasitoid through observing parasitoid emergence. If an individual made it to pupation, they were considered to have survived into the larval phase when they were vulnerable to pathogens and parasitoids.

I distinguished between death by *LdNPV* and *Entomophaga* by observing symptoms. Death by *LdNPV* was characterized by dead individuals typically hanging from the lid of the cup by their middle prolegs (Figure 7, left) (Reardon and Hajek 1998). Individuals that were infected with *Entomophaga* tend to hang from the sides of the cup head down by their back prolegs. Body fluids were pooled in the head region, and approximately a day after death, spores were present on the setae, or hair-like projects on the body (Figure 7, right) (USDA 1993).



Figure 7: Body configuration on deceased individual of *Lymantria dispar* in death by *LdNPV* (left) and death by *Entomophaga* (right).

Statistical analysis

I conducted an analysis to compare survivability among fragment size. I classified the data as binomial because individuals either died by an introduced pathogen (either *Entomophaga* or *LdNPV*) or survived (pupation or different cause of death, e.g., parasitic infection). Fragment size was categorized into small (< 100 ha), medium (100-200 ha), and large (> 200 ha). I used R to run a binomial generalized linear model to determine if fragment size (as a continuous variable) affected on survival of collected larvae. Another chi-square was run to determine if fragment size (as a categorical variable) had an effect on cause of death between *Entomophaga* and *LdNPV*.

CHAPTER FOUR

Results

In the binomial generalized linear model comparing the survival of *Lymantria dispar* from either pathogen (*LdNPV* or *Entomophaga*) in relation to forest fragment size, there was a negative relationship between forest fragment size and *L. dispar* survivability from either pathogen ($X^2 = 12.635$, $df = 1$, $p = 0.0004$). As forest fragment size increases, mortality due to the combined effects of the two pathogens (*LdNPV* or *Entomophaga*) increased (Figure 8).

No effect of fragment size on whether death occurred by *LdNPV* or by *Entomophaga* was found ($X^2 = 0.3075$, $df = 1$, $p = 0.5792$). The proportion of collected *Lymantria dispar* that died of *LdNPV* and *Entomophaga* at each fragment was 12.23% and 53.81% for small (< 100 ha) fragments, 11.88% and 80.20% for medium (100-200 ha) fragments, and 25.87% and 69.23% for large (> 200 ha) fragments, respectively (Table 1). Although these ratios were not significantly related to forest fragment size, *Entomophaga* was found to be responsible for a higher proportion of deaths than *LdNPV* at every forest fragment size. Of all death outcomes, 76.98% were caused by *Entomophaga*.

Forest fragment size	Dead by <i>LdNPV</i>	Dead by <i>Entomophaga</i>	Dead by parasite	Survived to pupation
Small (< 100 ha)	21.23%	53.81%	8.62%	16.24%
Medium (100-200 ha)	11.88%	80.20%	2.97%	5.00%
Large (> 200 ha)	25.87%	69.23%	2.10%	2.80%

Table 1: The proportions of mortality the outcomes per forest fragment size class for sampled *Lymantria dispar*. Outcomes included death from infection of pathogens *LdNPV* or *Entomophaga*, parasitic infection, and survival to pupation.

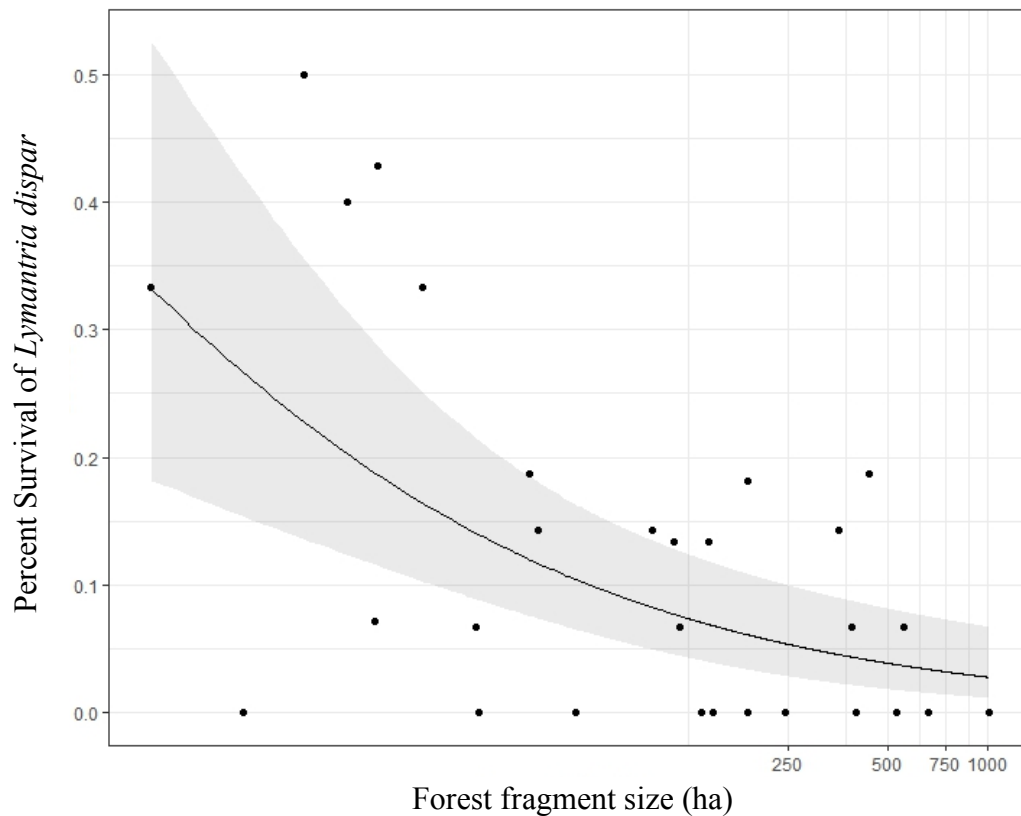


Figure 8: *Lymantria dispar* had lower survival in large than small forest fragments. An effect of fragment size on survival of collected larvae was found ($X^2 = 10.146$, $df = 1$, $p = 0.001446$).

CHAPTER FIVE

Discussion

In this study, it was found that forest fragment size is tied to the proportions of death from pathogens *Entomophaga* and *LdNPV* in *Lymantria dispar*. Survival of *L. dispar* was negatively related to fragment size, indicating that forest fragmentation in the region of eastern Connecticut may inhibit pathogen control of this species. This relationship is possibly caused by altered microhabitat conditions in forest fragments, including reduced moisture, increased wind exposure, and altered vegetation structure in smaller fragments. In these ways and others, fragmentation may have facilitated historical spread of *L. dispar*.

The ratios of these two pathogens were not significantly different between fragment size classes. This unexpected result indicates that there is likely not a single physical or biological factor associated with large fragments that would promote the spread of a fungal pathogen or a viral pathogen at differentiated levels. Rather, a more complex system is at play. In the sampled forest fragments, size on its own does not appear to be an indicator of which pathogen is more deadly to host *L. dispar*. Since mortality due to both of these pathogens were increased in larger fragments, my results indicate that larger forests may be important for restricting the spread of *L. dispar*.

Together, these results are indicative of an intricate and interconnected system between the pathogens, host, biological community, and physical environment. In the context of conservation, unfragmented forests are favorable for maintaining biodiversity and forest health. It appears that larger forests may assist in limiting the spread of

Lymantria dispar. These results should be used to inform management plans to control outbreak and spread of invasive species in the future.

Management planning

A general trend of invasive species is that the effects on ecosystems often change over time. These changes often start with an acute phase immediately after a new species arrives, which is followed by a chronic phase that begins after the species is more established. This establishing typically includes various ecological and evolutionary processes coming into play (Strayer et al. 2006). Nearly 150 years and generations after *Lymantria dispar* was introduced to North America, its effects are still devastating, but are constantly changing with the introduction of pathogens and other interspecies interactions. For this reason, it is increasingly important that effective management is implemented for *Lymantria dispar*.

Species eradication is most often the favored strategy for managing invasives (Zavaleta et al. 2001), and has long been a management goal for *Lymantria dispar*. Strategies implemented for eradication, like poisons and trapping, will often have consequences for entire ecosystems that are unexpected or are undesirable. These consequences may not be apparent until long after the control efforts have started. Refined and integrated approaches to invasive removal that account for ecological context may improve recovery results (Zavaleta et al. 2001). For forest-defoliating species, like *Lymantria dispar*, this is particularly true, as their impact to local ecosystem health varies widely from year to year. Poorly planned biocontrol application can result in increased densities over time (Reilly et al. 2013). A successful management strategy

should follow population responses to control efforts in both short and long term monitoring.

As human society becomes more globally connected, non-native species are introduced at an increasing rate. In making management plans for harmful invasive species, biological, ecological, and economic information is often lacking. As a crisis discipline, conservationists must frequently make rapid decisions based on general principles, rather than concrete specifics of the non-native species (Primack 2014). A current general ecological principle assumes that most non-native species do not successfully establish in new habitats, and only 2.5 of these species establish in the United States each year (Aukema et al. 2010). Further, invasive species that pose high risk to ecosystem structure and function only occurs once every two years. Using data and literature from established and well-researched species, like *Lymantria dispar*, is a helpful strategy for creating management plans for non-native species that are new or not well represented in the literature (Tobin et al. 2011).

Limitations

A few limitations were experienced in conducting this research. This study did not calculate the density of *Lymantria dispar* in each forest fragment. Therefore, the density-dependent spread of *LdNVP* is not documented, and cannot account for the difference between prevalence of virus or fungus in each fragment. We do not know why fragment size does not appear to influence whether virus or fungus was more prevalent or effective at killing *Lymantria dispar*, although it is likely a consequence of population densities and microhabitat factors. Additionally, identifying cause of death between pathogen types was qualitative and symptomatic. While this strategy was sufficient, a

more reliable swabbing technique may have been more precise. Lastly, a larger sample size from a smaller collection time period would have lended to data reliability, but was not feasible, as collection was strenuous and time-intensive, and there was limited available lab space.

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