

Disentangling the impacts of exotic plants and habitat disturbance on native plant richness and abundance.

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Abstract:

Invasive plants are widely cited as a major threat to native plant communities, and the correlation between plant invasions and a subsequent decline in native species is well documented at some scales. However, one outstanding question is the degree to which invasive species are a driver of native plant declines versus a correlate of other drivers, such as habitat disturbance. These two hypotheses to explain the dominance of invasive species in communities have been termed the ‘driver’ and ‘passenger’ models, respectively. In order to understand the impacts of plant invasion on native plants we need more studies that consider the role of correlated environmental predictors, which may play unseen roles in the response and recovery of native plant communities frequently attributed to invasion alone. Using a large database of plant community and environmental data from sites across Southern Ontario, I used path analyses to examine the direct and indirect relationships between disturbance, exotic and native plant richness, and relative abundance. Counter to my initial predictions, I found support for both the *partial passenger* and *partial driver* models of invasive dominance, while *full passenger* models were outright rejected. The causal hypotheses consistent with the data indicated significant relationships between native and exotic species richness and native and exotic relative abundance across models. An exploratory analysis, which examined species-specific models, found that the data was consistent with seven out of twelve causal hypotheses. Models that could not be rejected were split almost evenly across *full passenger*, *partial passenger*, and *partial driver* models. Model support varied according to the species included in the dataset suggesting that the best fit underlying model of invasive dominance likely varies by species. While the *partial passenger* and *partial driver* models were recurrently consistent with the data, no single model described the underlying patterns of invasive dominance across all systems.

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List of Abbreviations:

AIC:..... Akaike Information Criterion
AICc:Adjusted Akaike Information Criterion
APA: Abundance of *Alliaria petiolata*
ATA: Abundance of *Arisaema triphyllum*
CCA: Abundance of *Circaea canadensis*
d - sep: Directed Separation
D:..... Habitat Disturbance
DAG: Directed Acyclic Graph
EA: Exotic Relative Abundance
ESR: Exotic Species Richness
NA: Native Relative Abundance
NSR: Native Species Richness
p: *p* - Value
PA: Path Analysis
PC:..... Path Coefficient
SE: Standard Error
SEM: Structural Equation Modeling

Chapter 1

1.1 General Introduction and Literature review:

Anthropogenic activity is rapidly degrading the natural environment. Along with climate change, pollution, agrochemicals, and habitat loss, the proliferation of invasive species is a prominent ecological problem (Wilcove et al., 1998; Gurevitch and Padilla, 2004; The Millennium Ecosystem Assessment Panel, 2005). Human activities like agriculture, transportation, and urbanization cause global movements of species that invade ecological communities, often with unforeseen consequences (Tilman and Lehman, 2001). More than 13,000 introduced plant species currently persist outside of their native range, many of which have the potential to become invasive (van Kleunen et al., 2015; Dawson and Schrama, 2016). Invaders can have both direct and indirect impacts on native species and ecosystem processes. For example, the invasive vine *Pueraria montana* (common name: Kudzu vine) was introduced to the Southern United States from Japan by farmers following its promotion as a preventative solution to soil erosion, but it eventually became a ruthless invader (Stewart, 1997). Kudzu vine directly affects nearby trees and shrubs as a structural parasite by growing on neighboring plants to reach light (Forseth and Innis, 2004), killing native plants and homogenizing biotic communities (Virginia Department of Conservation and Recreation, 2001; Forseth and Innis, 2004). It can also indirectly impact the community as a nitrogen fixer by increasing the available nitrogen in the soil, thereby excluding plants adapted to low nitrogen conditions (Forseth and Innis, 2004).

A large body of research has been dedicated to understanding the interactions between invasive plants and their new communities, the resulting effects on native plant community structure and functional diversity, and the mechanisms that underlie these effects (Mack and D'antonio, 1998; Levine et al., 2003; Gurevitch and Padilla, 2004; MacDougall and Turkington, 2005; Stinson et al.,

2006; van Kleunen et al., 2015; Dawson and Schrama, 2016). A fundamental goal of invasion biology has been to improve our ability to determine which species will eventually become invasive and in which ecosystems.

1.2 Exotic/Invasive Species and Their Impacts on Natives:

A common problem among studies of non-native species is the lack of consensus on the definitions of a variety of related terminology (Mack et al., 2000; Colautti and MacIsaac, 2004; Ricciardi, 2012). For instance, ‘alien’, ‘exotic’, and ‘introduced’ may be used interchangeably with ‘invasive’ in one study but may each have very distinct interpretations in others (Colautti and MacIsaac, 2004). Therefore, for the purpose of this thesis, I refer to ‘invasives’ as dominant or widespread non-native plants that have adverse effects on the invaded habitat (Mack et al., 2000). I hereafter refer to ‘exotics’ as any non-native plant, that is neither dominant nor considered harmful to their introduced habitat. When referring to specific studies I use the same terminology as the author.

Plant invasions can impact the community structure and ecosystem functioning of existing plant communities, in some cases leading to a reduction in native plant abundance and diversity (Mack et al., 2000; Levine et al., 2003). Some native plant populations are especially vulnerable due to pre-existing factors such as poor competitive nature, limited geographical ranges, fragmented habitat, or habitat disturbance (Welk et al., 2002; Yelenik et al., 2004).

Invasive species are frequently cited as a leading cause of extinction of natives (Wilcove et al., 1998; Mack et al., 2000; Didham et al., 2005; Stinson et al., 2006); however, little evidence exists to support the hypothesis that the presence of invasives alone is a threat to native plants (Levine et al., 2003; Gurevitch and Padilla, 2004).

The correlation between plant invasions and subsequent declines in native growth and richness is well documented at some scales (Vitousek and Walker, 1989; Stinson et al., 2006; Hejda et al., 2009). A study by Stinson et al. (2006) tested the impacts of the invasive plant *Alliaria petiolata*, and its trait allelopathy, defined as the production of toxic secondary compounds that can harm the surrounding biota (Oliver et al., 1999), on the growth of four native tree seedlings (*Acer rubrum* L., *A. saccharum* Marsh., *Fraxinus americana* L., and *Fagus grandifolia* Ehrh.) in forested plots near Waterloo, Ontario. Their results showed that *A. petiolata* significantly reduced native seedling growth by disrupting belowground mutualisms with arbuscular mycorrhizal fungi (Stinson et al., 2006). In a related study exploring the impacts of invasion on community structure and species composition, Hejda et al. (2009) compared species richness, evenness, and diversity between 260 invaded and non-invaded sites across various regions of the Czech Republic, ranging from lowland meadows to sub-alpine meadows. They found that invaded plots had lower species richness, evenness, and diversity than non-invaded plots (Hejda et al., 2009). While these studies describe patterns consistent with a mechanism of invasive dominance and native suppression that is common among invaded communities, few studies have thoroughly examined the mechanisms by which invasions could lead to native species decline.

Indeed, there is open discord as to whether invasives tend to be a driving source of native declines, or whether they are masking or profiting from the impacts of other environmental variables (Klironomos, 2002; Didham et al., 2005; MacDougall and Turkington 2005). Invasive and native plants may interact with each other and other environmental variables in multiple ways. There is a strong possibility that a third factor could drive both the invasion and the decline in natives, making it appear as if the two are directly related when they are actually independent.

One environmental factor that could be responsible for driving both the dominance of invasives and the suppression of natives is habitat disturbance.

1.3 Environmental Disturbance Impacts on Native and Invasive Plants:

In past reviews of the environmental factors correlated with invasions, disturbed habitats have been found to host large numbers of invasive species (Mack, 1986; Mooney et. al., 1986; Hobbs and Huenneke, 1992; Lozon and MacIsaac, 1997; Rejmanek, 1989). Multiple experimental studies have also found a strong negative correlation between disturbance and native species richness (Brown and Boutin, 2009; Driscoll, 2017). A study by Brown and Boutin (2009) examined how past and present land use and disturbance (selective cutting, vegetation clearing) impact species richness and composition of forested communities on old agricultural land. While recent disturbance had no apparent impacts on native richness, they found that historically, partially cleared sites (moderately disturbed) had the highest native species richness, while fully cleared sites (heavily disturbed) had the highest invasive richness (Brown and Boutin, 2009). In a similar study, Biswas and Mallik (2010) tested the effects of habitat disturbance (clear-cut-caused windthrow and ground exposure) on plant richness and functional diversity for riparian and upland forested communities in northwestern Ontario. They found that in both riparian and upland sites species richness was significantly lower in areas of high, compared to moderate, disturbance intensity (Biswas and Mallik, 2010). The results of both studies suggest that while low to moderate disturbance may be beneficial to some species of native plants, high disturbance levels generally have a negative impact on native species richness, and can favour invasion (Brown and Boutin, 2009; Biswas and Mallik, 2010).

In addition to its role in native species decline, disturbance has also been shown to promote the establishment and range expansion of invasive species (D'Antonio, 1993; Rodgers and Parker,

2003; MacDougall and Turkington, 2005). Environmental disturbances may drive invasions by altering nutrient availability, by suppressing natural pathogens and herbivores, or by removing native species that may be superior competitors than exotics (Hobbs, 1989; Rejmanek, 1989; D'Antonio, 1993). In a field experiment conducted on four of the Georgia Sea Islands in the United States, Rodgers and Parker (2003) tested the impacts of human disturbance on the distribution of the invasive plants in exposed dune and inland forest habitats. Across four study islands, in both habitat types, they found an average invasive species cover of approximately 18% in severely disturbed sites, compared to 1% cover in less disturbed locations, suggesting that human disturbance significantly increased the overall cover of invasives on the islands (Rodgers and Parker, 2003). In another study, Lembrechts et al. (2016) examined how elevational ranges of native and exotic species differ between disturbed (roadsides) and undisturbed plots. They found that the elevational ranges of exotic species were on average broader in disturbed (roadsides) compared to undisturbed areas, demonstrating how environmental disturbances may promote invader range expansions (Lembrechts et al., 2016). In another experiment, D'Antonio (1993) examined three processes (soil disturbance, herbivory, and competitor identity) hypothesized to impact the invasion of different coastal plant communities in California (coastal scrub, grassland, and backdune) by the exotic plant *Carpobrotus edulis* L. (Bolus) (Aizoaceae). Results showed that site soil disturbance (soil turnover) at grassland sites promoted seedling emergence of *C. edulis* and indicated that soil disturbance was required for the establishment of the invasive species at these sites, while soil disturbance at coastal scrub or backdune sites did not support the establishment of *C. edulis* (D'Antonio, 1993). While it is evident that disturbance plays a role in the establishment and expansion of exotics in newly invaded systems (Mack, 1986; Mooney et al., 1986; Rejmanek, 1989; Hobbs and Huenneke, 1992; Lozon and MacIsaac, 1997; D'Antonio,

1993; Rodgers and Parker, 2003; Lembrechts et al., 2016), the precise effects of disturbance on native and invasives and their interaction are still relatively unstudied (Hobbs, 1989; D'Antonio, 1993).

Environmental disturbance seems to play a complex role in the web of interactions between native and exotic plant communities. While some natives may tolerate, or even thrive under low or moderate levels of disturbance (Brown and Boutin, 2009; Biswas and Mallik, 2010), higher levels may encourage the establishment and spread of invasives (Rodgers and Parker, 2003; Lembrechts et al., 2016) and reinforce patterns of invasive dominance and native decline within certain plant communities (Brown and Boutin, 2009; Biswas and Mallik, 2010).

1.4 Driver and Passenger Models:

Despite a myriad of studies that have looked at how invasive plants impact native plant growth, reproduction, abundance, and distribution, many questions remain about the mechanisms underlying these interactions (Roberts and Anderson, 2001; Levine et al., 2003; Gurevitch and Padilla, 2004; Stinson et al., 2006; Goodell and Parker, 2017). Two main models have been described to explain the major routes by which the dominance of invasive plants might correlate with the decline of local native plants: the 'driver' and 'passenger' models (MacDougall and Turkington, 2005). The driver model describes a scenario where an invasive species becomes dominant through its superior competitive ability, in turn reducing native species abundance and richness (MacDougall and Turkington, 2005; Fourie, 2008). The passenger model, on the other hand, describes a scenario where invasive dominance is reached due to the suppression of natives via other environmental factors or processes, such as habitat disturbance, or spillback from pathogen accumulation (Colautti et al., 2004; Mangla and Callaway, 2007; Flory and Clay,

2013), by which invasives are relatively unaffected or even promoted (Seabloom et al., 2003; MacDougall and Turkington, 2005). A key prediction of the driver model is that the experimental removal of dominant exotic species should result in the eventual return of native vegetation (Didham et al., 2005; MacDougall and Turkington, 2005). Conversely, the passenger model predicts that the reduction or removal of invasive species will have little or no influence on overall native abundance and richness, as direct interactions between native and invasives are weak or non-existent in this model (Didham et al., 2005; MacDougall and Turkington, 2005). As predicted by both models, native plants are suppressed in part due to invasives' greater ability to access the limiting resources within that system, either due to direct competitive ability or other indirect environmental stressors (e.g., dispersal barriers) that are more limiting to non-dominant natives than dominant invasives. It is difficult in any given system to determine whether, and how, natives are impacted via direct (driver), indirect (passenger), or some variant of both mechanisms of invasive dominance (Didham et al., 2005; MacDougall and Turkington, 2005).

Over the last decade, many field studies have reported evidence appearing to support either the passenger or driver models (Seabloom et al., 2003; Didham et al., 2005; MacDougall and Turkington, 2005). A highly-cited, multi-year field study by MacDougall and Turkington (2005) tested the impacts of biomass reduction treatments (mowing and weeding) of two invasive grasses, *Poa pratensis* (L.) and *Dactylis glomerata* (L.) on the relative abundance and species richness of native plants in meadows of the Cowichan Garry Oak reserve in southwestern British Columbia, Canada. They found that competition with invasive grasses was not the main factor limiting native species recruitment and recovery, and that this major prediction of the driver model was not supported by their study (MacDougall and Turkington, 2005). Instead, many natives were recruitment limited, or limited by other ecological factors such as fire suppression.

The authors interpreted their result as support for the passenger model, concluding that species assemblages in their study were structured by a complex web of interacting factors that included competition as well as disturbance (MacDougall and Turkington, 2005). There is additional support for the passenger model from other field studies. For example, in a seed addition experiment, Seabloom et al. (2003) compared the ability of exotic annual grasses to exploit disturbances (i.e., gopher digging and grassland burns) and compete for resources (using nitrogen additions), to the ability of five native perennial grasses, and determined how this affected their relative dominance. Their results suggest that recruitment limitations in native perennials, rather than competitive exclusion, better explained invasive dominance in their study system (Seabloom et al., 2003).

While the aforementioned studies offer support for the passenger model, others have supported the driver model (Vitousek et al., 1987, Vitousek and Walker, 1989; Fourie, 2008; Morris et al., 2008). The driver model implicitly assumes strong biotic interactions between invasive and native species, such that invasive dominance is a direct consequence of competitive exclusion (Didham et al., 2005; MacDougall and Turkington, 2005). Species that act primarily as drivers of native declines are generally considered to introduce new traits or processes to the invaded habitat (Vitousek et al., 1987; Chapin et al., 1995, 1996). For example, a study that explored the consequences of plant invasion on the native plant community at Hawaii Volcanos National Park found that the ability of the invasive *Myrica faya* (Aiton.) to support nitrogen fixing bacteria led to an increase in the overall bio-availability of nitrogen in the invaded areas, positively impacting both the invasive and the native plant community (Vitousek and Walker, 1989). One prediction of the driver model is that the removal of dominant exotic species will eventually result in the return of native flora (Didham et al., 2005). A study by Fourie (2008)

demonstrated support for this prediction, finding that removal of the dominant invasive tree *Acacia longifolia* in native fynbos communities, which possesses the novel ability to fix nitrogen in its invaded range, resulted in rapid native species recovery.

Based on this conflicting evidence, it seems that there is still much work to do to determine the mechanisms by which invasive species influence native plant communities, and the role of third factors in this relationship. Moreover, exploring the role of disturbance and other ecosystem properties in interactions between native and exotic flora is critical to the development of effective invasive management strategies and native recovery.

1.5 Invasive Management Practices:

The conflicting evidence for and against the driver and passenger models of invasive dominance are problematic for the development of recovery plans and the implementation of strategic invasive management practices (Gurevitch and Padilla, 2004; Didham et al., 2005; Rand et al., 2015). Without data-supported conclusions on the mechanisms that underlie how invasive species impact native plant ecosystems, it is difficult to develop appropriate invasive plant control methods (Didham et al., 2005; Rand et al., 2015). If the management of invasives within a system is structured around the assumption that the invasives are driving native decline when in actuality they are only passengers, investment in invasive removal may not result in measurable changes in native cover (Didham et al., 2005; MacDougall and Turkington, 2005). This is particularly concerning when considering the extensive resources invested in invasive management globally. For instance, a 2019 report from the Canadian Invasive Species Centre states that Ontario municipalities and conservation authorities spend approximately \$50.8 million annually on the management of invasive species (Vyn and ISC, 2019). How do we disentangle

the impacts of invasives from the other site-specific factors that could be driving native plant decline?

1.6 Structural Equation Modeling and Path Analysis:

For many invaded ecosystems, controlled field experiments are not feasible. Where controlled experiments are difficult to perform, researchers must utilize other tools to study their systems. One such tool is Structural Equation Modeling (SEM). SEM is a statistical modeling technique used to analyze systems often involving multiple causality, but where standardised field or lab experiments are not practical (Shipley, 2000a). An attractive feature of SEM is that it enables researchers to model complex relationships among many variables, where any variable may be both a causal variable (parent or causal ancestor) and a dependent variable (descendant), also referred to as a ‘mediators’ of the causal effect (Shipley, 2000a; Hertzog, 2018). Other benefits of SEM are that it allows for the comparison of direct, indirect, and total effects and the inclusion of unmeasured or unknown variables, known as latent variables (See Table 1.1; Shipley, 2000a). While controlled experiments are considered the gold standard for identifying causal relationships, the development of SEM has made it a reasonable alternative approach when experimentation is not possible.

Structural equation modelling (SEM) has evolved substantially since its invention by Sewall Wright in 1918, driven by the rise and intensification of computing power and complexity (Wright, 1921; Shipley, 2000a). While the use of SEM to explore complex relationships has been popular in the social sciences since the early 1980s (Bean, 1980; Tanaka, 1987), its use has only recently become more accepted and common place in the biological sciences, including ecology (Mitchell, 1992; Shipley, 2000a; Kharouba et al., 2015; Lefcheck, 2016).

Path analysis (PA) is a type of SEM that involves converting a hypothesized path model, known as a directed acyclic graph (DAG), into a set of linear equations that follow the hypothesized causal structure of the DAG (Table 1.1; Pearl, 1988; Gonzalez-Voyer and Hardenberg, 2013; Shipley, 2000a). From these sets of specified linear equations for each DAG, path coefficients can be estimated from the data (Pearl, 1988; Gonzalez-Voyer and Hardenberg, 2013; Shipley, 2000a). R software ('lavaan' Package (Rosseel et al., 2019); 'piecewiseSEM' package (Lefcheck et al., 2019); R, version 3.6.0 (R Core Development Team 2019)) can be used to derive the expected patterns of covariance among the variables in the causal model. In SEM, the model's free parameters are estimated using maximum likelihood methods, minimizing the difference in the observed and expected covariance matrices of the model and the actual data (Shipley 2000a; Gonzalez-Voyer and Hardenberg, 2013). In this way, SEM can deal with complex models, allowing for the inclusion of latent variables (See Table 1.1; Shipley 2000a). However, SEM does have some limitations in that it requires large sample sizes (i.e., at least 5x greater than the number of parameters to estimate; Bentler, 1995; Shipley, 2000a), the variable relationships must be linear, and data that are not multivariate normal are difficult to handle (Shipley, 2000a). Due to these drawbacks, Shipley (2000b) developed an alternative method of PA which he calls *d*-sep testing, based on a technique known as directed separation (*d*-separation; Table 1.1).

1.7 Confirmatory Path Analysis and the d - separation:

Confirmatory PA is a type of SEM based on the notion of directed separation (*d*-separation), initially described by Sewall Wright around 1920 (Table 1.1; Shipley, 2000a). While PA cannot deal with latent variables (See Table 1.1), it has other benefits (Shipley, 2000a, 2000b). Since PA is based on *d* - separation, it can be used for non-normally distributed data, non-linear variable relationships, and small sample sizes (Pearl, 1988; Shipley, 2000a).

Directed separation is an approach to PA developed by Judea Pearl and colleagues in 1988 (Pearl, 1988; Verma and Pearl, 1988). *D* - separation is a characteristic of sets of variables within a causal graph, indicating the independence between sets when one is conditioned upon (Pearl, 1988; Verma and Pearl, 1988; Shipley 2000a). Causal conditioning refers to the changing of state of a variable from 'on' to 'off' and vice versa, either blocking or allowing the causal influence of one set of variables on another (Table 1.1; Pearl 1988; Shipley, 2000a). So, if the variable B along the path $A \rightarrow B \rightarrow C$ is 'on' (based on arrow direction), then by conditioning on B, the indirect causal influence of A on C is blocked by changing the state of variable B to 'off'. In this way, the technique of *d* - separation can give us the required set of claims for any set of variables within a causal graph to be independent, when conditioned on by another set of variables (Pearl, 1988; Shipley, 2000a). This set of claims indicating the conditional independence of all variables within the causal graph is known as the basis set (Table 1.1; Pearl 1988; Shipley, 2000a). Each claim within a basis set can be tested using appropriate data-specific approaches (correlation tests, linear models, etc.) and the *p* - values combined to calculate Fisher's Critical Value (Fisher's *C*). Fisher's *C* statistic indicates whether a causal model is consistent with the data, allowing inconsistent DAGs to be rejected (Shipley, 2000a). The use of SEM and PA is one approach to establishing the drivers of native species decline in the absence of experiments.

1.8 Summary:

The spread of invasive species is a widely accepted ecological threat, often with unforeseen consequences (Wilcove et al., 1998; Gurevitch and Padilla, 2004; Stinson et al., 2006). Invaders can have both direct and indirect impacts on native species and ecosystem processes. We must consider both the direct and indirect effects of invasive plants along with other environmental

variables to predict how ecosystems will respond to the arrival of new species, and to develop tactful invasive management and native conservation practices. The use of statistical modeling techniques, such as PA, enable us to more thoroughly examine these systems that involve multiple causality, but where controlled field experiments are often not feasible.

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Chapter 2

2.1 Introduction:

Invasive species are widely listed as a threat to native plant communities (Wilcove et al., 1998; McCune et al., 2013). While some studies have established a consistent pattern of invasive dominance and native decline within plant communities (Mack et al., 2000; Didham et al., 2005; Stinson et al., 2006), invasive plants are often listed as threats simply due to their co-occurrence with native or rare plants, without strong evidence indicating that they are directly responsible for their decline. The correlation between species invasion and native decline may instead be driven by other factors, such as land use or habitat degradation (Didham et al., 2005; MacDougall and Turkington, 2005). It is very likely that invasive and native species interact with each other through multiple pathways. Indeed, there is still little consensus as to whether invasive species are the drivers of declines in native plant abundance and diversity (the driver model; MacDougall and Turkington, 2005) or whether they are simply passengers profiting from the effects of environmental factors responsible for the pattern (Didham et al., 2005; MacDougall and Turkington, 2005).

The pattern of species invasion and native decline in a community may be reinforced by the direct and indirect interactions of site-specific factors, such as habitat disturbance, with both invasive and native plants. Human and environmental disturbances can disrupt native plant communities, contributing to the decline in native plants and the range expansion of invasive species (Klironomos, 2002; Callaway et al., 2004; MacDougall and Turkington, 2005; Wolfe and Klironomos, 2005; Zobel and Öpik, 2014). Invasive plants may mediate some effects of habitat disturbance on native plants, through disturbance-encouraged invasive spread (Lembrechts et al., 2016) for example, which may have a larger impact on native decline than the direct impacts of

disturbance alone (MacDougall and Turkington, 2005). Without multi-year manipulated field studies, it is nearly impossible to disentangle the complex web of interactions between native and invasive plants.

For systems that involve multiple causality, the statistical modeling technique of confirmatory path analysis can be used to examine complex relationships among variables (Shipley, 2000a). Performing a path analysis to compare relative impacts of disturbance and exotic abundance/richness on native species will allow me to parse out where each direct and/or mediated effect has the strongest impact on native plant communities (Shipley, 2000a, 2000b). Exploring the web of interactions involved in invasive dominance patterns, and its associated impacts on natives, is crucial for directing management and conservation efforts. For example, if invasive competition is not the limiting factor for natives, then even complete invasive removals may have little or no effect on the abundance and diversity of native plants (Didham et al., 2005; MacDougall and Turkington, 2005).

2.1.1 Significance:

In order to disentangle the impacts of invasive species on native plants from other factors, it is important to examine the mechanistic relationships between invasives, natives, and potential third variables. Due to the potentially damaging impacts of species invasions, randomized manipulative studies are not feasible. Although many have looked at the effects of both invasive species and other correlated factors on native species in the field (MacDougall and Turkington, 2005; Stinson et al., 2006; Lembrechts et al., 2016) and others have used statistical models, including path analysis to establish the drivers of invasion (Mitchell, 1992; White et al., 2012; Peoples and Goforth, 2017), the mechanisms underlying species invasion and native decline are still relatively unknown. This study uses path analysis to investigate the intertwining effects of

environmental factors on native plant species. The results could potentially point to areas where possible management strategies might be best focused or avoided to minimize unneeded spending, while best managing invasive species and promoting native species conservation and recovery.

2.1.2 Objectives and Hypotheses:

I aimed to examine the direct and indirect mechanisms by which invasive plants impact native plant species while considering the impacts of a third factor, environmental disturbance. Using a large set of pre-existing field survey data, I examined the relative impacts of invasive species and habitat disturbance on native plant abundance and species richness. The dataset used in the analyses, groups plant abundance/richness data into two categories, either ‘native’ or ‘exotic’, where ‘exotic’ includes data collected for all non-native plants within that plot. For this reason, when I refer to models using ‘exotic’ richness/abundance, those variables are inclusive of both data on invasive species (as defined in Ricciardi, 2012) and those that are simply non-native. Path analysis enabled me to test multiple models of invasion and compare their relative fit to the data which would be otherwise difficult, due to the infeasibility of controlled field experiments.

2.2 Methods:

2.2.1 Data Collection and Description:

Through a collaboration with Dr. Joseph Bennett at Carleton University and Dr. Jenny McCune at the University of Lethbridge, I was granted access to a large-scale database describing the plant community at 282 1-hectare (ha) forest plots across Southern Ontario (Tables 2.1, 2.2; Figure 2.1). Plant community data was collected by Dr. Jenny McCune, Hanna Rosner-Katz, and their team of field assistants over four summers during the years of 2014, 2015, 2017, and 2018 (as described in McCune et al., 2017). Briefly, each plot surveyed was a 1-ha piece of private or protected forested land (Figure 2.1). All vascular plant species present at each site were recorded

and placed into three non-mutually exclusive ‘either-or’ categories: native or exotic (with some unknowns), rare or not, disturbance associated or not. A coarse estimate of each species abundance was also recorded based on a 5 category scale: 1 - very rare (1 or 2 individuals), 2 - rare (2 - 10 individuals), 3 - infrequent (< 10 scattered individuals), 4 - common (> 10 but not dominant), 5 - dominant (prominent throughout). Sites were described using field notes on past and current land use (e.g., farming, recreation, logging) and disturbance indicators (e.g., roads/trails, trash, cut stumps, wind-thrown trees). The area of land within a 500m radius of each site center that was forested (in both 1954 and 2013) determined using GIS, was also recorded (Table 2.1).

Upon receiving the dataset, I compiled existing notes on disturbance at each site into a human habitat disturbance proxy variable (here after referred to as ‘*Field-measured Disturbance*’), and used forested area within a 500m radius of each site to create a second disturbance proxy (here after referred to as ‘*Non-forested Area*’). *Field-measured Disturbance* is a field note compiled factor, generated by scoring sites for the presence or absence of any evidence of the three human disturbance indicators common across sites: human trails/roads, trash, or selective cutting/logging (stumps) (Table 2.2). Plots with evidence of any single indicator, or combination of indicators, were scored as one for disturbance, and those with no evidence of any of the three indicators were scored as zero. The *Non-forested Area* disturbance proxy (following Zhang et al., 2010) was generated by subtracting amount of forested area at each site from the total possible forested area within a 500m radius (78.54 ha) of any site (Table 2.1).

2.2.2 Path Analysis and Structural Equation Modeling approach:

Directed acyclic graphs (DAGs) representing the hypothesized causal links among the variables of interest were described and tested using the assembled database (Verma and Pearl, 1988; Shipley, 2000a; Tables 2.1, 2.2; Figures 2.2, 2.3). To test these hypotheses, confirmatory path analyses were performed to assess whether the correlations among the set of variables of interest were consistent with the hypothesized causal links among those variables, as defined by the DAGs (Table 2.1; Figures 2.2, 2.3). Briefly, this was done by converting the DAGs into a set of individual linear models that follow the *d*-separation claims (See Tables 1.1, 2.3) and performing a series of multiple regressions to test the overall model, and to calculate individual estimates for the direct and indirect relationships between variables.

Figure 2.2 illustrates the six model hypotheses for the analysis, each of which predicts a different relationship between the five variables: two different proxies for habitat disturbance (D), native plant relative abundance (N_A), exotic plant relative abundance (E_A), native species richness (N_{SR}), and exotic species richness (E_{SR}). Solid lines hypothesized direct effects of one variable on another in the direction of the arrow. Dashed lines indicate indirect effects of one variable on another (as mediated by a third variable) in the direction of the arrow (See Appendix A).

2.2.3 Statistical Analysis:

All data analyses were carried out in R, version 3.6.0 (R Core Development Team 2019).

Model residuals were analyzed (using QQ plots and the Shapiro-Wilk Test) for violations of normality ($p < 0.05$) and the equal variance assumptions of path analysis ($p < 0.05$). The following response variables were square root transformed to correct for violating the assumptions of normality of residuals: exotic and native species richness, exotic and native relative abundance.

To test competing causal hypotheses comparing the relationships between different habitat disturbance proxies and exotic/native species abundance and richness, I performed a confirmatory path analysis, which estimates causal links among correlated variables (Pearl, 1988; Mitchell, 1992; Shipley, 2009; Gonzalez-Voyer, 2014). Due to the structure of the data (i.e., use of binary variables), classical structural equation modeling with maximum likelihood statistics ('lavaan' Package in R (Rosseel et al., 2019)) was not used (Shipley, 2000a, 2003, 2013). Instead I used a combination of linear models (lm function, 'DAAG' package in R (Maindonald and Braun, 2015)) and generalized linear models (glm function, 'MASS' package in R (Ripley et al., 2019)), without random or mixed effects, to test the hypotheses of conditional independence in our models using the d - separation technique (Verma and Pearl, 1988; Shipley 2000a, 2000b, 2003).

I tested the fit of each entire model (basis set) using Fisher's C statistic. If the path diagram is consistent with the data (i.e., all independence claims are supported) then C is distributed as a X^2 statistic with $2k$ degrees of freedom, where k is the number of d - separation claims in the basis set (Verma and Pearl, 1988; Pearl, 1988; Mitchell, 1992; Shipley 2000a, 2013; Gonzalez-Voyer, 2014; Appendix B). A significant difference ($p < 0.05$) between the observed and predicted pattern of conditional independencies in the basis set indicates the model is inconsistent with the data and leads to a rejection of the model (Pearl, 1988; Mitchell, 1992; Shipley, 2000a, 2000b). I selected the best fitting model based on the Fisher's C and Akaike's information criterion (See Appendix C) where K is the total number of free parameters in the model and n is the sample size (Shipley, 2000a, 2013). After determining the best fit causal structure, the path coefficients were calculated by regressing each variable on each of its direct causes (psem function, 'piecewiseSEM' package in R (Lefcheck et al. 2019)), following the path

diagram structure (Figures 2.2, 2.3). Path coefficients were then standardised to allow for magnitude comparison (Mitchell, 1992; Shipley, 2000a).

I tested three possible path models and the conditional independences (i.e., statistical independence after accounting for other variables) of the two habitat disturbance proxies and native and exotic species richness and abundance (Tables 2.1, 2.4, 2.8; Figure 2.2). Habitat disturbance might directly influence native plant abundance/richness and exotic plant abundance/richness with no causal link between the two (Figure 2.2, Models 1, 4). Two models which test this hypothesis of invasive dominance are the *full passenger* abundance model and the *full passenger* species richness model (Figure 2.2; Models 1, 4). Alternatively, habitat disturbance could directly influence native plant abundance/richness, which in turn affects exotic plant abundance/richness, with no direct link between habitat disturbance and exotic plant abundance/richness (Figure 2.2; Models 2, 5). This hypothesis was tested through the *partial passenger* abundance model and the *partial passenger* richness model (Figure 2.2; Models 2, 5). Conversely, habitat disturbance could influence invasive plant abundance/richness directly, which in turn affects native plant abundance/richness, with no direct link between habitat disturbance and native plant abundance/richness (Figure 2.2; Models 3, 6). The *partial driver* abundance model and the *partial driver* richness model were used to test this hypothesis (Figure 2.2; Models 3, 6). All six variant passenger and driver models using abundance and species richness were tested twice, once with each of the two disturbance proxies: *Field-measured Disturbance* and *Non-forested Area* (Table 2.2).

2.2.4 Additional Exploratory Analyses:

After testing the consistency of models 1 - 6 (Figures 2.2, 2.3) with the data, I decided to analyze nine additional models in order to better understand the results. These additional analyses tested alternative casual hypotheses including the relative abundance of three individual species with

different life histories/invasion status (See Appendix D). For example, I was interested in whether the fit of a particular causal structure would change if I included the abundance of a single exotic species, rather than the relative abundance of all exotics. To explore this question, I tested the direct effect of the cover-class abundance of a common exotic species – *Alliaria petiolata* (garlic mustard), and the direct and indirect effects of *Field-measured Disturbance* on the relative abundance of all natives (Appendix D, Table D.2). Additionally, I was interested in whether the fit of a particular causal structure would change if I included the abundance of one frequent and abundant native rather than all natives, and whether the fit of these models would differ if I used natives of two distinct ecotypes – disturbance associated and non-disturbance associated. A disturbance associated species was defined as one which has the following mentioned in their habitat description: disturbed sites, roads, roadsides, railroads, recently disturbed sites, meadows, ditches, or anything else denoting disturbed habitat (Michigan Flora Online). *Full passenger*, *partial passenger*, and *partial driver* abundance models were tested to determine the direct effect of the relative abundance of all exotic species, and the direct and indirect effects of *Field-measured Disturbance*, on the cover-class abundance of one disturbance associated native – *Circaea canadensis* (enchanter’s nightshade; See Appendix D, Table D.6). Lastly, the *full passenger*, *partial passenger*, and *partial driver* abundance models were also tested to determine the direct effect of the relative abundance of all exotic species, and the direct and indirect effects of *Field-measured Disturbance*, on the cover-class abundance of one non-disturbance associated native – *Arisaema triphyllum* (jack-in-the-pulpit; See Appendix D, Table D.9).

2.3 Results:

2.3.1 Descriptive Statistics:

There was a strong, negative, linear relationship between exotic relative abundance (defined as the total abundance of all exotic species, as a percentage of the summed abundance of all species present) and the relative abundance of native plants in a plot ($r = -0.959$, $n = 282$, $p = 2.20 \times 10^{-16}$; Figure 2.4). In contrast, the number of exotic plant species and the number of native plant species exhibited a positive relationship ($r = 0.215$, $n = 282$, $p = 2.71 \times 10^{-4}$; Figure 2.5). There was a negative relationship between the forested area within a 500m radius of a plot in hectares and the relative abundance of exotic plants in the plot ($r = -0.326$, $n = 282$, $p = 2.12 \times 10^{-8}$; Figure 2.6), and a positive relationship with the relative abundance of native plants in a plot ($r = 0.378$, $n = 282$, $p = 5.16 \times 10^{-11}$; Figure 2.7). Similarly, there was a negative, linear relationship between the forested area (ha) within 500m of a plot and exotic species richness in the plot ($r = -0.215$, $n = 282$, $p = 2.71 \times 10^{-4}$; Figure 2.8), and a positive, linear relationship between forested area (ha, 500m radius) and the richness of native species in a plot ($r = 0.178$, $n = 282$, $p = 2.77 \times 10^{-3}$; Figure 2.9).

Native and exotic relative abundances across sites ($n = 282$) averaged $81.0 \% \pm 8.77$ SD and $13.8 \% \pm 7.76$ SD, respectively. Plot native species richness averaged 81.8 species ± 25.9 SD, while exotic richness averaged 15.6 species ± 9.07 SD across all sites.

2.3.2 Comparing Model Fit Using Fisher's C statistic:

When the three sets of abundance and richness models (*full passenger*, *partial passenger*, and *partial driver*), using the *Field-measured Disturbance*, are compared by their individual Fisher's critical statistic (Fisher's C) null probabilities, we can see which models are consistent with the data (Table 2.4). Looking only at the three abundance models, both the *full passenger* model and the *partial passenger* model have null probabilities below the alpha value of 0.05 (Table 2.4: $p_1 =$

2.22×10^{-16} , $p_2 = 0.0389$). However, while the *full passenger* model can be clearly rejected (Table 2.4: $p_1 = 2.22 \times 10^{-16}$), the *partial passenger model* is only just rejected (Table 2.4: $p_2 = 0.0389$). The *partial driver* abundance model is statistically consistent with the data (Table 2.4: $p_3 = 0.0723$), and I therefore fail to reject it.

When the three models are compared for the species richness dataset, using their individual Fisher's C and null probabilities, only the *full passenger* model is rejected, with a null probability substantially lower than the alpha value (Table 2.4: $p_4 = 3.60 \times 10^{-4}$). Both the *partial passenger* and the *partial driver* richness models are consistent with the data, and I therefore fail to reject them (Table 2.4: $p_5 = 0.288$, $p_6 = 0.405$).

Looking at the Fisher's C statistics and their null probabilities for the *full passenger*, *partial passenger*, and *partial driver* models using *Non-forested Area*, all six models tested were rejected (Table 2.5). Therefore, none of the *full passenger*, *partial passenger*, or *partial driver models* for both abundance and richness data were consistent with the data (Table 2.5).

2.3.3 Comparing Model Fit Using $\Delta AICc$:

By comparing $\Delta AICc$ values separately for each of the two sets of passenger-driver models with the two different response variables (full passenger, partial passenger, and partial driver models for abundance and species richness) which use *Field-measured Disturbance*, I can draw several conclusions. Looking at the three abundance models (Figure 2.2), the *partial driver* abundance model has the lowest $\Delta AICc$, although the *partial passenger* abundance model is technically indistinguishable from it ($\Delta AICc < 3$; Burnham and Anderson, 2004, 2010; Shipley, 2013). The *full passenger* model for abundance has essentially no support ($\Delta AICc > 10$) compared to the *partial passenger* abundance model and the *partial driver* abundance model (Table 2.6). Looking only at the three models with species richness as a response (Figure 2.2), the *partial driver* model

has the lowest Δ AICc, but again, the *partial passenger* model is not distinguishable from the *full passenger* model, and the *partial driver* model has no support in comparison (Table 2.6).

After comparing the model fit for the first set of models using *Field-measured Disturbance* with both the probability of the Fishers *C* and Δ AICc scores, I determined that comparing model fit by either method yields essentially the same results (Tables 2.4, 2.6). Based on this, the fit of models testing relationships between *Non-forested Area*, native and exotic abundance and richness, as well as all models in the exploratory analysis (See Appendix D), were determined and compared using the null probability of the Fisher's *C* alone (Table 2.5).

2.3.4 Overall Model Fit:

The path analyses are consistent with multiple alternative mechanistic links between habitat disturbance, native and exotic species richness, and relative abundance (Tables 2.7, 2.5; Figure 2.3). When comparing models that describe the relationship between *Field-measured Disturbance* and native and exotic relative abundance, the *partial driver* model was the best fit (Table 2.4, Figure 2.3). However, there was no single best fit model describing the relationship between *Field-measured Disturbance* and native and exotic species richness (Table 2.4, Figure 2.3).

2.3.5 Full Passenger Models:

The *full passenger* models for relative abundance and richness were tested and rejected for both disturbance metrics; *Field-measured Disturbance* and *Non-forested Area* (Tables 2.4, 2.5; Figure 2.3).

2.3.6 Partial Passenger Models:

The *partial passenger* models were tested using the two alternative disturbance proxies for both relative abundance and richness (Tables 2.4, 2.5; Figure 2.3). When using *Non-forested Area*, the *partial passenger* model was rejected for both richness and relative abundance (Table 2.5).

When using *Field-measured Disturbance*, the *partial passenger* model for abundance was rejected, while I failed to reject the *partial passenger* model for richness (Table 2.4, Figure 2.3). In the richness *partial passenger* model, the data are consistent with a positive influence of native species richness on exotic species richness (Table 2.7: PC = 0.0752, SE = 0.0204, $p = 3.00e-4$). In this same model, the data are consistent with no direct influence of *Field-measured Disturbance* on native species richness (Table 2.7: PC = 4.68, SE = 4.30, $p = 0.277$). The data are also consistent with *Field-measured Disturbance* having a weak indirect effect on native species richness (Table 2.8: PC = 1.18).

2.3.7 Partial Driver Models:

Two *partial driver* models, for abundance and richness, were tested with the two habitat disturbance proxies (Tables 2.4, 2.5; Figure 2.3). When using *Non-forested Area*, both the abundance and richness *partial driver* models were rejected (Table 2.5).

When using *Field-measured Disturbance*, the *partial driver* model for both abundance and richness was supported (Table 2.4, Figure 2.3). For the *partial driver* model with relative abundance, the data are consistent with exotic relative abundance negatively influencing native relative abundance (Table 2.7: PC = -1.08, SE = 0.0190, $p < 1.00 \times 10^{-4}$). For this same model, the data are also consistent with no impact of disturbance on exotic relative abundance (Table 2.7: PC = 1.56, SE = 1.29, $p = 0.225$). Lastly, the data are consistent with *Field-measured Disturbance* having an indirect negative effect on native plant abundance (Table 2.8: PC = -1.69).

For the *partial driver* model with the richness dataset, the data are consistent with exotic species richness positively influencing native species richness (Table 2.7: PC = 0.616, SE = 0.167, $p = 3.00 \times 10^{-4}$; Figure 2.3). In this model, the data are not consistent with an effect of

Field-measured Disturbance on exotic species richness (Table 2.7: PC = 1.91, SE = 1.50, $p = 0.203$).

Finally, for this same model, the data are consistent with *Field-measured Disturbance* having a positive indirect impact on exotic species richness (Table 2.8: PC = 0.352).

2.4 Discussion:

2.4.1 General Discussion:

I tested six different causal hypotheses representing variations of the passenger and driver models of invasive dominance (MacDougall and Turkington, 2005), each proposing a different relationship between six variables: native and exotic relative abundance, native and exotic species richness, and habitat disturbance (measured in two different ways). The path analyses revealed that the two measurements of habitat disturbance were inconsistent in terms of their effects on native and exotic richness as well as native and exotic relative abundance. I therefore did not find consistent support for the *full passenger* model of invasive dominance. I failed to reject a total of three out of twelve causal hypotheses, one of which supports the *partial passenger* model of invasive dominance, and two that support the *partial driver* model. All supported models included significant interactions between exotic and native abundance/richness (Figures 2.3, 2.4). Overall, I consistently found more support for models consistent with the *partial driver* rather than the *full passenger* mechanism of invasive dominance.

2.4.2 Full Passenger, Partial Passenger, and Partial Driver Models:

There is little consensus in the literature as to whether invasive species are the main drivers of declines in native richness and abundance in nature, or whether they may be passengers of changes driven by other environmental variables, such as habitat disturbance (Levine et al., 2003; Gurevitch and Padilla, 2004; MacDougall and Turkington, 2005). Counter to my expectations (MacDougall and Turkington, 2005), all four models with a causal structure indicative of a *full passenger* model, where changes in native relative abundance or richness are

the direct result of changes in habitat disturbance alone, with no influence of exotics (Figure 2.2, Models 1, 4), were outright rejected. The strong rejection of these models suggests that, for this dataset, a *full passenger* model is likely not the underlying mechanism of invasive dominance. While consistency of the *full passenger* model with the data was expected based on the results of a similar study that found strong support for the passenger model (MacDougall and Turkington, 2005), the rejection of these models is not completely surprising considering the extensive existing support for the driver model and its variations (Vitousek and Walker, 1989; Forseth and Innis, 2004; Fourie, 2008). In addition to their failure to reject the passenger model, MacDougall and Turkington (2005) also found results consistent with a more interactive or mixed partial passenger/driver model. They found that the percent cover of some native species increased following exotic removal, suggesting that the growth of those natives was likely limited by competitive exclusion by exotics for light, space, and nutrients (MacDougall and Turkington, 2005). Therefore, while it is possible that the rejection of all *full passenger* models indicates that within this dataset, changes in native abundance and richness may be limited by exotic competition rather than by environmental variables having more detrimental effects on natives than on exotics (Vitousek and Walker, 1989; Fourie, 2008), it may also be that the passenger mechanism of invasive dominance may have been otherwise supported if species-specific or site ecotype effects were accounted for by the tested models (MacDougall and Turkington, 2005).

In contrast to the *full passenger* models, one out of four models with a causal structure indicative of a *partial passenger* model of invasive dominance (MacDougall and Turkington, 2005), whereby changes in native relative abundance or richness are the direct cause of changes in habitat disturbance, and an indirect result of changes in exotic relative abundance and richness was not rejected (Figure 2.2, Models 2, 5). Therefore, I am unable to reject the *partial passenger* model, involving additive or synergistic effects, as an underlying mechanism of invasive

dominance for the richness dataset (Didham et al., 2005; MacDougall and Turkington, 2005; Bauer, 2012). The failure to reject these partial passenger models is also supported by MacDougall and Turkington's (2005) study, which found that for some native species, a more interactive model (rather than a *full passenger* model) may be the best description of the underlying mechanism of invasive dominance. Further, since complete passenger and driver models of invasive dominance can be thought of as extremes on a continuum of generally more interactive or synergistic models, it makes sense that *partial passenger* models would not be rejected in this analysis (Didham et al., 2005; MacDougall and Turkington, 2005; Bauer, 2012).

Consistent with previous studies (Vitousek and Walker, 1989; Fourie, 2008), two of four models with a causal structure indicative of a *partial driver* model of invasive dominance, whereby changes in native relative abundance or richness are the direct cause of changes in exotic relative abundance or richness, rather than direct changes in habitat disturbance (Figure 2.2, Models 3, 6), were not rejected. The failure to reject these models suggests that a *partial driver* model may be the underlying mechanism of invasive dominance in the abundance or richness datasets. While these results oppose my initial predictions, these results are reinforced by other studies whose findings also suggest underlying driver models of invasive dominance (Vitousek and Walker, 1989; Fourie, 2008; Hejda et al., 2009). For example, Vitousek and Walker (1989) found that the ability of the invasive *Myrica faya* to support nitrogen fixing bacteria led to an overall increase in available nitrogen in invaded areas, suggesting that competitive exclusion rather than impacts from non-interactive factors was likely a main cause of invasive dominance in that system. Similarly, the support for the *partial driver* models may suggest that for the abundance and/or richness data, exotic dominance could have more to do with strong biotic interactions between species (Vitousek and Walker, 1989; MacDougall and Turkington, 2005;

Fourie, 2008), than with impacts of environmental variables such as disturbance (Seabloom et al., 2003; MacDougall and Turkington, 2005).

All three models of invasive dominance (*full passenger*, *partial passenger*, and *partial driver*) were rejected for both abundance and richness data when using the *Non-forested Area* metric of disturbance. One possible reason why all of these models were rejected may have to do with the nature of the *Non-forested Area* variable. *Non-forested Area* was intended to be used as a proxy for habitat disturbance within the models, however, disturbance alone is not the only reason why a plot may have a high non-forested area. For instance, while plots were specifically chosen to be on mostly forested land, some plots may have partially consisted of urbanized areas, old agricultural fields, or grasslands, that would naturally have less forested area than a plot completely within a forest. Therefore, while it is possible that none of the models accurately describe the underlying mechanism of invasive dominance for the data tested, it may also be partially due to the imperfect disturbance proxy, *Non-forested Area*, that was used for these analyses.

2.4.3 Patterns Across Supported Models:

A closer look at the direct and indirect effects within the supported *partial driver* and *partial passenger* models reveals some interesting patterns. Counter to the widely found negative influence of disturbance on native richness (Gurevitch and Padilla, 2004; Stinson et al., 2006; Brown and Boutin, 2009), the models that were consistent with the data showed no effect of habitat disturbance on native species richness (Tables 2.7, 2.8; Figure 2.3, Models 5, 6). While there is no obvious reasoning for finding no effect of habitat disturbance on native species richness (Figure 2.3), it may be partially due to the disturbance adapted natives within the total native dataset tested here, which have not been distinguished from non-disturbance associated

natives in the main analysis (See Appendix D). Further, the lack of any effect detected (Figure 2.3) could be related to a lag in the impacts of disturbance on native richness (e.g., via extinction debt, Kuussaari et al., 2009; Gilbert and Levine, 2013). Disturbance may be generating a long-term extinction debt, where future declines in native richness occur due to delayed species impacts, while native richness appears temporarily unaffected (Vellend et al., 2006; Kuussaari et al., 2009; Gilbert and Levine, 2013; Kitzes and Harte, 2015).

The only significant correlation across all non-rejected models is that between native richness/abundance and exotic richness/abundance (Figure 2.3). This itself is not surprising, as invasives and natives can affect each other directly through competition and indirectly through other organisms and environmental variables (e.g., habitat disturbance, mutualisms; MacDougall and Turkington, 2005; Stinson et al., 2006; Hejda et al., 2009). Further, the failure to detect any effect of *Field-measured Disturbance* on either natives or exotics for either the abundance and richness dataset (Figure 2.3) suggests that the *Field-measured Disturbance* variable used in these analyses does not appear to greatly influence native or exotic richness/abundance. There is no obvious reason for this result, as disturbance frequently impacts both native and exotic productivity, often in opposite ways; e.g., by promoting invasive richness and spread and suppressing natives (Rodgers and Parker, 2003; D'Antonio, 1993; Biswas and Mallik, 2010). Alternatively, it has also been shown that moderate habitat disturbance can positively impact native richness (Brown and Boutin, 2009; Biswas and Mallik, 2010). Effects of disturbance on native and exotic plants can differ widely across systems based on variables such as species, location, and timing (Gurevitch and Padilla, 2004; Bauer, 2012). This may also help explain the failure to detect an effect of disturbance on natives or exotics.

2.4.4 Counterintuitive Results:

Within some of the non-rejected path models, there are multiple path coefficient estimates that seem counterintuitive. Curiously, these counterintuitive coefficients are found in both of the supported richness models, but not in the supported abundance model (Figure 2.3). In the *partial passenger* richness model, the data are consistent with a positive influence of exotic richness on native richness, while in the *partial driver* richness model the data are consistent with native richness positively influencing exotic richness (Table 2.7). Although there seems to be no obvious explanation for the direction of effect between these variables, it is possible that these results may simply be an artifact of the data used in the analysis. While this thesis attempts to explain why invasives would dominate and lead to a reduction in natives, this pattern does not exist in the raw data. Instead, there is a positive relationship between exotic species richness and native species richness, likely caused by some other unmeasured variable, such as site soil fertility (Roberts and Gilliam, 1995). This unexpected relationship in the raw data may have made this a difficult system to test the ‘drivers of native decline’ in the first place.

In addition, it is possible that these results may be due to the lack of good measurements of key factors within this analysis. For example, these results could be mediated by many sites which may have had intermediate disturbance, which would not have been possible for me to parse out with the use of the binary *Field-measured Disturbance* variable. Additionally, the unexpected results within the species richness dataset may be a consequence of how exotic (non-native) and invasive (non-native, dominant, and potentially harmful) plants’ richness/abundance were grouped together. If invasive plants had been analyzed separately from all other non-natives, it is possible the results may have been more intuitive. This supposition is supported by the more intuitive results found in the exploratory analysis models using the invasive species A.

petiolata. The *partial driver* model was consistent with no significant effect of *A. petiolata* on native relative abundance, and the *partial passenger* model was consistent with the converse (Appendix D: Table D.3).

Supported models from the exploratory analyses also showed some counterintuitive path coefficients. For example, the supported *partial passenger* exploratory analysis model for *A. triphyllum*, was consistent with a negative impact of native *A. triphyllum* on all exotics (Appendix D: Figure D.3). Again, while there is no obvious reason for this, it is possible that these non-intuitive path coefficients may be the result of the lack of a strong disturbance metric, a key variable in the analyses. Had I used a better metric of disturbance, perhaps soil fertility (Runkle, 1985; Roberts and Gilliam, 1995), it is possible that the results may have allowed for a clear interpretation. Further, if results were driven by variables such as site fertility, for which I lacked data and was therefore not included in any analysis, then this may present a serious caveat to my results, which should be considered.

2.4.5 Support from Exploratory Analysis:

The exploratory analysis tested three causal hypotheses representing variations of the passenger and driver models of invasive dominance, each proposing a different relationship between five possible variables: total native or exotic abundance, disturbance adapted native (*Circaea canadensis*, *Arisaema triphyllum*) or invasive (*Alliaria petiolata*) abundance, and *field-measured disturbance*. The path analyses showed a variety of species-specific effects on overall model fit (Appendix D: Tables D.4, D.6, D.9).

I had predicted that best fit model of invasive dominance for the two disturbance associated species would be the *partial driver* model. However, among species-specific models using *A. petiolata* or *C. canadensis*, there was no single best fit model which explained the causal

relationship (Appendix D: Tables D.2, D.6; Figures D.1, D.2). These results support those of the main analysis, offering support for both the *partial passenger* and *partial driver* model of invasive dominance (Appendix D: Tables D.2, D.6). Further, the analyses for both *A. petiolata* and *C. canadensis* also support the *full passenger* model, otherwise completely rejected in the main analysis (Tables 2.4, 2.5). This shows that the fit of the causal structure for the *full passenger* model did change when using the *A. petiolata* and *C. canadensis* datasets, in place of total native and exotic abundance data, suggesting that life history of a species may influence which causal hypothesis is the best fit for those data. Therefore, it is possible that while rejected in the main analysis, the *full passenger* model of invasive dominance was among the best fit models in both sets of species-specific models for *A. petiolata* and *C. canadensis*, because both of these species are considered disturbance associated (Michigan Flora Online).

Disturbance associated plants, both native and exotic, tolerate and may even thrive under various levels of disturbance (D'Antonio, 1993; Grime, 2001; Brown and Boutin, 2009; Biswas and Mallik, 2010). While high disturbance has been linked to the successful invasion and spread of *A. petiolata* (Nuzzo, 1992; Munger, 2001), it has also been shown to decrease the abundance of many native species (Brown and Boutin, 2009; Biswas and Mallik, 2010; Driscoll, 2017). This may help explain the *full passenger* models being consistent with the data for models looking only at the invasive *A. petiolata*, suggesting that invasive dominance may be reached due to the direct impacts of disturbance which positively impact disturbance associated *A. petiolata* (Nuzzo, 1992; Munger 2001), and negatively impact the grouped abundance of natives (Biswas and Mallik, 2010). Further, while *C. canadensis* is considered a disturbance-associated native (Grime, 2001), it is also possible that this species, like other natives, may only tolerate low disturbance and can still suffer declines in abundance under higher disturbance levels (Brown and Boutin,

2009). For example, a study by Brown and Boutin (2009) examined the effects of historical and recent disturbances of varied intensity (i.e., past land use, grazing, selective cutting, roads) on the richness of native and exotic plants in abandoned woodlots near Ottawa, Canada. Their results showed that native richness was highest in historically partly cleared sites and lower in historically fully cleared sites, suggesting while those natives can thrive under moderate levels of disturbance, high levels can still negatively influence their richness (Brown and Boutin, 2009). Similarly, it may be that the *full passenger* model of invasive dominance is supported when looking at *C. canadensis*, if it is sensitive to higher levels of disturbance (Brown and Boutin, 2009; Biswas and Mallik, 2010). Therefore, the support found for the *full passenger* model in addition to other models supported in the main analysis may be due to inclusion of species with particular life histories and/or those that have not been accounted for within the models.

Unlike the other species-specific models tested, those using *A. triphyllum* did have a single best fit model – the *partial passenger* model. Here, the *partial passenger* model was consistent with the data, possibly because *A. triphyllum* is not disturbance associated (Michigan Flora Online). This species may be less likely to tolerate any disturbance it encounters and therefore may experience reduced abundance in disturbed settings. Disturbance can reduce the cover of natives, and in turn the competitive vigor between invasives and natives, by leaving spatial openings and nutrient abundance, ultimately enabling an increase of exotics (Jauni et al., 2014). Therefore, while competition between native and exotic plants may play a role in the exotic dominance, it may be harder to detect in systems with non-disturbance associated species than in systems with disturbance associated ones, as the direct impacts of disturbance on natives may overshadow any other competitive effects.

The findings of the exploratory analysis reinforce and help explain previous conclusions (See Chapter 2: Discussion), suggesting that between the *full passenger*, *partial passenger*, and *partial driver* models, whether a model is a consistent fit with data or not depends partially on the particular species involved, and further suggests that no single model of invasive dominance will best describe the underlying pattern of invasive dominance across all systems (Gurevitch and Padilla, 2004; Bauer, 2012).

2.4.6 Implications:

The main findings of this study include the rejection of all *full passenger* models and moderate support for both the *partial passenger* and *partial driver* models of invasive dominance. Among the three tested models of invasive dominance (*full passenger*, *partial passenger*, and *partial driver*) using *Field-measured Disturbance*, there was no single causal model that best fit the species richness data, while the *partial driver* model was the only supported causal model for the abundance data. Among the three tested models of invasive dominance using *Non-forested Area*, no casual model was consistent with both abundance and richness data. Most models failed to separate the effects of disturbance on exotics versus natives and did not allow me to easily distinguish between models postulating a direct effect of exotics on natives and the converse. Species-specific analyses for the disturbance associated plants, *A. petiolata* and *C. canadensis*, supported all three models of invasive dominance. However, analyses using the non-disturbance associated native *A. triphyllum* were consistent with only the *partial passenger* model. The overall results of the exploratory analyses support the main conclusions and help further explain some of the counterintuitive results. This study demonstrates the difficulty in establishing the causal relationships between habitat disturbance, native and exotic species richness, and abundance. Overall, the results of this study emphasize the complexity of invasive systems while

adding tentative support for either a *partial driver* model or *partial passenger* model of invasive dominance in the tested datasets.

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Chapter 3

3.1 Study Limitations and Future Directions:

Confirmatory path analysis enables the user to examine complex relationships among sets of variables for systems which may otherwise be difficult to study (Shipley, 2000). While the use of path analysis was crucial to this study and offers many benefits in terms of statistical analyses, there are also limitations. For example, while the results of path analysis can tell us about the correlations between variables within my models, these correlations must not be overinterpreted, as the causality between the variables is still essentially unknown. Controlled experimental studies in the field are the gold standard for establishing causality.

The occurrence of multiple counterintuitive path coefficients across my results suggest there may be an underlying problem. While these unexpected results may be an artifact of the data, there are multiple caveats that should also be considered. In particular, it is possible that the unexpected positive relationship between native and exotic species richness in the raw data may be driven by variables not included in any of the analyses. This possibility should be kept in mind as to not over-interpret model path coefficients that I am not entirely confident in.

Another caveat concerning the validity of the analysis results and interpretation is the lack of good measurements of key factors within the analysis. Perhaps most importantly, my study used two metrics to establish a proxy for habitat disturbance (*Field-measured Disturbance* and *Non-forested Area*), both of which are imperfect. *Field-measured Disturbance*, as a binary variable, is a very coarse estimate of disturbance within plots. While I had hoped the interpretation would be strengthened by the fact that a second set of analyses was performed with an alternative disturbance proxy (*Non-forested Area*), this second disturbance metric used was also imperfect.

While human habitat disturbance does tend to strongly correlate with forested area (Zhang et al., 2010), there are other reasons why a plot may have low forested area. For instance, the presence of a field, marsh, or urbanized area within that plot. Future studies should aim to use less coarse estimates of habitat disturbance, and ideally create causal path diagrams before data collection, in order to gather the most informative data based on the diagrams designed (Shipley, 2000). For instance, the inclusion of a larger number of disturbance indicators, or multiple types of disturbance (human/environmental) may be of particular interest.

Future studies could further investigate habitat-specific effects. The richness, abundance, and disturbance data used in this study were collected across a large geographic area (Ottawa to Windsor, ON) and includes sites from several different ecotypes (e.g., Carolinian, Mixed Forest). Site-specific effects could also be investigated by the inclusion of multiple dominant species within each habitat, replacing total exotic or native abundance and richness variables used in this analysis. Further, future studies could investigate the effects of scale as greater environmental heterogeneity of large sites may make it harder to detect competition compared to smaller sites.

3.2 Conclusions:

The establishment and spread of invasive species is a widely accepted ecological threat, often with unforeseen consequences (Wilcove et al., 1998; Gurevitch and Padilla, 2004; Stinson et al., 2006). However, there is still much work to do to determine the mechanisms by which invasive species influence native plants, and the role of non-interactive environmental factors within this relationship (Gurevitch and Padilla, 2004; MacDougall and Turkington, 2005). This study is one of the first to use path analysis to investigate the intertwining impacts of environmental factors and exotic plants on native species. While the study rejects the *full passenger* model of invasive dominance, I failed to provide clear support for the *partial passenger*

over the *partial driver* model (or vice-versa). Further exploration of the role of disturbance and other ecosystem properties in community interactions between native and exotic flora will be critical to the development of effective invasive management strategies and native recovery.

3.3 References:

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Table 1.1 Definitions for path analysis related terminology.

Term	Definition as applies to this paper
Directed Acyclic Graph (DAG)	A diagram of variables linked by unidirectional arrows that indicate the hypothesized causal links between all variables included (Shiple, 2000).
Latent Variables	Any variable that is unknown or unmeasured and included in the DAG (Shiple, 2000).
Directed Separation (d – sep)	A path analysis technique that gives the required list of claims for any set of variables within a causal graph to be independent, when conditioned on another set of variables (Pearl, 1988; Verma and Pearl, 1988; Shipley, 2000). Also used as a characteristic describing certain sets of variables within a DAG, when conditioned upon (Shiple, 2000). For example, if a set of variables is ‘ d -separated’ when conditioned on, then those variables are independent of each other.
Causal Conditioning	An action of blocking or allowing the causal influence of one set of variables on another set within a DAG (Pearl, 1988; Shipley, 2000). When a set of variables is conditioned on, it changes its state from active to inactive or the converse. This means if a vertex is active in its natural state, then when conditioned on the causal flow of information from one variable to the other will be blocked (no effect).
Conditional Dependence/Independence	A characteristic of a set of variables when conditioned upon (Shiple, 2000). If two variables are d -separated when conditioned on another set of variables, then they are conditionally independent. If two variables are not d -separated when conditioned on another set of variables, then they are conditionally dependent.
Basis Set	The set of claims indicating the conditional independence of all variables within a DAG (Shiple, 2000).

Table 2.1 Description of variables from the data collection (not all used in confirmatory path analysis).

Variables	Description
Plot	Plot name.
Year	Year the plot was surveyed.
Latitude	Latitude in UTM NAD83 zone 17N.
Forested areas within 500m in 1954	Total area forested within 500m of the plot, in hectares, in 1954. Maximum possible is $\pi(\text{radius})^2 = 78.54\text{ha}$.

Table 2.2 Description of variables used in the confirmatory path analyses.

Variables	Description
Native Relative Abundance	The total abundance of all native species, as a percentage of the summed abundance of all species present.
Exotic Relative Abundance	The total abundance of all exotic species, as a percentage of the summed abundance of all species present.
Native Species Richness	The total number of native species present
Exotic Species Richness	The total number of exotic species present.
<i>Field-measured Disturbance</i>	A binary measurement of human habitat disturbance created by scoring sites for the presence or absence of any combination of the following three disturbance indicators: human trails, logging, and trash.
<i>Non-forested Area</i>	Forested area within 500m of each plot in hectares, subtracted from total possible forested area (78.54 ha), to create a habitat disturbance proxy representing non-forested area (ha) within 500m of each plot (See Table 2.1).
Relative Abundance of Exotic <i>Alliaria petiolata</i>	The relative abundance of one exotic species – <i>Alliaria petiolata</i> . * Abundance Scale: 1 = very rare (1 or 2 individuals only), 2 = rare (more than 2 but less than 10 individuals), 3 = infrequent (more than 10, scattered around plot), 4 = common (common throughout but not dominant), 5 = dominant (visible and prominent throughout plot).
Relative Abundance of native <i>Circaea canadensis</i>	The relative abundance of one disturbance associated native plant, <i>Circaea canadensis</i> .
Relative Abundance of native <i>Arisaema triphyllum</i>	The relative abundance of one non-disturbance associated native plant, <i>Arisaema triphyllum</i> .

Table 2.3 A basis set with the implied *d* - separation statements for the path diagrams shown in Figure 2.2.

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Non-adjacent variables are the variables in each path diagram that do not have a direct effect between them. Parent variables are those that are causing the effect on another variable. D-separation statements describe the independence claims for the variables in each path diagram. The notation of the *d*-separation statements is as follows: the non-adjacent variables are listed in the round brackets; the pipe indicates the pair of variables are *d*-separated conditional on the following parent variable in the braces. Example: (x, y) | {z} can be read as: x and y are *d*-separated, conditional on z. The *d* - separation statements are the same for both abundance and richness *full passenger* models, *partial passenger* models, and *partial driver* models, using either *Field-measured Disturbance* or *Non-forested Area*.

Model ID	Non - adjacent variables	Parent variables of either non - adjacent variable	<i>d</i> - separation statement
FP	E, N	D, D	(E, N) {D}
PP	D, E	None, N	(D, E) {N}
PD	D, N	None, E	(D, N) {E}

Table 2.4 Model fit (Fisher's *C*) of six competing path models with two different response variables and *Field-measured Disturbance* (Figure 2.2).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Shown is the Fisher's *C* statistic with the df and null probability (*p* - value) associated with each model in parentheses. Significant null probabilities (*p* > 0.05) are bolded.

Response Variable	Model ID	<i>C</i> (df, <i>p</i> - value)
Abundance	FP	72.3 (2, 2.22x10 ⁻¹⁶)
	PP	6.49 (2, 0.0389)
	PD	5.25 (2, 0.0723)
Species Richness	FP	15.9 (2, 3.60x10 ⁻⁴)
	PP	2.49 (2, 0.288)
	PD	1.81 (2, 0.405)

Table 2.5 Model fit of six competing path models with two different response variables using *Non-forested Area* (Figure 2.2).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Shown is the Fisher's *C* statistic with the df and null probability (*p* – value) associated with each model in parentheses.

Response Variable	Model ID	<i>C</i> (df, <i>p</i> – value)
Abundance	FP	72.3 (2, 2.22 x10 ⁻¹⁶)
	PP	8.05 (2, 0.0179)
	PD	20.7 (2, 3.19 x10 ⁻⁵)
Species Richness	FP	23.6 (2, 7.43 x10 ⁻⁶)
	PP	23.6 (2, 7.41 x10 ⁻⁶)
	PD	19.1 (2, 7.07 x10 ⁻⁵)

Table 2.6 Model fit (Δ AICc) of six competing path models for two different response variables using *Field-measured Disturbance* (Figure 2.2).

Where K (the number of free parameters needed to fit the model) is 5 for all models and the difference (Δ) in AICc is relative to the model with lowest AICc. Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*.

Response Variable	Model ID	Δ AICc by Response Variables
Abundance	FP	68.5
	PP	1.30
	PD	0
Species Richness	FP	14.4
	PP	0.70
	PD	0

Table 2.7 Path coefficients (mean) with standard error, and standardised coefficients for direct causal links associated with the best fit models using *Field-measured Disturbance* (Figure 2.3). Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Each tilde indicates the direction of the causal effect: where the variable after the tilde is affecting the variable in front of it. Significant paths are bolded ($p < 0.05$).

Model ID	Response Variable	Direct Causal Links	Mean (SE)	Standardised Mean	p - value
PD	Abundance	Exotics ~ <i>Field-measured Disturbance</i>	1.56 (1.29)	0.0725	0.225
		Natives ~ Exotics	- 1.08 (0.0190)	- 0.959	<1.00e-04
PP	Species Richness	Natives ~ <i>Field-measured Disturbance</i>	4.68 (4.30)	0.0650	0.277
		Exotics ~ Natives	0.0752 (0.0204)	0.215	3.00e-04
PD		Exotics ~ <i>Field-measured Disturbance</i>	1.91 (1.50)	0.0760	0.203
		Natives ~ Exotics	0.616 (0.167)	0.215	3.00e-04

Table 2.8 Decomposed effects for indirect causal links associated with the best fit models using *Field-measured Disturbance* (Figure 2.3).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Indirect causal links are the effect of one variable on another as mediated by a third variable. Each tilde indicates the direction of the causal effect, mediated by a third: where the variable after the tilde is the causal parent of the variable in front of it (Appendix A).

Response Variable	Model ID	Indirect Causal links	Decomposed Effects	Standardised Decomposed Effects
Abundance	PD	Native ~ <i>Field-measured Disturbance</i>	- 1.69	- 0.0696
Species Richness	PP	Exotics ~ <i>Field-measured Disturbance</i>	0.352	0.0140
	PD	Native ~ <i>Field-measured Disturbance</i>	1.18	0.0164

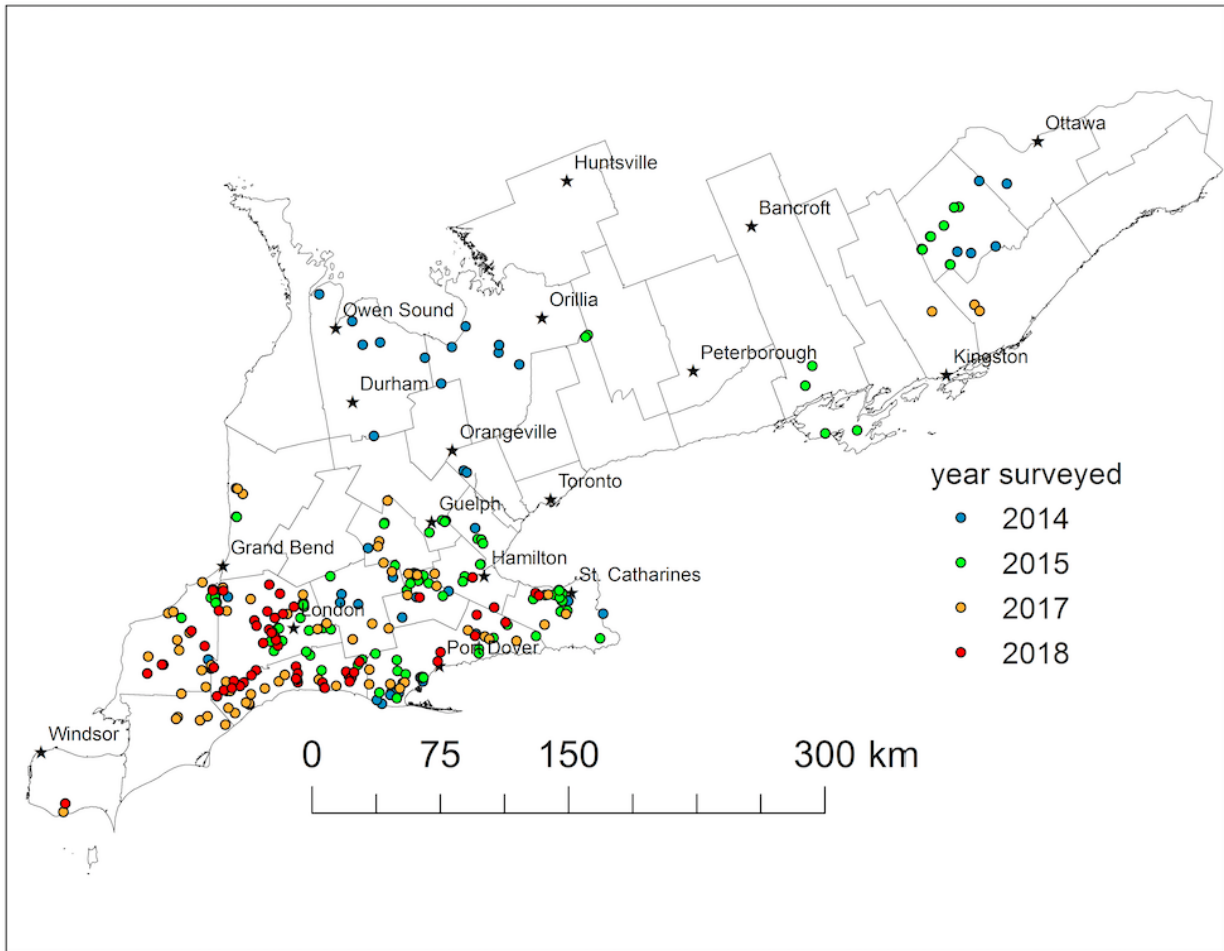


Figure 2.1 Map of North America showing the study area, sites, and year surveyed. Points show one-hectare forested plots surveyed across Ontario. Point colour indicates the year each plot was surveyed.

*Full Passenger
Abundance Model*



*Partial Passenger
Abundance Model*



*Partial Driver
Abundance Model*



*Full Passenger
Richness Model*



*Partial Passenger
Richness Model*



*Partial Driver
Richness Model*



Figure 2.2 Six alternate causal path models of the relationship between habitat disturbance, native and exotic species richness/relative abundance.

Directed acyclic graphs depicting possible relationships between *Field-measured Disturbance* and/or *Non-forested Area* (D), native plant relative abundance (N_A), exotic plant relative abundance (E_A), native species richness (N_{SR}), and exotic species richness (E_{SR}). Solid lines indicate direct effects and dashed lines indicate indirect effects as a result of the direct effects with the mediator variables.

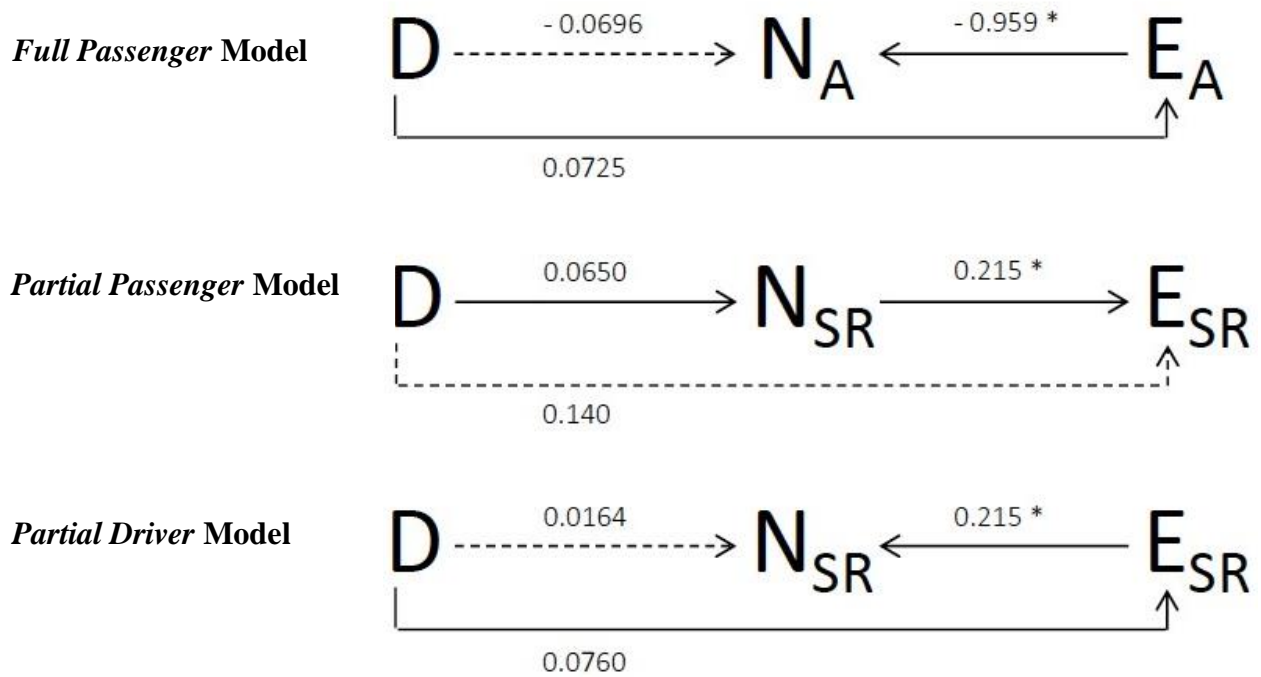


Figure 2.3 The three supported path models of all six (Figure 2.2) testing the direct and indirect relationships between *Field-measured Disturbance (D)*, exotic species richness (ESR), exotic relative abundance (EA), native species richness (NSR), and native relative abundance (NA).

Solid lines indicate direct causal paths and dashed lines indicate indirect paths as a result of the direct effects with the mediator variables. Path coefficients with an asterisk indicate significant casual paths ($p < 0.05$). Shown are the standardised path coefficients. Path coefficients for direct and indirect causal links with p – values are in Tables 2.6, 2.7.

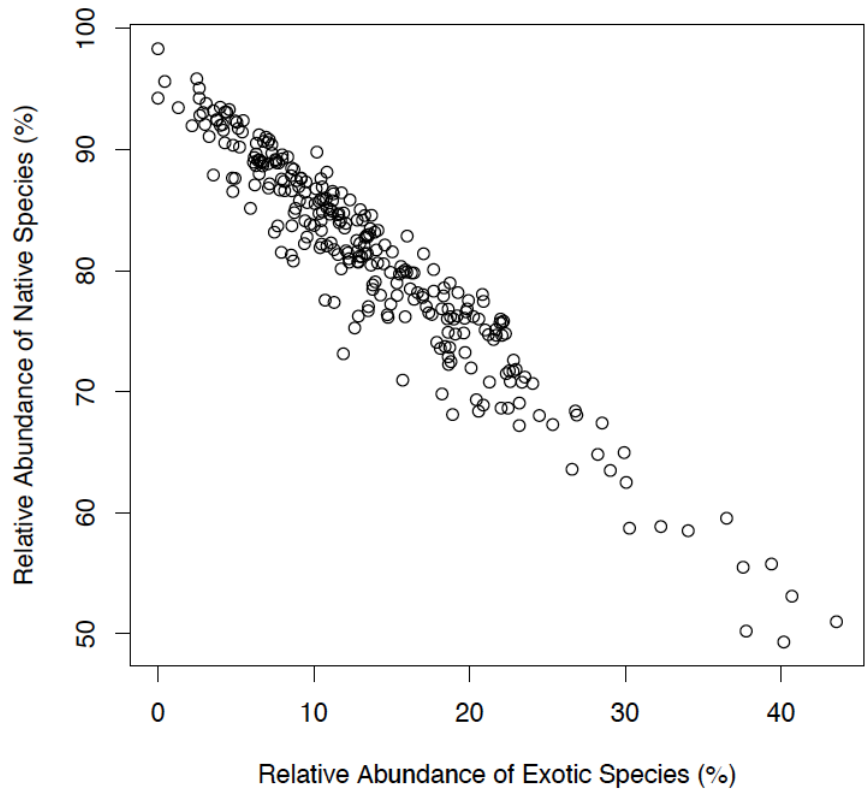


Figure 2.4 The correlation between native and exotic relative abundance as a percentage of the total summed abundance of all species present.

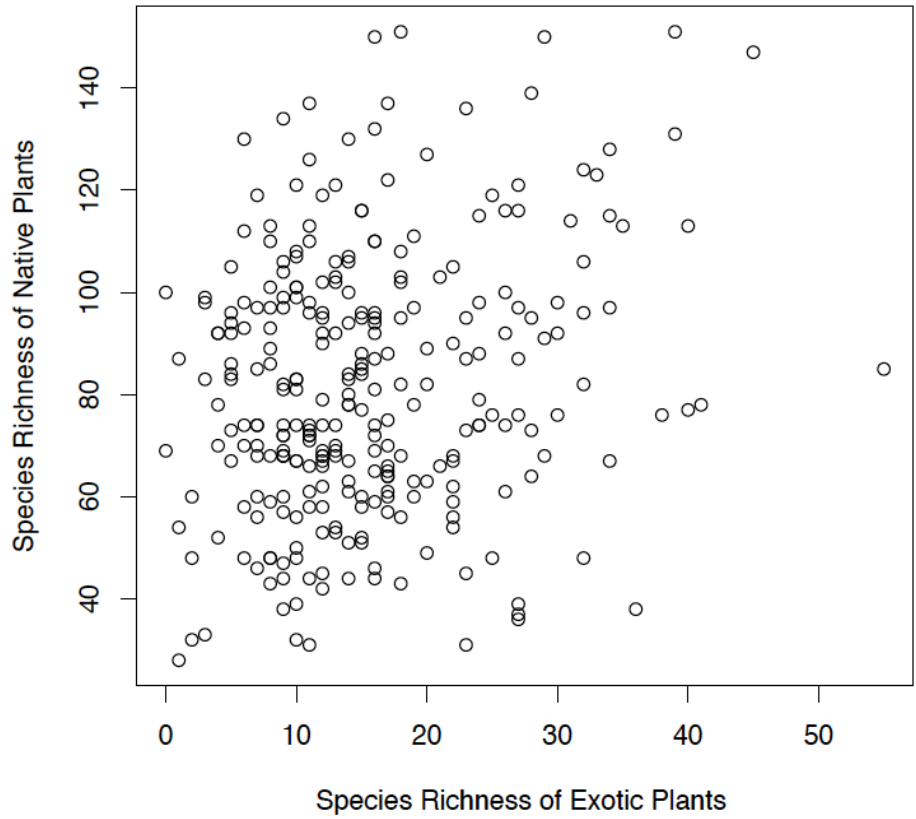


Figure 2.5 The correlation between native and exotic species richness (the total number of native or exotic species present).

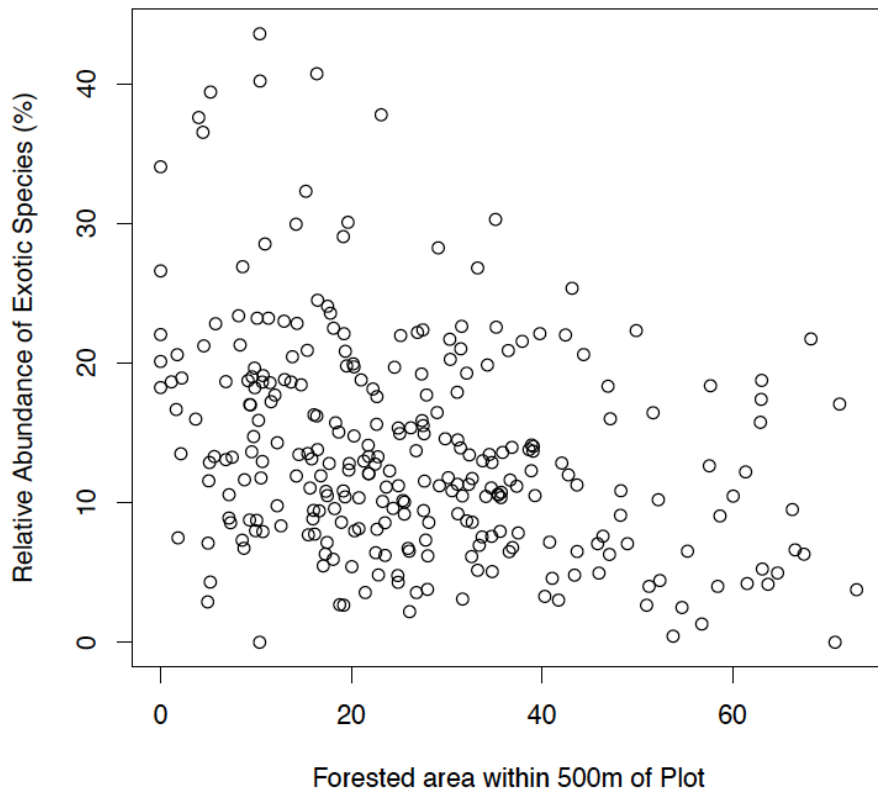


Figure 2.6 The correlation between the forested area within a 500m of a plot in hectares and the relative abundance of exotic species in the plot (% of the total summed abundance of all species present).

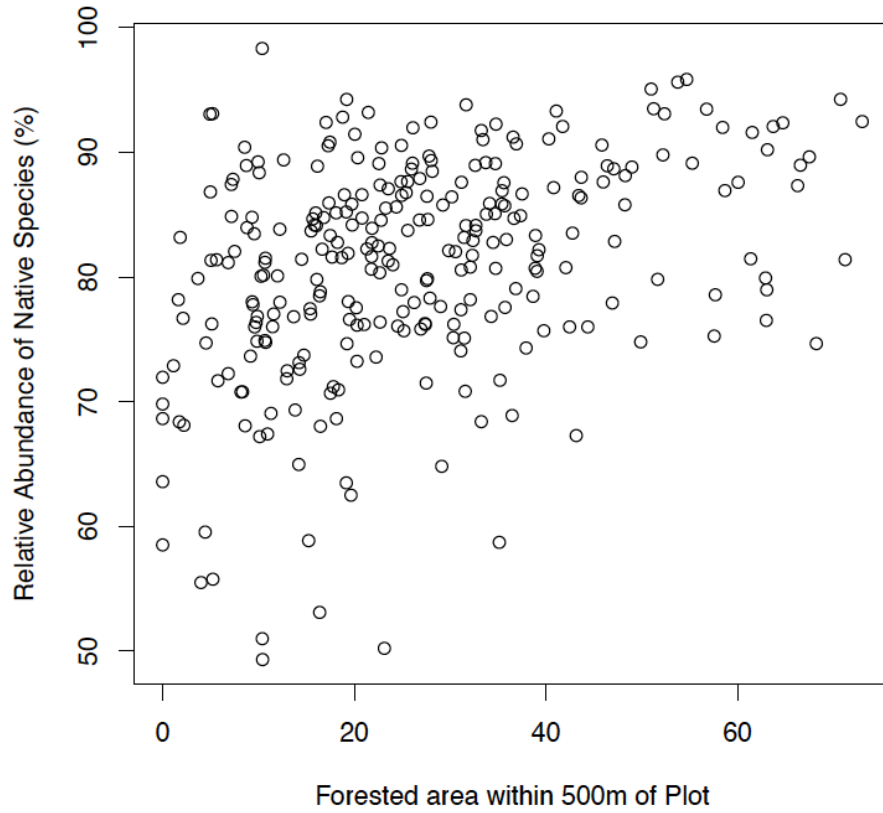


Figure 2.7 The correlation between the forested area within a 500m of a plot in hectares and the relative abundance of native species in the plot (% of the total summed abundance of all species present).

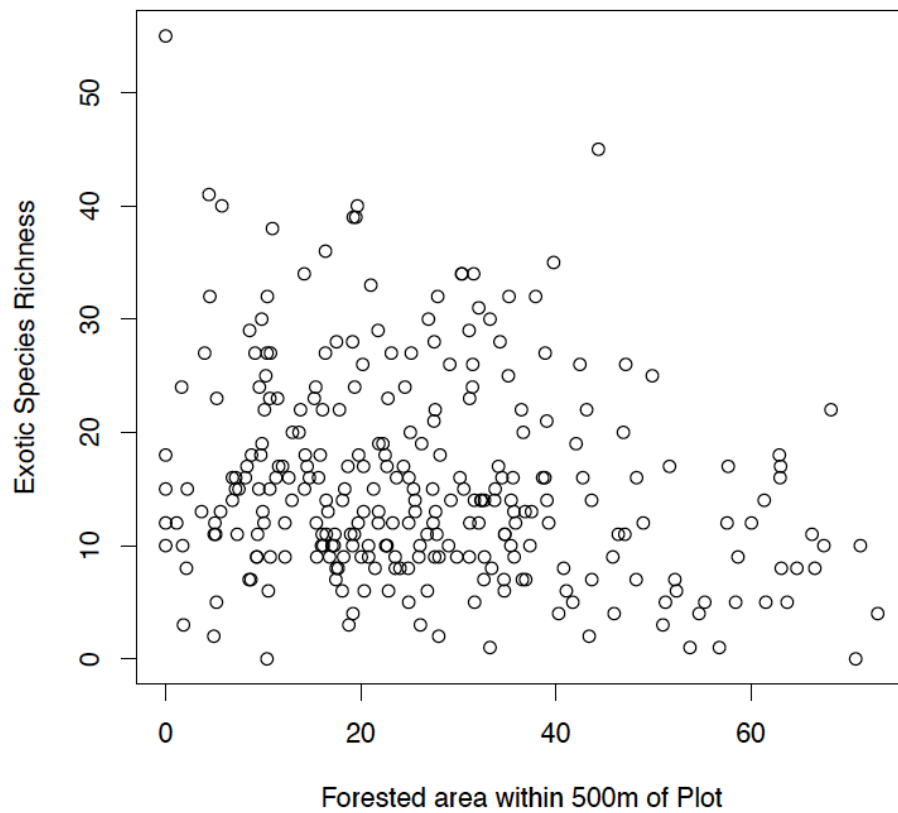


Figure 2.8 The correlation between the forested area (ha) within 500m of a plot and exotic species richness (the total number of exotic species present) in the plot.

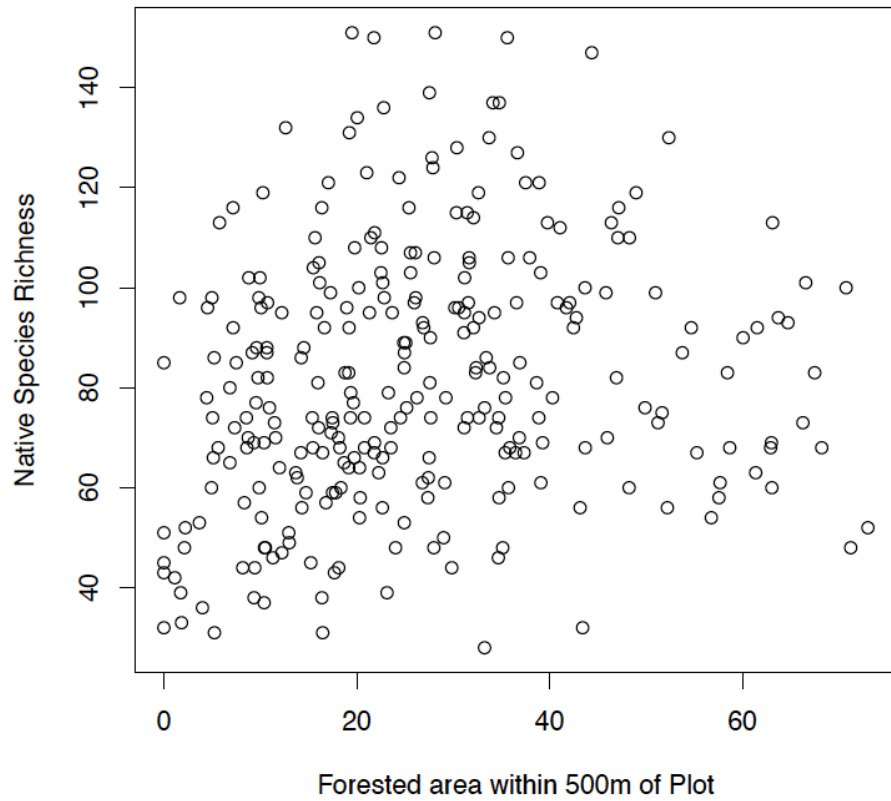


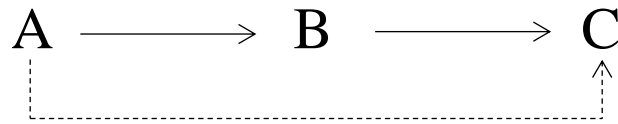
Figure 2.9 The correlation between the forested area (ha) within 500m of a plot and native species richness (the total number of native species present) in the plot.

Appendices:

Appendix A – Calculating Indirect Causal Links from Path Diagrams:

To calculate the indirect links within a path diagram, the path coefficients of direct links along any indirect path are multiplied together.

Example: Indirect effect $ac = ab * bc$



Appendix B – Calculating Fisher’s Critical Value:

The Fisher’s Critical Value (C Statistic) and its null probability are calculated following the two mathematical formulas below (Pearl, 1988; Verma and Pearl, 1988; Mitchell, 1992; Shipley 2000a, 2013; Gonzalez-Voyer, 2014). These calculations were done on the statistical software program R, version 3.6.0 (R Core Development Team 2019). Where $[L(M(\Theta);D)]$ is the likelihood of the model given the empirical data when the estimated parameters of the probability distribution maximize this likelihood, where p_i is the null probability of the i_{th} d – separation claim in the basis set, n is the number of independence claims in the basis set, and C is Fisher’s critical value (Shipley, 2013).

$$-2 \ln [L (M (\hat{\Theta}) ; D)] = -2 \sum_{i=1}^n \ln (p_i) = C$$

Appendix C – Calculating Model AIC and AICc Scores:

The C statistic can be used to calculate the AIC and AICc (AIC variant standardised based on sample size) score for any path model (Shipley, 2013). The AIC and AICc were calculated following the mathematical formulas below using the statistical software program R, version 3.6.0 (R Core Development Team 2019). Where $[L(M(\Theta);D)]$ is the likelihood of the model given the empirical data when the estimated parameters of the probability distribution maximize this likelihood, where C is Fisher's critical value, K is the total number of free parameters to be estimated, and n is the sample size (Shipley, 2013).

$$AICc = -2 \ln [L (M (\Theta) ; D)] + 2K = C + 2K$$

$$AICc = -2 \ln [L (M (\Theta) ; D)] + 2K (n / (n - K - 1)) = C + 2K (n / (n - K - 1))$$

Appendix D – Exploratory Analyses:

D.1 Introduction:

Because some of the results from the main analysis were unexpected and difficult to interpret, I decided to perform a more refined test of hypotheses that specify particular plant life history types. Three additional analyses were performed. The first uses one common disturbance associated exotic species – *Alliaria petiolata*. The second uses a highly disturbance associated native – *Circaea canadensis*, and the last uses one non-disturbance associated native – *Arisaema triphyllum*. These three additional analyses were performed to see if the results change if I remove the bulk of either the native or exotic community to look at species-specific effects of three species with differing life history types.

D.2 Results:

D.2.1 Overall Model fit:

Overall model fit was tested for three sets of exploratory models. The first set of models use the relative abundance of all natives and cover-class abundance of a single exotic species – *A. petiolata*, while the second and third set of models use relative abundance of all exotics and cover-class abundance of a single native, either disturbance associated (*C. canadensis*), or not (*A. triphyllum*). From the first set of exploratory models, using cover-class abundance of *A. petiolata*, all three models were found to be consistent with the data, with no single best fit model among the three (Table D.2; Figure D.1). The second set of exploratory models using *C. canadensis* shows that all three models are consistent with the data, with no single best fit model among the *full passenger*, *partial passenger*, and *partial driver* models (Table D.6: $p_1 = 0.151$, $p_2 = 0.280$, $p_3 = 0.158$). Lastly, from the third set of exploratory models using cover-class

abundance of *A. triphyllum*, only the *partial passenger* model was found to be consistent with the data (Table D.9; Figure D.3).

D.2.2 Full Passenger Models:

From the first set of exploratory models using the cover-class abundance of a single exotic species – *A. petiolata*, the null probabilities of the Fisher's *C* indicate that only the *full passenger* model was not rejected (Table D.2; Figure D.1). The path analysis revealed that for this model, the data are consistent with *Field-measured Disturbance* not influencing either the cover-class abundance of the exotic *A. petiolata* (Table D.3: PC = 0.194, SE = 0.237, $p = 0.414$), or the relative abundance of natives (Table D.3: PC = - 0.958, SE = 1.45, $p = 0.511$).

From the second set of exploratory models using a single disturbance associated native species – *C. canadensis*, the *full passenger* model was again found to be consistent with the data (Table D.6; Figure D.2). For this *full passenger* model, the data are also consistent with no significant influence of *Field-measured Disturbance* on either the relative abundance exotics (Table D.7: PC = 1.56, SE = 1.285, $p = 0.225$), or the cover-class abundance of the disturbance associated native species – *C. canadensis* (Table D.7: PC = 0.235, SE = 0.154, $p = 0.129$).

D.2.3 Partial Passenger Models:

From the first set of exploratory models using cover-class abundance of a single exotic species – *A. petiolata*, the *partial passenger* model was found to be consistent with the data (Table D.2; Figure D.1). For this *partial passenger* model, the data are consistent with no influence of *Field-measured Disturbance* on native relative abundance (Table D.3: PC = - 0.958, SE = 1.45, $p = 0.511$), and no influence of native relative abundance on the cover-class abundance of

A. petiolata (Table D.3: PC = - 0.0147, SE = 0.00970, $p = 0.131$). For the same model, the data are consistent with a positive indirect effect of *Field-measured Disturbance* on the cover-class abundance of *A. petiolata*, as mediated by the relative abundance of natives (Table D.4: PC = 0.00354).

For the second set of exploratory models using a single disturbance associated native species – *C. canadensis*, the *partial passenger* model was found to be consistent with the data (Table D.6; Figure D.2). In this *partial passenger* model, the data are consistent with no significant influence of *Field-measured Disturbance* on a disturbance associated native (Table D.7: PC = 0.235, SE = 0.154, $p = 0.129$). Further, the data are consistent with no significant influence of *C. canadensis* on exotic relative abundance (Table D.7: PC = 0.765, SE = 0.496, $p = 0.124$). In addition, the data are also consistent with a positive indirect effect of *Field-measured Disturbance* on exotic relative abundance, as mediated by the disturbance associated native species – *C. canadensis* (Table D.8: PC = 0.00833).

From the third set of exploratory models using a single non-disturbance associated native species – *A. triphyllum*, the *partial passenger* model was the only model of the three in this set that I failed to reject (Table D.9; Figure D.3). The path analysis for this *partial passenger* model indicates that it is consistent with the cover-class abundance of the single non-disturbance associated native species – *A. triphyllum*, not being significantly influenced by *Field-measured Disturbance* (Table D.10: PC = 0.319, SE = 0.196, $p = 1.05$). The data are also consistent with *A. triphyllum* having a significant negative influence on exotic relative abundance (Table D.10: PC = - 1.61, SE = 0.380, $p < 0.001$). In the same model, the data are consistent with *Field-measured Disturbance* having a negative indirect effect on exotic relative abundance, as mediated by native abundance (Table D.11: PC = - 0.0238).

D.2.4 Partial Driver Models:

From the first set of exploratory models using the cover-class abundance of a single exotic species – *A. petiolata*, the null probabilities of the Fisher's *C* indicate that I cannot reject the *partial driver* model (Table D.2; Figure D.1). For the *partial driver* model, data are consistent with no influence of *Field-measured Disturbance* on the abundance of *A. petiolata* (Table D.3: PC = 0.194, SE = 0.237, $p = 0.414$), and no significant influence of the relative abundance of *A. petiolata* on native relative abundance (Table D.3: PC = - 0.554, SE = 0.366, $p = 0.131$). For this same model, the data are consistent with a negative indirect effect *Field-measured Disturbance* on native relative abundance, as mediated by the relative abundance of *A. petiolata* (Table D.4: PC = - 0.00441).

From the second set of exploratory models using a single disturbance associated native species – *C. canadensis*, the *partial driver* model was found to be consistent with the data (Table D.6; Figure D.2). This model is consistent with no significant effect of *Field-measured Disturbance* on the relative abundance of exotics (Table D.7: PC = 1.56, SE = 1.29, $p = 0.225$), and no significant effect of exotic relative abundance on *C. canadensis* cover-class abundance (Table D.7: PC = 0.0110, SE = 0.00710, $p = 0.124$). Further, the data are consistent with a positive indirect effect of *Field-measured Disturbance* on the cover-class abundance of *C. canadensis*, as mediated by the exotic relative abundance (Table D.8: PC = 0.00666).

Table D.1 A basis set with the implied d – separation statements for the *full passenger*, *partial passenger*, and *partial driver* models for *Alliaria petiolata*.

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Non-adjacent variables are the variables in each path diagram that do not have a direct effect between them. Parent variables are those that are causing the effect on another variable. D-separation statements describe the independence claims for the variables in each path diagram. The notation of the d -separation statements is as follows: the non-adjacent variables are listed in the round brackets; the pipe indicates the pair of variables are d -separated conditional on the following parent variable in the braces. Example: $(x, y) \mid \{z\}$ can be read as: x and y are d -separated, conditional on z. Where N = native relative abundance, AP = relative abundance of the exotic *Alliaria petiolata*, and D = *Field-measured Disturbance* (Figure D.1).

Model ID	Non – adjacent variables	Parent variables of either non – adjacent variable	d – separation statement
FP	AP, N	D, D	$(AP, N) \mid \{D\}$
PP	D, AP	None, N	$(D, AP) \mid \{N\}$
PD	D, N	None, AP	$(D, N) \mid \{AP\}$

Table D.2 Model fit of three competing path models: *full passenger*, *partial passenger*, and *partial driver* models for *Alliaria petiolata*.

Models test the direct and indirect relationships between *Field-measured Disturbance* (D), native relative abundance (N_A), and cover-class abundance of a single exotic species *Alliaria petiolata* (AP_A) (Figure D.1). Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Shown is the Fisher's *C* statistic with the df and null probability (*p* – value) associated with each model in parentheses. Significant null probabilities ($p > 0.05$) are bolded.

Model ID	<i>C</i> (df, <i>p</i> – value)
FP	3.93 (2, 0.140)
PP	1.61 (2, 0.447)
PD	1.17 (2, 0.558)

Table D.3 Path coefficients (mean) with standard error, and standardised coefficients for direct causal links associated with the best fit models for *Alliaria petiolata* using *Field-measured Disturbance* (Figure D.1).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Significant paths are bolded ($p < 0.05$). Each tilde indicates the direction of the causal effect: where the variable after the tilde is the causal parent of the variable in front of it.

Model ID	Direct Causal Links	Mean (SE)	Standardised Mean	p – value
FP	Natives ~ <i>Field-measured Disturbance</i>	- 0.958 (1.45)	- 0.0393	0.511
	<i>Alliaria petiolata</i> ~ <i>Field-measured Disturbance</i>	0.194 (0.237)	0.0489	0.414
PP	Natives ~ <i>Field-measured Disturbance</i>	- 0.958 (1.45)	- 0.0393	0.511
	<i>Alliaria petiolata</i> ~ Natives	- 0.0147 (0.00970)	- 0.0901	0.131
PD	<i>Alliaria petiolata</i> ~ <i>Field-measured Disturbance</i>	0.194 (0.237)	0.0489	0.414
	Natives ~ <i>Alliaria petiolata</i>	- 0.554 (0.366)	- 0.0901	0.131

Table D.4 Decomposed effects of indirect causal links associated with the best fit models for *Alliaria petiolata* using *Field-measured Disturbance* (Figure D.1).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Indirect causal links are the effect of one variable on another as mediated by a third variable. Each tilde indicates the direction of the causal effect of one variable on another, mediated by a third: where the variable after the tilde is the causal parent of the variable in front of it (Appendix A).

Model ID	Indirect Causal Links	Decomposed Effects	Standardised Decomposed Effects
PP	<i>Alliaria petiolata</i> ~ <i>Field-measured Disturbance</i>	0.0141	0.00354
PD	Natives ~ <i>Field-measured Disturbance</i>	- 0.107	- 0.00441

Table D.5 A basis set with the implied *d* - separation statements for the full passenger, partial passenger, and partial driver models for *Circaea canadensis* and *Arisaema triphyllum*. Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Non-adjacent variables are the variables in each path diagram that do not have a direct effect between them. Parent variables are those that are causing the effect on another variable. D-separation statements describe the independence claims for the variables in each path diagram. The notation of the *d*-separation statements is as follows: the non-adjacent variables are listed in the round brackets; the pipe indicates the pair of variables are *d*-separated conditional on the following parent variable in the braces. Example: (x, y) | {z} can be read as: x and y are *d*-separated, conditional on z. Where E = exotic relative abundance, N = relative abundance of the native *Circaea canadensis* or the native *Arisaema triphyllum*, and D = *Field-measured Disturbance*.

Model ID	Non - adjacent variables	Parent variables of either non - adjacent variable	<i>d</i> - separation statement
FP	E, N	D, D	(E, N) {D}
PP	D, E	None, N	(D, E) {N}
PD	D, N	None, E	(D, N) {E}

Table D.6 Model fit of three competing path models: *full passenger, partial passenger, and partial driver models for *Circaea canadensis*.*

Models test the direct and indirect relationships between *Field-measured Disturbance* (D), exotic relative abundance (E_A), and cover-class abundance of a single disturbance associated native species - *Circaea canadensis* (CCA) (Figure D.2). Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Shown is the Fisher's *C* statistic with the df and null probability (*p* - value) associated with each model in parentheses. Significant null probabilities ($p > 0.05$) are bolded.

Model ID	<i>C</i> (df, <i>p</i> - value)
FP	3.78 (2, 0.151)
PP	2.55 (2, 0.280)
PD	3.69 (2, 0.158)

Table D.7 Path coefficients (mean) with standard error, and standardised coefficients for direct causal links associated with the best fit models for *Circaea canadensis* using *Field-measured Disturbance* (Figure D.4).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Direct causal links are the direct effect of one variable on another. Significant paths are bolded ($p < 0.05$). Each tilde indicates the direction of the causal effect: where the variable after the tilde is the causal parent of the variable in front of it.

Model ID	Direct Causal Links	Mean (SE)	Standardised Mean	p - value
FP	<i>Circaea canadensis</i> ~ <i>Field-measured Disturbance</i>	0.235 (0.154)	0.0906	0.129
	Exotics ~ <i>Field-measured Disturbance</i>	1.56 (1.285)	0.0725	0.225
PP	<i>Circaea canadensis</i> ~ <i>Field-measured Disturbance</i>	0.235 (0.154)	0.0906	0.129
	Exotics ~ <i>Circaea canadensis</i>	0.765 (0.496)	0.0919	0.124
PD	Exotics ~ <i>Field-measured Disturbance</i>	1.56 (1.29)	0.0725	0.225
	<i>Circaea canadensis</i> ~ Exotics	0.0110 (0.00710)	0.0919	0.124

Table D.8 Decomposed effects of indirect causal links associated with the best fit models for *Circaea canadensis* using *Field-measured Disturbance* (Figure D.2).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Indirect causal links are the effect of one variable on another as mediated by a third variable. Each tilde indicates the direction of the causal effect, mediated by a third: where the variable after the tilde is the causal parent of the variable in front of it (Appendix A).

Model ID	Indirect Causal links	Decomposed Effects	Decomposed Standardised Effects
PP	Exotics ~ <i>Field-measured Disturbance</i>	0.180	0.00833
PD	<i>Circaea canadensis</i> ~ <i>Field-measured Disturbance</i>	0.0172	0.00666

Table D.9 Model fit of three competing path models: *full passenger*, *partial passenger*, and *partial driver* models for *Arisaema triphyllum*.

Models test the direct and indirect relationships between *Field-measured Disturbance* (D), exotic relative abundance (E_A), and the cover-class abundance of a single non-disturbance associated native species - *Arisaema triphyllum* (AT_A) (Figure D.3). Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Direct causal links are the direct effect of one variable on another. Shown is the Fisher's C statistic with the df and null probability (p - value) associated with each model in parentheses. Significant null probabilities ($p > 0.05$) are bolded.

Model ID	C (df, p - value)
FP	22.2 (2, 1.54×10^{-5})
PP	4.71 (2, 0.0950)
PD	6.12 (2, 0.0469)

Table D.10 Path coefficients (mean) with standard error, and standardised coefficients for direct causal links associated with the best fit models for *Arisaema triphyllum* using *Field-measured Disturbance* (Figure D.3).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Direct causal links are the direct effect of one variable on another. Also shown are the *p* - values for each bivariate relationship; significant paths are bolded (*p* < 0.05). Direct causal links are the direct effect of one variable on another. Each tilde indicates the direction of the causal effect: where the variable after the tilde is the causal parent of the variable in front of it.

Model ID	Direct Causal Links	Mean (SE)	Standardised Mean	<i>p</i> - value
PP	<i>Arisaema triphyllum</i> ~ <i>Field-measured Disturbance</i>	0.319 (0.196)	0.0969	0.105
	Exotics ~ <i>Arisaema triphyllum</i>	- 1.61 (0.380)	- 0.246	< 0.001

Table D.11 Decomposed effects of indirect causal links associated with the best fit models for *Arisaema triphyllum* using *Field-measured Disturbance* (Figure D.3).

Model ID indicates the underlying model of invasive dominance, where FP = *Full Passenger*, PP = *Partial Passenger*, PD = *Partial Driver*. Direct causal links are the direct effect of one variable on another. Indirect causal links are the effect of one variable on another as mediated by a third variable. Each tilde indicates the direction of the causal effect, mediated by a third: where the variable after the tilde is the causal parent of the variable in front of it (Appendix A).

Model ID	Indirect Causal links	Decomposed Effects	Standardised Decomposed Effects
PP	Exotics ~ <i>Field-measured Disturbance</i>	- 0.514	- 0.0238

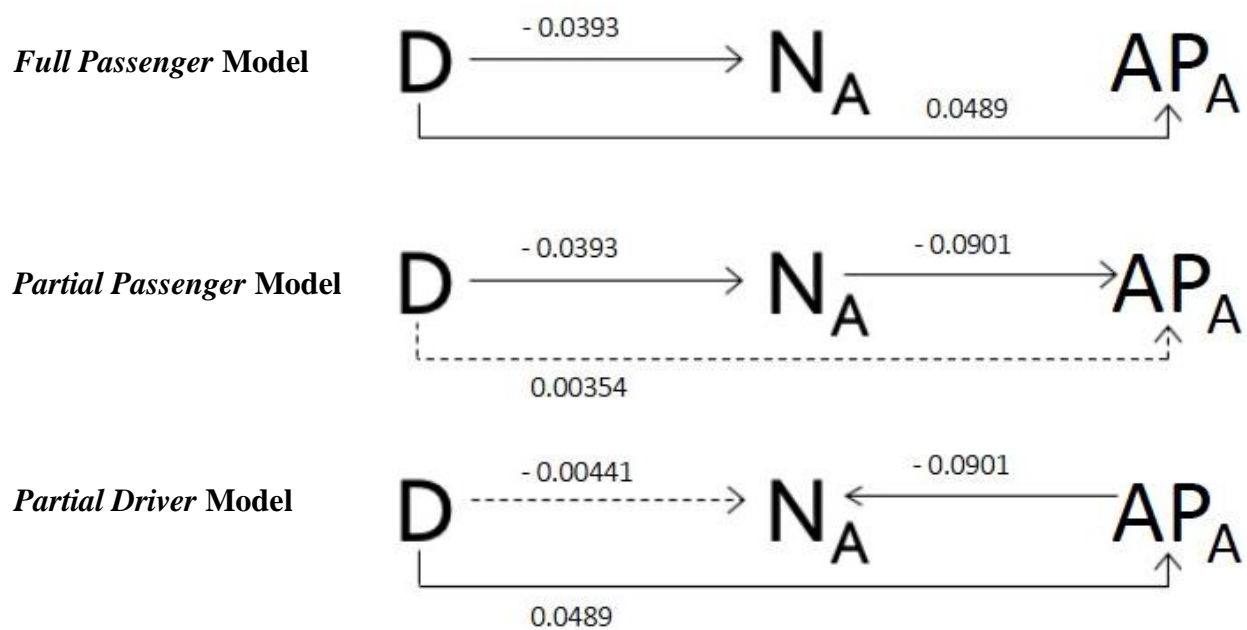


Figure D.1 The supported path models testing the direct and indirect relationships between *Field-measured Disturbance* (D), native relative abundance (NA), and cover-class abundance of a single exotic species *Alliaria petiolata* (APA).

Solid lines indicate direct causal paths and dashed lines indicate indirect paths as a result of the direct effects with the mediator variables. Path coefficients with an asterisk indicate significant casual paths ($p < 0.05$). Shown are the standardised path coefficients. Path coefficients for direct and indirect causal links with p - values are in Tables D.3 and D.4.

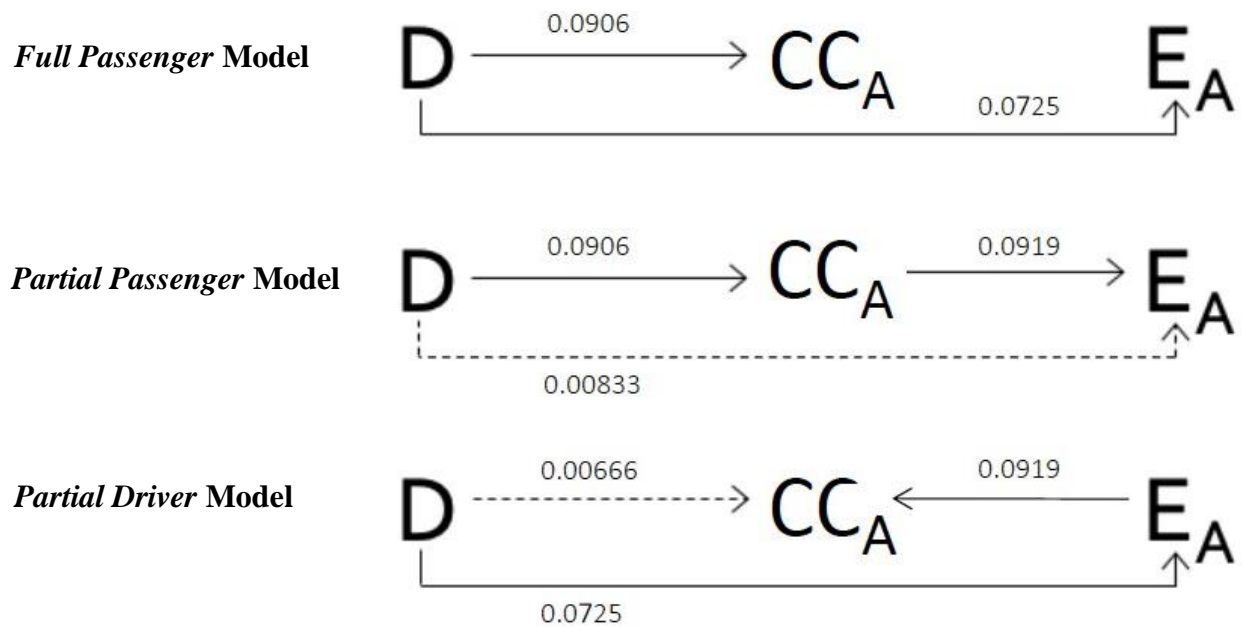


Figure D.2 The supported path models testing the direct and indirect relationships between *Field-measured Disturbance* (D), exotic relative abundance (EA), and the cover-class abundance of a single disturbance associated native species - *Circaea canadensis* (CCA). Solid lines indicate direct causal paths and dashed lines indicate indirect paths as a result of the direct effects with the mediator variables. Path coefficients with an asterisk indicate significant casual paths ($p < 0.05$). Shown are the standardised path coefficients. Path coefficients for direct and indirect causal links with p - values are in Tables D.7 and D.8.



Figure D.3 The supported path model testing the direct and indirect relationships between *Field-measured Disturbance* (**D**), exotic relative abundance (**E_A**), and the cover-class abundance of a single non-disturbance associated native species - *Arisaema triphyllum* (**AT_A**).

Solid lines indicate direct causal paths and dashed lines indicate indirect paths as a result of the direct effects with the mediator variables. Path coefficients with an asterisk indicate significant casual paths ($p < 0.05$). Shown are the standardised path coefficients. Path coefficients for direct and indirect causal links with p - values are in Tables D.10 and D.11.