**Introduction**

Invasive species negatively impact natural ecosystems and cause economic harm (Pimentel et al. 2000). Resource managers are tasked to mitigate these impacts, but are often constrained by the amount of money and person hours they can dedicate to invasive species management. This it is vital that management strategies are efficient and effective. Key to developing such strategies is having a fundamental understanding of the patterns and processes of range expansion of non-native invasive species (Sakai et al. 2001; Theoharides & Dukes 2007), which has been the focus of much research. One remaining gap in our knowledge of species invasions is a full understanding of the processes governing population dynamics during the transition from establishment of self-sustaining populations in a novel region to the rapid expansion in abundance and area of occupancy characteristic of invasive species. The period of time between population establishment and the beginning of rapid expansion is commonly referred to as the lag-phase (also referred to as lag-time, lag duration, or lag), and is considered a period when rates of population growth, both in numbers and in area, are relatively small (Kowarik 1995; Crooks & Soulé 1999; Sakai et al. 2001; Pysek & Hulme 2005; Theoharides & Dukes 2007).

In order to understand processes governing population dynamics during a lag-phase, it is first necessary to identify the lag-phase. Quantifying the lag-phase for a species has many challenges. Assuming a non-native species establishes in an environment suitable for growth and reproduction, and ignoring potential positive density dependence effects (i.e. Allee effects), population size should initially increase exponentially (Figure 1A). Exponential growth can be described as *N(t) = N(0) Rt*, where *t =*time-step, *N(t)* = the population size at time-step *t*, and *R* is the population growth rate. A visual examination of population size through time for an exponentially growing population, suggests that there is period of time early in the population growth trajectory during which the population size remains relatively similar to *N(0)* (Figure 1A *- R* = 1.2 for the black dots), and that this period is followed by a transition to one in which the population size rapidly increases. Crooks and Soulé (1999) describe this as “the shallow portion early in the growth curve when the population is growing relatively slowly in absolute number” and define this as the **inherent lag**. In fact, this pattern is common to all exponential growth curves, and thus all growing populations should appear to have at least an inherent lag-phase. However, because a mathematical definition of inherent lag is lacking, it is challenging to apply this term. In the case of exponential population growth, a plot of the *log* of population size versus time yields a linear relationship (Figure 1B – *R* = 1.2 for black dots). Thus, it is clear that the population growth rate is constant through time and there is no distinct transition point that can define the shift from the inherent lag-phase to the population explosion phase. Furthermore, the visual interpretation of the inherent lag-phase depends on the portion of the curve examined. The inset in Figure 1A shows the same curve (*R* = 1.2) from time points 1 to 20, demonstrating that what might be called an inherent lag-phase in this case is very different (shorter) than based on the population size trend over 40 time points.

While an inherent lag cannot be explicitly defined mathematically, it is a useful term when comparing a population growth curve to one that shows an **extended lag**. An extended lag phase in one in which population growth early in the growth curve is less than it is later. The grey dots in Figures 1A and B are growth curves for a population whose initial growth rate is *R* = 1 and increases to *R =* 1.2 during the first 20 time steps. As is the case for population growth with constant *R*, the growth curve of Population Size versus Time is non-linear (Figure 1A). However, in this case the growth curve of the *log* of population size versus Time is also non-linear during the time period when *R* is increasing. The non-linear portion of the curve, where the slope of the growth curve is more shallow and the curve is concave up, is considered evidence for an extended lag (Crooks & Soulé 1999). Patterns of population growth for many invasive species show evidence of an extended lag phase. The potential factors causing an extended lag phase are not well understood; several ecological and evolutionary processes may be involved (Mack et al. 2000; Sakai et al. 2001; Pysek & Hulme 2005; Gurevitch et al. 2011)). A brief extended lag may be explained by time constraints intrinsic to population growth and establishment, such as generation time and time to first reproduction (i.e., the time required for a population to achieve a stable age distribution). However, many observed lag-phases are longer than these processes may explain. In a recent study on lag-phase dynamics of weedy species in New Zealand, Aikio and colleagues (2010a) point out that “the potential biological and environmental mechanisms underlying the lag-phase have been the focus of considerable speculation but limited empirical support.” Historical biodiversity data from herbaria and museums could be applied to address this lack of empirical support and further our understanding of the population dynamics of the lag-phase. These data can be used to re-construct patterns of spatial spread of invasive species, which are linked to increases in population size.



Figure 1. Population size versus time relationship in a simple exponential population growth example. Black dots represent constant population growth rate *R* = 1.2. Grey dots represent an increasing growth rate for the first 20 time steps from *R* = 1.0 to *R* = 1.2, then constant *R* = 1.2 from time points 20 to 40. (A) Population size versus time. Inset plot is Population size (N) versus time (t) for *R* = 1.2 for only the first 20 time steps. (B) Log (Population size) versus time. For constant *R*, note the non-linear relationship in (A) versus the linear relationship in (B). This relationship is non-linear in both (A) and (B) for a population with an increasing growth rate (grey dots).

Retrospective spatial analyses can yield insights into the ecological processes involved in the spread of non-native invasive species in novel regions and a rich data source for these types of analyses is the specimen holdings of herbaria. Information from herbarium records are used in several studies that estimate species rates of spread through time and space in introduced regions (e.g., (Delisle et al. 2003; Salo 2005; Miller et al. 2009; Crawford & Hoagland 2009; Newbold 2010; Aikio et al. 2010a, 2010b; Lavoie 2012), as well as to investigate native species expansions beyond historical range limits due to changing ecological conditions (e.g., (Feeley et al. 2011; Feeley 2012). Despite their utility, analyzing these data presents a number of challenges and determining whether a species had an extended lag-phase using these data is not a trivial task. One substantial challenge is that herbarium records may have been collected with unequal sampling effort in time and/ or space, resulting in biases in datasets compiled from these records. For example, historically there are documented periods of high and low specimen collection for herbaria in general (Prather et al. 2004). There may also be herbarium specific trends, such as a peak in collection activity following the opening of a herbarium or an emphasis on regional specimen collection. Other biases may emerge because of issues of convenience. A noted pattern in natural history collections is the large number of specimens collected near museums, herbarium, botanical gardens, and academic centers, as well as urban areas in general, where there is generally a higher concentration of naturalists (i.e., the “botanist effect”; REF). These potential biases makes it difficult to determine if observed trends in herbarium collections (e.g., increased number of records through time) are indicative of changes in the population size or range size of the species of interest or representative of trends in overall specimen collection. For example, Catling and Porebski (1994) found that observations of the plant *Frangula alnus* were generally concentrated around urban areas from the time this species was first observed in southern Ontario, late 1800s, up to the 1970s. This pattern may be the result of the fact that botanists were located near these areas, and thus their collections tended to come from these areas, or it may be that *F. alnus* grows well in ecological conditions near urban areas (i.e. disturbed environments), or some other explanation. Finally, while exponential growth is widely accepted as a null model for local population growth, there are many plausible null models for areal growth (i.e., spatial spread) for range expanding species. One commonly used null model is a reaction-diffusion model, which results in a description of spatial growth as a function of the radius of the population. Thus, the area of occupancy for a species spreading randomly on a landscape from a central point should increase as a square

in area linearly if the area undergoes a square-root transform.

From Crooks and Soule – “the square root transformation typically linearlizes the time course of spread of an invasive species” and these results appear to be quite robust.

Given the promise of the utility of natural history collections in general (Graham et al. 2004; Anderson 2012), and herbaria in particular (Lavoie 2012), it is not surprising that the effects of unequal sampling effort have been discussed in many recent studies that use herbarium records. Common to many of the methods used to address unequal sampling effort is to compare the trends in the distribution of records for a species of interest to other species that have similar habitat requirements – i.e. associated species (Miller et al. 2009). Using this method Catling and Porebski (1994) compared the pattern of collection records of *F. alnus* to that of *Rhamnus alnifolia* and showed that botanists were in fact collecting specimens well outside of urban areas during the time frame of the introduction and early spread of *F. alnus*. They thus concluded that *F. alnus* was in fact primarily located near urban areas during this time. More recent developments in analysis methods make it possible to account for many potential biases in a more robust manner than a simple visual comparison (e.g. (Delisle et al. 2003; Aikio et al. 2010b), facilitating the use of herbarium records to reconstruct patterns of range expansion for both non-native and native plants (e.g., (Miller et al. 2009; Larkin 2011). At least one of these methods (i.e., (Aikio et al. 2010a) was specifically developed and applied to identify the existence, and estimate the duration, of lag phases for invasive plants. Adopting and modifying these methods, I address some of the unanswered questions regarding the introduction and spread of the non-native invasive plant *Frangula alnus* (Glossy buckthorn)*.*

*Frangula alnus* is purported to have had an extended lag phase (Catling & Porebski 1994; Frappier et al. 2003b), and various mechanisms have been proposed to explain this observation. Howell and Blackwell (1977) suggested that the rapid expansion of *F. alnus* into Ohio, following an extended period of presence in the eastern United States may be associated with the rapid expansion of the non-native European starling. Lending support to this idea, European starlings have recently been linked to the spread the non-native invasive plant *Celastrus orbiculatus* (Oriental bittersweet) (Merow et al. 2011), which is also a woody fruit bearing plant. However, Catling and Porebski (1994) pointed out that the spread of *F. alnus*  in southern Ontario preceded the presence of European starlings, suggesting other mechanisms must be at play. While Howell and Blackwell’s speculation concerns the spread of *F. alnus* throughout the state of Ohio (>110,000 km2), Frappier and colleagues (2003b) speculate on a mechanism causing an observed extended lag phase in the invasion of a 250m2 forest plot, suggesting that the lag may be due to “early selection and adaptation” to the local ecological conditions. Despite these speculations, it remains unclear as to whether *F. alnus* did in fact have an extended lag phase.

In this study, I examined the range expansion of *F. alnus* throughout its novel range of northeastern North American. I compiled a dataset of historical occurrence observations of *F. alnus* consisting primarily of herbarium records, but also including some observations noted in the scientific literature. Using this dataset I calculated metrics related to the rate of spatial expansion of *F. alnus* throughout northeast North America employing modified methods of (Delisle et al. 2003; Aikio et al. 2010a) to account for unequal sampling effort of herbarium records. I used the results from this analysis to examine whether *F. alnus* shows evidence for having an extended lag phase. These findings are an important foundation for further analyses carried out in Chapters 4 and 6, in which I use linked population and species distribution models to examine the population dynamics of the lag-phase. While I am aware of three studies that examined aspects of the range expansion of *F. alnus* (Howell & Blackwell 1977; Catling & Porebski 1994; Larkin 2011), all of these studies were geographically more restrictive than the study I preset. I know of no previous study that investigated the range expansion of *F. alnus* throughout its entire novel range.

**Methods**

*Collection of Presence Records*

I assembled a dataset of occurrence records for *F. alnus* to investigate its spread throughout northeast North America. I collected historical presence records by 1) searching publicly available on-line databases of several herbaria, 2) requesting *F. alnus* record information from curators and collection managers of various herbaria and, 3) searching the Global Biodiversity Information Facility (GBIF), and 4) carrying out a literature search for all North American localities, using the keyword search terms “Frangula alnus” or “Rhammus frangula” in ISI Web of Science database. I only included presence records with information on the year and location (county level or finer) of observation in my dataset.

Using publicly available on-line databases, I accessed herbarium records from 30 herbaria (Table 1). Many herbaria manage on-line databases that include records from affiliated, but separate, herbaria. For example, the Wisconsin State Herbarium is located at the University of Wisconsin at Madison. A search of the database for this herbarium yields accession records from this herbarium (WIS), as well as the University of Wisconsin at Stevens Point herbarium (UWSP), the University of Wisconsin at Green Bay herbarium (UWGB), and the Morton Herbarium (MOR). Therefore, while 30 herbaria are represented in my dataset, a smaller number of databases were used to acquire these records. I contacted curators and collections managers at several herbaria directly to inquire about whether there were records for *F. alnus* in their collections. Curators or collection managers at three herbaria, Rutgers Chrysler Herbarium, Miami University of Ohio Herbarium, and Carnegie Mellon Herbarium, provided me with the record information for all *F. alnus* or *R. frangula* in their collections. One herbarium, Cornell University Herbarium, informed me that they do have records for this species in their collection, but they did not have resources to collect the information from these records. Another herbarium, Illinois State Herbarium, could not find accessions associated with regions of the state otherwise not represented in my dataset. I did not include information on these accessions, though they were available through an online database interface, because of this lack of verification.

In addition to collecting records from herbarium databases, I collected records accessed searching the Global Biodiversity Information Facility (GBIF), the Canada Biodiversity Information Facility (CBIF), and the Invasive Plant Atlas of New England (IPANE). Records collected from all three of these biodiversity databases were carefully examined, as they also included records accessed in other searches. For example, IPANE includes nearly all of the records for *F. alnus* that I acquired by searching the University of Connecticut’s Herbarium database.

I searched for historical records of *F. alnus* presence reported in published journal articles using the ISI Web of Science database. I used keyword search terms of “Frangula alnus” and “Rhamnus frangula”. From this literature search, I included 5 presence records reported in (Howell & Blackwell 1977; Taft & Solecki 1990; Catling & Porebski 1994). Howell and Blackwell (1977) investigated the history of the spread of *F. alnus* into and throughout Ohio, and reported that the first recorded observation was from Lake County, Ohio in 1927 (confirmed via search of Ohio State University Herbariam). Taft and Solecki (1990) reported that *F. alnus* was first recorded in the state of Illinois in 1912 (Sherff 1912, as cited in Taft and Solecki 1990) in Cook County (confirmed via search of Field Museum Herbarium). Catling and Porebski (1994) investigated the spread of *F. alnus* into and throughout southern Ontario. I was able to use data reported in this paper on the three earliest records of *F. alnus* presence in this region. While this study includes several references to records of *F. alnus* collected in the region through time, as presented I was unable to make use of this information because the temporal resolution of the records is too coarse. Most of the herbarium records used in this study are located in herbaria that do not have easily accessible databases and my attempts to contact these authors to acquire information about these records have gone unanswered.

|  |  |  |  |
| --- | --- | --- | --- |
| Table 1. Historical presence record sources and counts | | | |
| Source | Herbarium Code | Record Count | Accession Method |
|  | A | 2 |  |
|  | ACAD | 8 |  |
|  | B | 1 |  |
|  | BKL | 35 |  |
|  | CHIC | 3 |  |
|  | CHRB | 10 |  |
|  | CM | 68 |  |
|  | CONN | 85 |  |
|  | F | 28 |  |
|  | GH | 5 |  |
|  | HAM | 7 |  |
|  | KANU | 3 |  |
|  | MAD | 1 |  |
|  | MASS | 22 |  |
|  | MO | 2 |  |
|  | MOR | 43 |  |
|  | MSC | 25 |  |
|  | MT | 22 |  |
|  | MU | 57 |  |
|  | NCBS | 3 |  |
|  | NEBC | 63 |  |
|  | NY | 5 |  |
|  | QK | 2 |  |
|  | RM | 2 |  |
|  | US | 3 |  |
|  | UWGB | 16 |  |
|  | UWSP | 6 |  |
|  | W | 2 |  |
|  | WIS | 85 |  |
|  | YU | 4 |  |
| Literature Search |  | 5 |  |

*Georeferencing of Historical Presence Records*

Most of the presence records in my compiled dataset did not have latitude and longitude values noting where the specimen was collected. However, many records had descriptive information, which I used to assign latitude and longitude values to the collection location. This process is commonly called georeferencing. I primarily used the GoogleEarth software (REF) to georeference records (*sensu* (Garcia-Milagros & Funk 2010), however some cases required additional Internet searches on named locations, such as unique building names or geographic features. The descriptive location information allowed for varying degrees of precision in the final latitude and longitude value assigned to a record. At a minimum, all records of specimens collected in the United States had enough information to be assigned to the county the specimen was collected in. For records with *only* county level information, I assigned the US Census Bureau designated latitude and longitude values to the record. For records of specimens collected in Canada, I relied on the information included with the specimen to assign county equivalent values. To achieve finer spatial resolution, some information allowed for assigning values for the township the specimen was collected in, where as others allowed for assigning precise locations. I assigned location uncertainty values using guidelines from the Biogeomancer Consortium (BioGeomancer Consortium 2006) to all of the records I georeferenced. I carried out analyses using different subsets of the compiled dataset based on the spatial resolution of the presence record (described further below).

*Number of Records Through Time*

Trends in the number of records added to an herbaria through time can be used to infer rates of spread for non-native invasive species and to determine if a species experienced an extended lag phase (Pysek & Prach 1993; Aikio et al. 2010a). I calculated the cumulative number of records reported per year in the dataset of compiled historical *F. alnus* presences and plotted the log of the cumulative number of records through time against years. I fit linear, quadratic, and cubic regression lines to these data, and used the likelihood ratio to determine which model was the best fit. Using the cumulative records through time data, I calculated an annual rate of growth for the cumulative number of presence records by dividing the cumulative number of records at year *t+1* by the cumulative number of records at year *t*. The mean rate of growth was calculated as the geometric mean of the annual growth rates. Additionally, I calculated 10-year moving window geometric mean growth rates, which minimizes the influence of extreme inter-annual fluctuations in growth rates. This likely yields more accurate rates for the earliest period of the invasion, during which time calculations are made using a relatively small number of records.

*Area of Occupancy Through Time*

I examined the spatial pattern and rate of range expansion of *F. alnus* throughout its novel range using the dataset of compiled historical *F. alnus* observations described above. To do this I created a map of equal sized grid cells for the area of interest (Longitude: -97.0 – -62.0 degrees; Latitude: 38.0 – 48.0 degrees) using the Quantum GIS software (REF). Each grid cell was 5 x 5 arc minutes, which is generally reported as 10 x 10 km. Because a unit of longitude is smaller at higher latitudes than at lower latitudes, the area of each grid cell decreases towards the poles. The area for each grid cell ranges from ca. 67 km2 to ca. 57 km2. While acknowledging this difference, I am assuming it does not have a substantial affect on my analysis. For the remainder of this analysis I used the R statistical programing environment (REF) with additionally functions from the ‘rgdal’, ‘raster’, and ‘dismo’ packages (REFS). Each record in the compiled dataset was assigned membership to one grid cell based on its latitude and longitude value. If a grid cell contained at least one occurrence of *F. alnus*, it was considered occupied. I calculated multiple occupancy measures, including total area occupied per decade and the cumulative area occupied from time of first introduction to the present. In calculating the latter measure, I assumed that once a grid cell was classified as occupied, it would not later be classified as unoccupied. Similar measures have been used in other studies investigating the spread of invasive species (Pyšek & Prach 1995; Weber 1998; Delisle et al. 2003) (REFS – there’s at least two more to go here). Further, given the difficulty of removing *F. alnus* and the lack of reported successful eradications, this is a reasonable assumption (REFS). I calculated the rate of growth for the area of occurrence analogously to how I calculated the rate of growth of the number of records (see *Number of Records Through Time*). In these calculations, the cumulative number of records was substituted with the cumulative number of occupied gird cells and the square root of the cumulative number of grid cells versus time (years) was plotted. Assuming areal growth is a random diffusion process, this relationship should be linear. A deviation from linearity that is concave up indicates a period of time earlier in the history of the species presence during which spatial spread is slower than random diffusion. Likewise, a concave down curve indicates a period of time earlier in the history of the species presence during which spatial spread is more rapid than random diffusion.

*Occupied Counties Through Time*

Many records contained only enough spatial information to georeference the collection location to the county in which it occurred. Furthermore, georeferencing records to county requires substantially less time and effort than higher levels of precision. Thus, analyzing spatial patterns of herbarium records at the county level makes the compilation and use of large datasets more achievable given limited time and resources, while still providing insights into the patterns and processes of species invasions (e.g., (Barney 2006). Similar to the calculations of *Area of Occupancy Through Time*, I calculated the cumulative number of counties occupied through time for the compiled dataset. Again, I assumed that once *F. alnus* was found in a county, the county was henceforth considered occupied. I calculated the growth rate for the cumulative number of counties occupied in a manner similar to how I calculated the rate of growth of the number of records (see *Number of Records Through Time*).

*Accounting for Unequal Sampling Effort in Time and Space*

The potential effects of unequal sampling effort complicate the interpretation of observed patterns in historical presence locations. One method for addressing these effects is to compare trends in records of a species of interest to trends for a species, or group of species, whose range and population size should be in equilibrium with their environment (e.g., native species) (Delisle et al. 2003). In this study, the species of interest is *F. alnus*. I have chosen the following group of associated native species, each of which has similar habitat requirements as *F. alnus*:

* Speckled Alder - *Alnus incana*
* Smooth Alder - *Alnus serrulata*
* Alderleaf Buckthorn - *Rhamnus alnifolia*
* Meadow Willow - *Salix peiolaris*
* Witch Hazel - *Hamamelis virginica* (syn. *macrophylla*)
* White Ash - *Fraxinus americana*

These species represent woody plants that are likely to be observed in ecological conditions where *F. alnus* is observed. As noted above, Catling and Porebski (1994) compared the distribution of record collections for Alderleaf Buckthorn to that of *F. alnus* as a comparison. Similarly, Meadow Willow was used in a paired comparison with *F. alnus* in a study on the effects of invasive and native species on wetland species diversity (Houlahan & Findlay 2004). The other species in this group are found in ecological conditions conducive to the growth of *F. alnus* (personal observations **and reference various tree guides**). To construct the associated species dataset I searched GBIF for all records that were located within the area of interest described in *Area of Occupancy Through Time*. Additionally, I collected all records for these species reported in the following herbaria databases: University of Wisconsin, Ohio State University, University of Minnesota, the Morton Arboretum Herbarium, Michigan State University, and Brooklyn Botanical Gardens. These records were georeferenced to the county level. Grouping these records from all of these species into one dataset, I calculated the metrics for the number of records through time, the area of occupancy through time, and the number of counties occupied through time, as described above.

I compared the trends for *F. alnus* and the group of associated species for both area of occupancy through time and counties occupied through time in a similar manner to (Delisle et al. 2003). Delisle and colleagues (2003) similarly used herbarium records to investigate the spread of six non-native species in Quebec, Canada. They compared trends in area of occupancy through time by dividing the cumulative number of occupied 10x10 km grid cells for each non-native plant by the cumulative number of cells occupied by a group of five native species, yielding a proportion of non-native to native occupied cells for each year of their study period. It is important to note that a major assumption in the interpretation of this analysis is that spatial growth of native plants in the herbaria dataset does not represent the spread for these plants, but rather represents the increase in spatial coverage of herbaria records in general (i.e., an increase in the number of locations where samples are collected). Thus, if the proportion of occupied cells between non-native and native plants is increasing through time, this represents periods during which the spatial coverage of records for the non-native plant outpaces the background increase in spatial coverage. This can be interpreted as the result of the non-native plant rapidly spreading in space. In this chapter I have employed a modification of this method to account for unequal sampling effort of *F. alnus.*

Several presence records for the group of associated species were located in areas where *F. alnus* has not been observed, most likely due to the larger niche breadth of some of the associated species compared to *F. alnus* (as suggested by examining the Biota of North America Program – North American Plant Atlas (REF) and should be confirmed by analysis in Chapter 4), for example *Fraxinus Americana* (White Ash). Including these records in my analysis has the effect of increasing the area of occupancy measures for the group of associated species compared to the possible area of occupancy for *F. alnus*. Similarly, the historical presence record dataset I manually constructed includes records of *F. alnus* from institutions from which associated species records were not collected (e.g., Miami University Herbarium and Rutgers Herbarium). The records acquired from these institutions are largely geographical restricted (for example, primarily located in the states of Ohio and New Jersey for the institutions mentioned), and these locations were not always represented well in the larger group of associated species dataset. Therefore, including these records has the effect of increasing the area of occupancy of *F. alnus* compared to the possible area of occupancy for the group of associated species. To account for both of these issues, I examined the ratio of cumulative area of occupancy of *F. alnus* and the associated group of species, limiting the records used to an area of coarse spatial overlap for both datasets. I defined the spatial overlap by creating a map of equal sized grid cells, again for the area of interest defined above, where each grid cell was 30 x 30 arc minutes (i.e., 0.5° or approximately 50 km). As described in *Area of Occupancy Through Time*, each record was assigned membership to one 30’ grid cell based on its latitude and longitude value. I then constructed restricted *F. alnus* and associated species occurrence datasets, in which only records that occurred in a 30’ grid cell occupied by at least one record from *both* datasets during the study period. Using these restricted datasets, I calculated the ratio of the increase in the cumulative area of occupancy between *F. alnus* and the group of associated species.

To compare the cumulative number of counties occupied through time, while accounting for similar concerns regarding falsely sampling regions in space that are unsuitable to *F. alnus*, I only included records from counties that were occupied at some time by both *F. alnus* and one of the associated plants. Doing this, the ratio of the cumulative number of counties occupied at the end of the study period has to be equal to one.

The growth rates for the cumulative number of grid cells occupied and the cumulative number of counties occupied were compared between *F. alnus* and the group of associated species. To compare the growth rates I divided the annual growth rate of *F. alnus* records by the annual growth rate of the entire group of associated species.

*Comparison of Number of Records through time*

In addition to comparing trends in the areal increase of *F. alnus* and the associated species, I also compared trends in the cumulative number of records through time. For each year of the study period I divided the cumulative number of *F. alnus* records by the cumulative number of associated species records. This correction method is similar to that proposed by (Delisle et al. 2003) and has been used in several studies to account of unequal sampling effort (e.g., (Mihulka & Pyšek 2001; Aikio et al. 2010a; Larkin 2011). As part of this comparison I compared the growth rate of the cumulative records through time for *F. alnus* and the group of associated species as I described above.

For both *F. alnus* and the group of associated species I calculated the proportional increase in the cumulative number of records for each year, by dividing the cumulative number of records for each year by the total number of records collected over the full study period. The proportional increase curves allow for direct comparison of the rates of increase in the number of records through time in the datasets. Assuming that *F. alnus* and the associated species are sampled with equal intensity in time, dividing the proportional increase of *F. alnus* by the increase for the associate species yields a value that may be interpreted as the relative percentage of *F. alnus* availability on the landscape compared to the associated species.

**Results**

I compiled a dataset of 749 occurrence records for *F. alnus* and 5548 occurrence records for the combined group of associated species. *Frangula alnus* specimens have been collected in much of northeast North America (Figure \_\_A\_\_), and collection locations for the group of associated species was largely inclusive of where *F. alnus* was collected. The earliest dated occurrence record for *F. alnus* was an herbarium specimen collected in 1879 in Hudson County, New Jersey (accessed from CHRB). The earliest dated occurrence record for an associated species was an herbarium record for *Hamamelis virginiana* collected in 1836 in Richland County, Ohio (accessed from CM). Only 36 associated species records pre-dated the first *F. alnus* record, representing less than 1% of the associated records. A total of 14 *F. alnus* specimens were deposited in 4 separate herbaria prior to 1900. Of these records, 12 were georeferenced to the metropolitan New York City area (many in the state of New Jersey) and the remaining 2 were collected in southern Ontario (as reported in (Catling & Porebski 1994).



Figure 2. \_\_A\_\_: Geographic locations of collected records for *F. alnus* and a group of associated species. Red points represent records from the compiled historical presence records for *F. alnus* and green points represent records from the compiled historical presence records for the group of associated species. Some locations were assigned geographic locations based on the latitude and longitude values of counties as defined by the US Census Bureau. Red outlined box delineates the study region

Based on recorded specimen collection dates, the number of herbarium specimens collected for both *F. alnus* and the group of associated species has increased through time (Figure \_\_B\_\_). For the group of associated species, there was a substantial increase in the number of records collected at the beginning of the 20th century, followed by another increase post 1950. There was a steady increase in the number of records collected per decade from the time of the first recorded presence of *F. alnus* in the United States to the end of the 20th century. For both groups, there was a dramatic decline in the number of records at the start of 21st century, which is a pattern that has been observed elsewhere as well (Prather et al. 2004).



Figure 3. \_\_B\_\_ Total number of records collected in each decade for *F. alnus* (grey bars) and the combined group of associated species (black bars).

The log cumulative number of records through time indicates that the rate at which records were added to herbaria for both *F. alnus* and the group of associated species does not fit an exponential growth relationship (i.e., a linear relationship) (Figure \_\_C\_\_ (A)). The best-fit regression models of log cumulative number of records versus time (years) were a cubic polynomial regression for *F. alnus* (R2 = 0.989, df = 124, P << 0.05) and a quadratic polynomial regression for the group of associated species (R2 =0.979, df = 174, P<<0.05 respectively), both indicating a departure from linearity. The cumulative number of records for the group of associated species increased steadily from the late 1800s to the present. The cumulative number of records for *F. alnus* increased rapidly from the late 1800s to approximately 1930. The ratio of the proportional cumulative increase in records between *F. alnus* and associates species indicates that *F. alnus* increased approximately log-linearly from 1920 to the present (Figure \_\_C\_\_ (C)). These findings are also supported by the ratios of the annual growth rates and ten year moving average (geometric mean) growth rates (Figure \_\_C\_\_ (B)), which show that the rate at which *F. alnus* collections occurred was generally slower than that of the group of associated species prior to approximately 1920, but faster during most of the 20th century.



Figure 4 \_\_C\_\_ (A) Log cumulative number of records through time. Linear (solid) and cubic polynomial (dot-dash) regression predictions are plotted over the cumulative increase curves. (B) Annual and 10 year moving window average (geometric mean) growth rates of herbarium records. (C) Ratio of the cumulative number of records of *F. alnus* versus associated species.

The cumulative number of occupied 5 arc min grid cells for *F. alnus* and the associated species, constrained to overlap within 30 arc min grid cells, increased through time for both datasets (Figure \_\_D\_\_). The rate of increase is slow for both *F. alnus* and the group of associated species until 1890, after which the number of occupied cells rapidly increases for the group of associated species. In contrast, the number of occupied cells continues to increase slowly for *F. alnus* until approximately 1920, as is demonstrated by the calculated difference between the two growth rates (Figure \_\_D\_\_(B)).

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Figure 5 \_\_D\_\_ (A) Square root of the cumulative number of grid cells through time. Shown here are the linear and polynomial regression lines for a models using year as a predictor variable and the square root of the cumulative number of grid cells occupied as the response variable. Linear regression predictions are shown for both *F. alnus* and the group of associated species. The best-fit polynomial regression fit is shown for each set (quadratic for *F. alnus* and cubic for the group of associated species) (B) Ratio of Growth Rates of Cumulative Occupied Grid Cells. Note that some extreme data points are not shown (those >1.2 or <0.8, but contribute to the moving window average values. (C) Ratio of square root of the 5 arc min grid cells occupied by *F. alnus* and associated species at a given time step. Occupied 5 arc min grid cells were constrained such that they were within 30 arc min grid cells containing members of both groups at least once during the study period.

A plot of the square root of cumulative occupied grid cells versus time supports a departure from a simple diffusion model of spatial spread in historical presence records (Figure \_\_D\_\_(A)). If a random diffusion process governed the spatial spread of herbaria record locations, a linear regression would be the best-fit model of the square-root of cumulative records versus time (Crooks & Soulé 1999). In contrast, the best-fit regression models of the square-root of the cumulative number of grid cells occupied, with year as the predictor variable, were a quadratic polynomial regression for *F. alnus* (R2 = 0.996, P << 0.05) and a cubic polynomial regression for the group of associated species (R2 = 0.990, P << 0.05), both indicating a departure from linearity.

The ratio between the cumulative number of grid cells of *F. alnus* and associated species shows that the rate at which *F. alnus* increased in area of occurrence is greater than the rate of increase in the area of occurrence for the group of associated species (Figure \_\_D\_\_(C)). After approximately 1910, *F. alnus* increased in area of occupancy at a rate greater than the associated species.Both the ratio of annual rate of growth and the 10 year moving window average (geometric mean) rate of growth of the cumulative number of occupied grid cells between *F. alnus* and the group of associated species indicates that prior to 1915, with exception of the earliest years of the *F. alnus* invasion, the rate at which new grid cells were considered occupied by ­*F. alnus* was lower than the corresponding rate for the group of associated species (Figure \_\_D\_\_(B)). From 1915 to the present, the rate at which grid cells are considered occupied by *F. alnus* was consistently higher than the corresponding rate of growth for the associated species.



Figure 6 \_\_E\_\_ (A) Square root of the cumulative number of counties through time. (B) Ratio of the rate of growth for cumulative occupied counties. (C) Square root of the ratio of the cumulative number of counties occupied by *F. alnus* versus the group of associated species.

The results for the analysis of the cumulative number of counties occupied were similar to the results of the analysis of the cumulative number of occupied grid cells. As noted in *Occupied Counties Through Time*, the compiled records dataset for both *F. alnus* and the associated species was subset to include records from counties that were occupied by both during the study period. The number of counties where herbarium samples were collected increased very rapidly during the late 19th to early 20th century, as indicated by rapid increase in the cumulative occupied counties for the associated species. The number of counties where *F. alnus* was found increased very slowly during the early part of the 20th century, but rapidly after 1940 (Figure \_\_E\_\_(A)). Assuming counties were selected as locations for herbarium specimen collections at random, the relationship between the square root of the cumulative number of occupied counties and time (years) should be linear for the associated species. However, this is not the relationship for either the associated species or *F. alnus* (Figure \_\_E\_\_(A)). To-do: Fit regressions and show that linear regression is not best fit.

The ratio of occupied counties between *F. alnus* and the associated species indicates that early in the invasion history, *F. alnus* was less frequently collected in newly sampled counties, but that for most of the 20th century the number of counties occupied by *F. alnus* has increased more rapidly than the number of counties occupied by associated species (Figure \_\_E\_\_(C)).

The difference in the rate of growth of cumulative occupied counties between *F. alnus*­ and the associated species shows a similar pattern to that reported for cumulative occupied grid cells (Figure \_\_E\_\_(B)). The rate at which counties are considered occupied is slower for *F. alnus* than the associated species early in the invasion history (prior to 1900) and faster during most of the 20th century (Figure \_\_E\_\_(B)).

Based on my compiled datasets, specimens were collected from previously unsampled counties for one of the associated species on average greater than 48 years prior to a the collection of a sample of *F. alnus*. While the distribution of years between sampling of an associated species and *F. alnus* is quite wide (Figure \_\_N\_\_), the first year one of the associated species was collected in a county is significantly earlier than the first year *F. alnus* was sampled in that county (Paired t-test, t = -15.57, df = 196, P << 0.05).



Figure 11 \_\_N\_\_ Frequency of the number of years between an observation of one of the associated species in a county and the observation of *F. alnus* in that county.

**Discussion**

The question of *how* *F. alnus* was introduced remains unanswered. Given its established use as both a medicinal plant (REFS) and as an ornamental (as suggested by the fact that *F. alnus* was planted in the U.S. Department of Agriculture arboretum as early as 1891, as well as discussion in (Sherff 1912)), it is likely that this species was purposely planted. In fact, low fertility cultivars of *F. alnus* are still available for purchase today (Jacquart & Knight 2010). A thorough investigation of seed catalogs and nursery records from the late 19th century may shed further light on this mystery, but was beyond the scope of this project. As is the case with many non-native species that naturalize in novel regions, there is little documented knowledge of the time or place that *F. alnus* was first introduced. While most literature related to *F. alnus* claims that it was likely first introduced during the mid-19th century, at least one source suggests it was introduced prior to 1800 (Converse 1984). The location of first introduction has been reported as “the eastern states” by (Howell & Blackwell 1977) and as Canada by (Frappier et al. 2003a). My findings suggest that a likely location of first introduction was the metropolitan New York City area, particularly in nearby areas of New Jersey. Specimens for 12 of 14 records in my dataset dating from before 1900 were collected in this region. Furthermore, based on reported years of specimen collection, *F. alnus* was present in this area more than a decade before it was first reported in southern Ontario, countering the claim of Canada as being the location of first introduction. However, locations in southern Ontario account for the remaining 2 of 14 records dating before 1900, indicating that introduction into the region was likely early during the spread of *F. alnus*. It is interesting to note that the region in which I found the first recorded observation was a large shipping and port area, raising the possibility that shipping played a role in an accidental introduction of this species. Many non-native plants have been introduced to port areas by the unloading of solid ballast (Barney 2006) (REF – Look in Rhodoria). However, this region also had a high population density, thus there may have been more people who purposely planted *F. alnus*.

Three previous studies have examined aspects of the range expansion of *Frangula alnus* using herbarium records as their primary data source (Howell & Blackwell 1977; Catling & Porebski 1994; Larkin 2011). All of these studies were geographically restricted in the range examined. Howell & Blackwell (1977) examined the spread of *F. alnus* (using the synonym *Rhamnus frangula*) into, and throughout, Ohio and found evidence that it likely first entered Ohio in the 1920’s, being observed first in Lake County (northeastern Ohio). The authors speculate that the spread of *F. alnus* westward through Ohio was facilitated by the range-expanding non-native bird the European Starling. Many bird species are noted to eat the fruit of *F. alnus* and defecate undigested seeds, and European Starlings in particular have been noted as eating these fruit (Ridley 1930 as cited in (Howell & Blackwell 1977)). These authors did not account for potential unequal sampling effort in herbarium records, but rather simply reported when and where *F. alnus* first appeared in Ohio. Catling & Porebski (1994) examined the historical spread of *F. alnus* in southern Ontario, Canada (also using the synonym *R. frangula*) and found that *F. alnus* was first recorded in London, Ontario in 1898 and Ottawa in 1899. Their data show *F. alnus* spread to other urban centers, but primarily remained confined to urban areas until the 1970’s. From the 1970’s to the early 1990’s (the time the study was published) *F. alnus* appeared to spread into natural areas outside of urban areas at an increased rate of spread compared to the rate of spread during the previous 70 years. The authors suggest that this observation may be indicative of a lag period in the spread of *F. alnus*. To address potential biases resulting from unequal sampling efforts, specifically for records collected prior to 1930, the authors visually compared the spatial distribution of the *F. alnus* records with that of native *Rhamnus alnifolia*, a species with similar habitat requirements. More recently, Larkin (2011) examined the lengths of lag phases for multiple (>200) species of non-native invasive species in the Wisconsin and the southern Lake Michigan region. In his analysis, Larkin applied the methods of (Aikio et al. 2010a). In the regional context of this study, the earliest record *F. alnus* was from 1941 and based on his analysis, was found to have had a 15-year lag phase.

Compared to previous work, my study examines the spread of *F. alnus* over a larger spatial area. The area of interest (described in *Area of Occupancy Through Time*) includes all collected observations of *F. alnus*, both historical and contemporary presences, with the exception of less than four presences located in Tennessee and Wyoming.

Additionally, the datasets I have compiled include many more sources than previous studies. Including these additional data in previous studies would have an effect on their results.

~~For example, using data from WisFlora and vPlants (two databases associated with WIS and CHIC, respectively) Larkin (2011) found that the earliest record of ­~~*~~F. alnus~~* ~~in the southern Lake Michigan region was 1941 and estimated that the species had a 15 year lag-phase, culminating in 1956. In my compiled dataset, the first record in this region is from 1912, which would expand the estimated lag-phase by 29 years, making the total lag-phase 44 years.~~

The results of Larking, in which there are different ‘Earliest records’, ‘Lag length’, and ‘Inflection years’ among the three regions studied indicates that invasion dynamics are very much governed by local processes.

**Make this point else where – perhaps in the caveats.** This raises the interesting point that in studies using herbarium data, limiting the data used to particular sources (i.e., particular herbaria or collections within herbaria) can result in misleading calculations of the real ecological processes going on in space.

Maximizing the use of historical biodiversity collections presents many challenges that the current study is certainly not immune to. First, unequal sampling effort is pervasive in most historical biodiversity collections (Reddy & Dávalos 2003) (ADD REFS). For herbaria in particular, there are many reasons for unequal sampling effort in specimen collection, some of which have been discussed above (i.e. the ‘botanist effect’). Other causes of unequal sampling effort include herbaria specific emphasis on regional collections or the targeting of specific taxonomic groups or places for collection. An example of the former is the Oberlin Herbarium collection (housed in the Ohio State Herbarium), which includes several thousand records primarily collected from within the state of Ohio. There are numerous examples of the latter, including several collections of orchids, bryophytes, mosses, and ferns, which seem to be groups of particular interest to plant collectors. While I cannot prevent these sorts of biases from being present in my compiled dataset, calculating the ratios of the cumulative number of grid cells and counties occupied for *F. alnus* and the associated species should correct for these biases. One potentiality that would not be corrected for in this case is if invasive species, including *F. alnus*, are sampled more intensely than native species for some time during the study period. This could have the effect of making the rate of *F. alnus* areal growth appear greater than it actually was. However, since I calculated these ratios using the *cumulative* number of occurrences (or counties), I expect that these effects would be most influential during early part of the study period. During this time, an intensive collection of non-native species may result in grid cells (or counties) being classified as occupied earlier than the associated species expected to already be present in these areas. It is unlikely that such surveys were undertaken during the early part of the study period, thus I believe my results are robust to these concerns. Assuming that the cumulative number of occupied grid cells or counties is representative of the area of extent is likely a valid assumption. With one notable exception (Cunard & Lee 2008), there are no documented examples of successful buckthorn eradication from an area the size of a 5x5 arc min grid cell, or a county. This supports the notion that once a location is occupied, it remains so. On the other hand, I am certain that some locations of historical *F. alnus* occurrences no longer have the species present because of changes in land-use (e.g., development of once woodland plots). This is the case for many of the records observed in the metropolitan New York region, the site of many of the earliest records. Disturbances, or removal of population from the landscape, due to anthropogenic influences may have a substantial effect on the spread of buckthorn throughout its novel region. However, *F. alnus* can be successful in very small, isolated, and disturbed plots within a urban or suburban land-use matrix (personal observation and (Del Tredici 2010).

A second challenge is that most herbaria do not have electronic databases of their holdings that are easily accessed by the public (i.e., a web-base search interface) and many do not have a complete electronic database of records within the institution (personal observation and (Lavoie 2012). There are several herbaria records that were not included in my compiled dataset because of lack of ease of acquisition. Nevertheless, given the extent of my data compilation in space and across institutions, I’m confident that the patterns and trends reported are accurate in general. I was able to collect records from some herbaria by directly contacting curators and collection managers. Many collection managers were happy to provide me with record information for *Frangula alnus*, in part because there were generally a small number of records, and some were able to provide me with information from records of the group of associated species. However, because of the large request entailed in collecting records for the associated species I was not able to collect these records from some herbaria. This is particularly problematic because I focused my direct contact efforts on herbaria that I either new *F. alnus* records were stored in (e.g. Miami University Herbarium) or herbaria in regions that I thought were lacking in records collected by other means (e.g. Cornell University to cover western New York state). In the case of the latter, I was unable to collect any record from this source. These collection issues mean that my analysis underestimates the amount of area occupied by *F. alnus*. Further collections may increase the accuracy of my results.

**Matt and Resit – I think this is a possible area I can put some more thought into. Yes, more sampling is certainly going to make my results more accurate, but I wonder if there is a way to test how robust my results are? Perhaps I could sample from other records collected, or perhaps I could sample from a distribution model result? The latter may be akin to a bootstrap process.**

Despite concern regarding the extent to which my compiled datasets approximate a complete representation of the area occupied by *F. alnus*, my results clearly support a rapid rate of spread for this species throughout its invasion history. Calculating the ratio of the cumulative number of grid cells and counties occupied between *F. alnus* and the group of associated species I was able identify time-periods associated with the expansion of *F. alnus* while accounting for potential unequal spatial and temporal sampling bias in occurrence record collection (Delisle et al. 2003). Based on these calculations, it seems likely that *F. alnus* has been expanding rapidly throughout its invaded range since the mid to late 1920s. A key assumption for this correction method is that the members of the group of associated species are in equilibrium with their environment. That is, these plants have a stable range distribution and have previously spread to all of the ecological conditions within the study range that they can survive and reproduce. There are some caveats to this assumption to consider, perhaps the most important being that the ecological conditions in my study region have certainly not been stable over the last 130 years. There have been substantial changes in land-use, no doubt resulting in changes to plant communities. However, given that the species chosen for the group of associated species have similar ecological requirements as *F. alnus*, I expect that any such changes would affect trends in these species and *F. alnus* equally. Thus, I am confident that these ratios are not strongly affected by such changes.

Provided the equilibrium assumption for the associated species is true, then the rate of the cumulative number of grid cells or counties occupied is not representative of the spread of these plants, but rather indicative of the spatial spread of the effort of herbarium specimen collectors. Therefore, if the cumulative number of grid cells (and counties) occupied by the associated species were appropriately represented by a random diffusion process (i.e., linear when taking the square root of the cumulative number of grid cells versus time), this would imply that specimen collectors moved randomly outward from a central point, perhaps an herbarium, collecting new records as they went. Neither the square root of the cumulative number of grid cells or counties fit such a relationship (Figures 8 and 12). However, it may be that piecewise linear regression would fit these curves, implying that early during the study period specimen collecting did spread out randomly on the landscape, but very rapidly, and later the accumulation of specimens from new areas continued to follow a random diffusion relationship, but with a much slower rate of spread. Combined with the dramatic increase in the cumulative number of records during earlier part of the study period (Figure 3), these patterns suggest that this was a period of high sampling effort, which coincides with beginning of an intense effort to collect specimens for herbaria (Prather et al. 2004).

The earliest occurrence records of *F. alnus* in the study region were collected during this period of high sampling effort, making it clear that this species was present in the novel range from what could be considered the beginning of intensive sampling effort for herbaria in areas with ecological conditions conducive to its growth. Nevertheless, ­*F. alnus* was uncommon across the study region at this time, and appears to remain uncommon until at least the 1920s. Assuming that cumulative occurrence curves for the associated species do in fact represent the spatial spread of collection effort, and that a collector would collect *F. alnus* if it were present during a survey, I can put into perspective these findings. This period appears to be a lag-phase for *F. alnus*, which is supported by the predicted periods of expansion resulting from the ratios of cumulative number of occupied grid cells and counties discussed above that follow it. Additionally, the calculated ratios of growth rates for the cumulative number of records, occupied grid cells, and occupied counties all show that the growth rate of *F. alnus* was smaller than that of the associated species before the 1920s and greater after (Figures 4, 10, and 14). Accepting this period as a lag-phase, the question remains as to whether it is a inherent or extended lag-phase (Crooks & Soulé 1999). If the number of herbarium records collected for a species is related to the population size of that species, then after correcting for the background rate of sampling and unequal effort, an extended-lag phase would show a non-linear relationship in the log-tranformed ratio of the cumulative number of records for *F. alnus* and the associated species. This appears to be the case for *F. alnus* early in its invasion history (Figure 6). If the start of the invasion of *F. alnus* were considered 1920, then the results would indicate that there was only an inherent lag-phase. However, given the pattern from 1879 to the 1920s, dominated by high fluctuations of the log of the ratio value, there is not a simple linear relationship over its complete invasion history.

The high fluctuations of ratio values for all comparisons presented above may be the result of the relatively small number of cumulative records for both *F. alnus* and the associated species during this time (shown by the size of the points in Figures 9 and 13). In this situation, the addition of a small number of records to either dataset can drastically change the ratio between them. The accumulation of *F. alnus* occurrences had a particularly large effect early in its invasion history, as is indicated by the ratio of growth rates, in which generally *F. alnus* records increase more slowly than the associated species from 1879 to the 1920s, but there are anomalous years in which the growth rate of *F. alnus* is much larger than that of the associated species (Figures 4 and 10). This is caused for example when the cumulative number of records for *F. alnus* goes from 4 to 10 from 1893 to 1894, resulting in a growth rate of R = 2.5. Comparatively, during this time the number of records for the associated species goes from 171 to 191, resulting in a growth rate of R = 1.12. It is difficult to determine if *F. alnus* did in fact start its invasion with a very high growth rate, then immediately slowed, or rather this result is only an artifact of the way I calculated growth rates.

TODO – Look at decadal patterns – this may make things more clear.

It is interesting to note that previous literature examining the spread of *F. alnus* have suggested different times marking the end of the lag-phase. As noted above, Larkin (2011) suggested the culmination of a lag-phase as 1956 in the southern Lake Michigan region. In southern Ontario, Catling and Porebski (1994) suggested the lag-phase ended in the 1970s. Importantly, no previous study addressing the lag-phase of ­*F. alnus* addressed whether the lag-phase was an inherent or extended lag. Both of these observations are far later than what I report here. However, these studies examined only a small area each of the invaded range. The patterns and processes of range expansion, particularly of lag-phase dynamics, likely vary depending on scale and local ecological conditions (Theoharides & Dukes 2007). Further analysis could entail using the datasets I have compiled, but restricting the calculations carried out here to regional levels. I examine these patterns from a different perspective in Chapter 6, where I use integrated species distribution and demographic models to investigate the local and regional population processes that result in the patterns I have found this chapter. In this way, I am able to examine how local population processes, such as individual plant survival, fruit production, and seed dispersal, propagate to regional patterns such as those discussed here.

Possibly – metapopulation size is increasing, but number of occupied populations shows a lag.

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