**Introduction**

Understanding the patterns and processes of range expansion is an important area of research in invasion ecology (Sakai et al. 2001), and has been the focus of many studies (as reviewed in (Pysek & Hulme 2005). Retrospective spatial analyses have been used to study the ecological processes involved in the spread of non-native invasive species in a novel region (REFS HERE). A rich data source for these types of studies is the specimen holdings of herbaria, which have been used to 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). Additionally, these data are used to investigate native species expansions beyond historical range limits due to changing ecological conditions (e.g., (Feeley et al. 2011; Feeley 2012). However, herbarium records may suffer from biases resulting from unequal sampling effort in time and/ or space, making it difficult to determine if observed trends (e.g., increased number of records through time for a species) are indicative of changes in range size or trends in overall specimen collection. The effects of unequal sampling effort have been a primary focus of several recent studies making use of herbarium records (Lavoie 2012). Developments in analysis methods make it possible to account for many observed biases (e.g. (Delisle et al. 2003; Aikio et al. 2010b) and to use herbarium records to reconstruct patterns of range expansion for both non-native and native plants.

A common pattern observed in the range expansion of many non-native invasive species is the presence of a substantial period of time, following initial establishment, during which population sizes are relatively small and area of occupancy is relatively low in the novel range. This period is followed by rapid range expansion and population density increases. The time period of small population size and low area of occupancy is referred to as a **lag phase** or **lag time** (Kowarik 1995; Crooks & Soulé 1999; Sakai et al. 2001; Pysek & Hulme 2005). All range expanding species should have at least an **inherent lag phase** (Crooks & Soulé 1999), due to time constraints inherent in population growth and establishment, such as generation time and time to first reproduction. However, many lag phases are observed to be longer than the predicted inherent lag phase. The potential factors causing an **extended lag phase** are not well understood; several ecological and evolutionary processes may be involved (e.g., the lag phase may last as long as it takes for the non-native species to adapt to the novel environment - (Pysek & Hulme 2005)). *Frangula alnus* (Glossy buckthorn) 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. Recently, European starlings have been linked to the spread the non-native invasive plant *Celastrus orbiculatus* (Oriental bittersweet) (Merow et al. 2011). 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.

Determining whether a species had an extended lag phase is not a trivial task. For non-native invasive plants, temporal trends in herbarium record collection are often cited as evidence for an extended lag phase, however it is difficult to distinguish signal from noise in these patterns. Recently methods have been developed that attempt to correct for potential biases in unequal sampling effort of herbarium specimens, and to identify periods of rapid range expansion for non-native invasive plant species (Delisle et al. 2003; Aikio et al. 2010a). Further, the method proposed by Aikio and colleagues (2010a) is specifically focused on identifying the existence of, and estimate the duration of, lag phases. In this study, I examine the range expansion of *F. alnus* throughout its novel North American range. I constructed a dataset of spatial observations of *F. alnus* consisting primarily of herbarium records, but also including some observations noted in the scientific literature. Using this dataset I calculate the rate of spatial expansion of *F. alnus* throughout northeast North America and examine the lag phase of this invasion, while accounting for unequal sampling effort of herbarium records using modified methods of (Delisle et al. 2003; Aikio et al. 2010a). 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 restricted compared to the whole invaded range. I know of no study that investigated the range expansion of *F. alnus* throughout its entire novel range.

**Methods**

*Collection of Presence Records*

I assembled a dataset of presence records for *F. alnus* to investigate its pattern of spread throughout northeast North America. I collected historical presence records by 1) searching publicly available on-line databases for various herbaria, 2) directly contacting curators for some herbaria and requesting *F. alnus* records, 3) searching the Global Biodiversity Information Facility (GBIF), and 4) carrying out a literature search for all North American localities, using the search terms “Frangula alnus” or “Rhammus frangula” in ISI Web of Science database. I only included records with information on the date and location 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. I **recently received records from Illinois as well, though only at the county level.** 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.

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. All records accessed via GBIF were also saved as a separate dataset used in this analysis (discussed below).

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”. In total, I included 5 presence records I found via a literature search. I extracted historical presence information from (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).  ~~As of 1955 it was known to have established in five counties in northeaster Illinois, and by 1978 it was established in 18 counties.~~ Sherff described the invasion of *F. alnus* into Skokie Bog, and which was speculated as the result of an introduction facilitated by birds carrying seeds from nearby Glencoe, where *F. alnus* was used as an ornamental plant (Sherff 1912). Catling and Porebski (1994) investigated the spread of *F. alnus* into and throughout southern Ontario. From this paper I was able to determine the three earliest records of *F. alnus* presence in this region. While this study includes several references to records of *F. alnus* through time in the region, as published 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. Herbarium Record Sources and Counts | | | |
| Herbarium | Herbarium Code | Record Count | Source |
|  | 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 Herbarium Specimens*

Most of the herbarium records I acquired did not have latitude and longitude values assigned to the location of specimen collection. However, many records had descriptive information that I used to assign a latitude and longitude value to the specimen collection location. I primarily used the GoogleEarth software (REF) to carryout this process (i.e., to georeference the specimen; *sensu* (Garcia-Milagros & Funk 2010). In some cases, georeferencing required additional Internet searches on named locations, such as unique building names or geographic features, to determine the latitude and longitude for a collection location. Descriptive location information allowed for varying degrees of accuracy and precision in the final latitude and longitude value assigned to a record. Some information allowed for assigning values for the township the specimen was located in, where as others allowed for assigning precise collection locations. I assigned location uncertainty values using guidelines from the Biogeomancer Consortium (BioGeomancer Consortium 2006). I used records with georeferencing uncertainty at the township level or lower for the primary analysis carried out in this chapter. However, I collected several herbarium records that could only be accurately georeferenced to the county level. Any analysis using these records is necessarily more spatially coarse than those using more accurately georeferenced records. However, many of these records are from regions of the country that are not otherwise represented in my analysis (e.g., Minnesota and Indiana). To take advantage of these data, I carried out an additional analysis using specimen locations referenced at the county level.A similar analysis with this spatial accuracy was carried out previously to answer similar questions (Barney 2006). Barney is also a case in which “cumulative geographic spread” was assumed – i.e. once a location was observed as being occupied, it remained occupied. **Still have to complete this analysis** **TODO –** Consider what you will do if you want to include the records for Illinois, which are only at the county level.

*Number of Records Through Time*

The total number of herbarium records reported through time can be used to infer the rate of spread of non-native invasive species (Pysek & Prach 1993; Aikio et al. 2010a). I calculated the total number of records reported per decade in the dataset of compiled historical *F. alnus* observations and the cumulative number of records reported for each year, from the year associated with the oldest presence record to the present. Using the cumulative records through time data, I calculated a rate of growth for the number of records. Annual growth rates were calculating by dividing the cumulative number of records for year *t+1* by the cumulative number of records for year *t*. The mean rate of growth was calculated as the geometric mean of the annual growth rates. While this process is similar to how growth rates are calculated in demographic analyses, I am not *directly* applying the growth rate calculated here to any underlying population process.

*Area of Occupancy Through Time*

I used the dataset of compiled historical *F. alnus* observations (described above) to examine the spatial pattern and rate of range expansion of this species throughout its novel range, from the time of first introduction to the present. Integral to this analysis was calculating the amount of area occupied by *F. alnus* through time. 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. **TO-DO: I should address this in my analysis, but it will require a substantial amount of new/additional scripting in R.**

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. This measure has been used in other studies investigating the spread of invasive species (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).

**TODO** – I’m using AOO as a measure here - it is important to consider what this may imply and perhaps discuss this further in the discussion section – also look at Gaston Refs to think about AOO more generally.

I calculated the rate of growth for the area of occurrence in a similar manner 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.

*Accounting for Unequal Sampling Effort in Time and Space*

Trends in the number of herbarium records observed through time and/or across space may be the result of unequal sampling effort. Through time there are documented periods of high and low specimen collection for herbaria in general. For example, the period during World War II is noted as a period low specimen collection (REF – I know I read this, but have to find the reference). There may also be herbarium specific trends, such as a peak in collection activity following the opening of a herbarium. Likewise, there may be unequal sampling across space for specimen collection. For example, there may be more specimens collected near herbarium, botanical gardens, or academic centers, as well as urban areas in general (i.e. the “botanist effect”; REF). The potential of the effects of unequal sampling effort complicate the interpretation of observed patterns in historical presence locations. For example, (Catling & Porebski 1994) found that *F. alnus* observations 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 results from the fact that botanists were located near these areas, and thus their collections tended to come from these areas (i.e., the “botanist effect”), or it may be that *F. alnus* has an affinity for ecological conditions near urban areas (i.e. disturbed environments), or some other explanation. It is important to correct for the mechanisms of this trend that may be due to unequal sampling effort. A simple method used to address this question is to compare 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. Recently, methods have been developed to address these concerns in a more robust manner than a simple visual comparison. These methods also rely on a comparison between the species of interest and a group of associated species. Thus, in addition to presence records for *F. alnus,* I have collected presence records for the following group of associated species:

* 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) examined Alderleaf Buckthorn as a comparison with to the distribution of *F. alnus*. Similarly, Meadow Willow was considered in a direct comparison of the effects of invasive and native species on wetland species diversity (Houlahan & Findlay 2004). Likewise, the other species listed above are species that are likely to be 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*.

One quantitative method for addressing unequal sampling effort uses a direct comparison between the area of occupancy through time for a species of interest and for a group of associated species (Delisle et al. 2003). Delisle and colleagues (2003) used their method to investigate the spread of six non-native species in Quebec, Canada, examining the increase in the area of invasion (“cumulative number of locations” in their text). They plotted the cumulative number of occupied locations versus time, referring to this as the “invasion curve”. To correct for unequal sampling effort in space and/or time, they constructed similar curves for five native species, whose ranges should be relatively static during the time-period investigated in the study. For each year in this time-period, the number of locations for the non-native species is divided by the total number of locations for the five native species, yielding a proportion of non-native to native number of locations. Periods during which this proportion is increasing through time are considered periods of invasion. Here I have employed this method to account for unequal sampling effort of *F. alnus*, and present a modification to better use this method with the historical presences dataset I have compiled, which includes records from many sources and spread over the large spatial extent.

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 Chapter 4 analysis), 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 that are not data providers for GBIF (e.g., Miami University Herbarium, University of Wisconsin Herbarium, and Rutgers Herbarium). The records acquired from these institutions are largely geographical restricted (for example, located in the states of Ohio, Wisconsin, and New Jersey for the institutions mentioned), and these locations were not always represented well in the larger GBIF search. 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 the latter issue, I carried analyses using a separate *F. alnus* dataset constructed of only records accessed via GBIF. 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.

**Results**

The earliest dated herbarium record in my compiled dataset was collected in 1879 in Hudson County, New Jersey (accessed from CHRB). I found a total of 14 specimens deposited in at least 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).

Records collected for *F. alnus* both by an extensive manual herbarium search and a GBIF query show a high level of overlap (Figure RECORD MAP). However, the manual search includes several regions not included in the GBIF query (e.g. Wisconsin, central Ohio, and south-central Pennsylvania). The spatial distribution of records from the GBIF query for the group of associated species is largely inclusive of both of the *F. alnus* datasets, with a notable exception of south-central Pennsylvania.



Figure 1. RECORD MAP: Geographic locations of collected records for *F. alnus* and a group of assocatied species.

The number of herbarium specimens collected for both *F. alnus* and the group of associated species has increased through time based on collection dates recorded with specimens (Figure RECORD NUMBERS). For the group of associated species collected via a GBIF search, there is a substantial increase in the number of records collected at the beginning of the 20th century. The number of records collected for this group increases slightly through the 20th century. Both the manually collected historical records and the records collected via a GBIF search show that there has been 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 all three groups, there is 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 (REF).



Figure 2. RECORD NUMBERS: Total number of records collected in each decade.

The cumulative number of occupied grid cells increases through time for both *F. alnus* datasets and the related group of species (Figure CELLS THROUGH TIME). Both *F. alnus* datasets do show a long period of time in which the cumulative area occupied appears to be small and remain stead (1880s to 1930s for the manual dataset and 1880s to 1960s for the GBIF dataset).

****

Figure 3. Cummulative number of grid cells occupied through time

There is a clear indication 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. This is true in comparisons of *F. alnus* occurrence to associated species occurrence for both of the *F. alnus* datasets (Figure RATIO CUMMULATIVE). However, for the *F. alnus* dataset collected via GBIF, there is an extended period of time during which the rate of increase for *F. alnus* and the group of associated species is approximately equal, followed by a dramatic increase in the rate of spread of *F. alnus*. **For discussion – this may be due to presence of non-herbarium records in GBIF and inclusion of invasive species surveys.**



Figure 4. RATIO CUMMULATIVE

Examining the ratio of the cumulative area of *F. alnus* and the group of associated species only at grid cells that included members from both datasets at some point during the study shows that the rate of increase for *F. alnus* increases more rapidly. **Discussion material – this may be indicative of the fact that the group of associated species are at equilibrium early on (i.e., mostly present in all cells), but that *F. alnus* becomes present in those cells later.**

****

Figure 5. RATIO OVERLAP - Ratio of grid cells occupied by *F. alnus* and associated species at a given time step, observed in grid cells in which members of both datasets appear at least once during the study period.

****

**Non-cumulative ratio of area, by decade:** This is the non-cumulative ratio of grid cells occupied by *F. alnus* based on records in the manually constructed dataset versus the grid cells occupied by the group of associated species based on the records acquired via GBIF. For both datasets, the number of occupied grid cells is grouped by decade. The size of each data point is scaled by the total number of grid cells occupied in that decade.

****

This plot shows the annual growth rate of the cumulative number of records for the three datasets. The mean growth rates are: All.GBIF (i.e. associated species) = 1.037, FRAL Herbarium (i.e. manually collected) = 1.050, and FRAL.GBIF (i.e *F. alnus* dataset via *only* GBIF) = 1.035. All growth rates are calculated based on the geometric means of the annual growth rates from 1879 to 2013.

****

This plot shows the annual growth rate of the cumulative number of occupied grid cells for the three datasets. The mean growth rates are: All.GBIF (i.e. associated species) = 1.033, FRAL Herbarium (i.e. manually collected) = 1.046, and FRAL.GBIF (i.e *F. alnus* dataset via *only* GBIF) = 1.041. All growth rates are calculated based on the geometric means of the annual growth rates from 1879 to 2013.

****

**Discussion**

The question of ­*why* *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, and other REFS), it is likely that this species was purposely planted. A thorough investigation of seed catalogs and nursery records from the late 19th century may shed further light on this mystery, but is 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. Based on the date of specimen collection reported on herbarium records, *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 in fact early during the document spread of *F. alnus*.

It is interesting to note that the region I propose as being the area of first introduction was a large shipping region. It is possible that shipping played a role in accidental introduction of this species, but this area was also one of high population density, where it may be more likely for people to plant it on purpose.

Three previous studies have examined aspects of the range expansion of *Frangula alnus*, all 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. They founnd evidence that it likely first entered Ohio in the 1920’s, being observed first in Lake County (northeastern Ohio). The authors conjecture that *F. alnus* spread westward through Ohio, its spread being facilitated by the range-expanding non-native European Starling, who likely ate *F. alnus* fruit and transported the seeds. These authors did not account for potential unequal sampling effort in herbarium records, but reported when and where *F. alnus* appeared in Ohio. Catling & Porebski (1994) examined the historical spread of *F. alnus* in southern Ontario, Canada (also using the synonym *R. frangula*) using herbarium records. They 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) it appeared to spread into natural areas outside of urban areas at a rate that was more rapid than its earlier rate of spread. 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 was found to have had a 15-year lag phase.

The important point to make with the Larkin study is that my dataset includes presence records from this region as early as 1912, which would expand the length of this lag phase by 29 years (making a 44 year lag phase). Another important point, and a point of comparison is that the method of Aikio et al. 2010, as applied by Larkin, is based on the total number of records observed, rather than the cumulative area of occurrence. Perhaps there is a comparison of abundance to AOO to be made here.

There are two points I should make here. One relates to results that are geographically restricted versus non-restricted and the other relates to studying one species very closely versus several more broadly.

*Study Caveats*

\* 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). Nevertheless, 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. However, because of the large request entailed in collecting records for the associated species group I did not collect these records from herbaria that I contacted directly. 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 this latter example, I was unable to actually collect herbarium records from this source. These collection issues mean that my analysis definitely underestimates the amount of area occupied by *F. alnus*. In the future, more data collection will 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 my be akin to a bootstrap process.**

Despite the concern regarding whether my sampling was complete, my results showing a rapid rate of spread of *F. alnus* are defensible. For one of the comparisons between the number of grid cells occupied by *F. alnus* versus the group of associated species selected only records from grid cells that were occupied by both groups at some point during the invasion history were considered.

\* Implications of measurement being based on AOO – There is a reasonable amount of literature dealing with the relationship between AOO and abundance. I don’t really want to get to far down this road, but it is clear that I am implying that since the area of occupancy has increased, so has the abundance of *F. alnus*. Clearly this \*\*must\*\* be true at a minimal level, since new individuals are required to inhabit new areas, thus increasing the abundance of the species. It may, however, be interesting to think about what patterns in abundance one might expect based on the changes in AOO, and to then compare them to the patterns of abundance that correspond to patterns of occupancy as determined by the linked spatial and population models in Chapter 5.

\* *Number of records through time versus cumulative number of grid cells occupied:* For the group of associated species, while the number of records recorded per decade tends to increase only slightly (Figure RECORD NUMBERS), the cumulative number of grid cells occupied steadily increases. This may be due to an overall increase in the area sampled for herbarium records through time.

\* Discuss the implications of using cumulative versus non-cumulative assumptions. Is the cumulative assumption valid? Is it valid to claim that once a location is classified as having an observation it is henceforth considered occupied? On the one hand, yes, I think this is a valid assumption, particularly for Glossy Buckthorn. With very few exceptions (Tom Lee’s work – *Is patience a virtue?*), there are no documented examples of successful buckthorn eradication from an area the size of my grid cells (or counties). On the other hand, I am certain that some locations that have historical buckthorn records no longer have buckthorn because they have become developed. 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, I think this effect is different from the effects of natural population extinctions, i.e. metapopulation dynamics.

**Literature Cited**

Aikio, S., R. P. Duncan, and P. E. Hulme. 2010a. Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos **119**:370–378. Retrieved March 7, 2013, from http://doi.wiley.com/10.1111/j.1600-0706.2009.17963.x.

Aikio, S., R. P. Duncan, and P. E. Hulme. 2010b. Herbarium records identify the role of long-distance spread in the spatial distribution of alien plants in New Zealand. Journal of Biogeography **37**:1740–1751. Blackwell Science Ltd. Retrieved April 3, 2013, from http://doi.wiley.com/10.1111/j.1365-2699.2010.02329.x.

Barney, J. N. 2006. North American History of Two Invasive Plant Species: Phytogeographic Distribution, Dispersal Vectors, and Multiple Introductions. Biological Invasions **8**:703–717. Retrieved April 28, 2013, from http://link.springer.com/10.1007/s10530-005-3174-9.

BioGeomancer Consortium. 2006. Guide to Best Practices for Georeferencing. Page 90 (A. D. Chapman and J. Wieczorek, Eds.). Global Biodiversity Information Facility, Copenhagen. Retrieved from http://scholar.google.com/scholar?q=related:tMogcSCUg5YJ:scholar.google.com/&hl=en&num=30&as\_sdt=0,5.

Catling, P. M., and Z. S. Porebski. 1994. The history of invasion and current status of glossy buckthorn, *Rhamnus frangula*, in southern Ontario. Canadian field-naturalist **108**:305–310. Retrieved from http://www.csa.com/partners/viewrecord.php?requester=gs&collection=ENV&recid=3759742.

Converse, C. K. 1984. ELEMENT STEWARDSHIP ABSTRACT for Rhamnus cathartica, Rhamnus frangula (syn. Frangula alnus). The Nature Conservancy, Arlington, The Nature Conservancy. Retrieved from http://146.201.97.143/GIST/ESA/esapages/documnts/franaln.rtf.

Crawford, P. H. C., and B. W. Hoagland. 2009. Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? Journal of Biogeography **36**:651–661. Retrieved March 1, 2013, from http://doi.wiley.com/10.1111/j.1365-2699.2008.02043.x.

Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. Pages 103–125 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. Invasive species and biodiversity management. Kluwer Academic Dordrecht, The Netherlands.

Delisle, F., C. Lavoie, M. Jean, and D. Lachance. 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. Journal of Biogeography **30**:1033–1042. Blackwell Science Ltd. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2699.2003.00897.x/full.

Feeley, K. J. 2012. Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. Global Change Biology **18**:1335–1341. Retrieved March 29, 2013, from http://doi.wiley.com/10.1111/j.1365-2486.2011.02602.x.

Feeley, K. J., M. R. Silman, M. B. Bush, W. Farfan, K. G. Cabrera, Y. Malhi, P. Meir, N. S. Revilla, M. N. R. Quisiyupanqui, and S. Saatchi. 2011. Upslope migration of Andean trees. Journal of Biogeography **38**:783–791. Blackwell Science Ltd. Retrieved March 13, 2013, from http://doi.wiley.com/10.1111/j.1365-2699.2010.02444.x.

Frappier, B., R. T. Eckert, and T. D. Lee. 2003a. Potential impacts of the invasive exotic shrub *Rhamnus frangula* L.(glossy buckthorn) on forests of southern New Hampshire. Northeastern Naturalist **10**:277–296. BioOne. Retrieved from http://www.bioone.org/doi/abs/10.1656/1092-6194(2003)010[0277:PIOTIE]2.0.CO;2.

Frappier, B., T. D. Lee, K. F. Olson, and R. T. Eckert. 2003b. Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. Forest Ecology and Management **186**:1–6. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S0378112703002743.

Garcia-Milagros, E., and V. A. Funk. 2010. Improving the use of information from museum specimens: using Google Earth© to georeference Guiana Shield specimens in the US National Herbarium. Frontiers of Biogeography **2**:71–77. Retrieved from http://www.biogeography.org/html/fb/FBv02i03/FBv02i03p71\_Garcia-Milagros.pdf.

Houlahan, J. E., and С. S. Findlay. 2004. Effect of invasive plant species on temperate wetland paint diversity. Conservation Biology **18**:1132–1138. Blackwell Science Inc. Retrieved from http://scholar.google.com/scholar?q=related:urUkz6nEodgJ:scholar.google.com/&hl=en&num=30&as\_sdt=0,5.

Howell, J. A., and W. H. J. Blackwell. 1977. The history of Rhamnus frangula (glossy buckthorn) in the Ohio flora. Castanea **42**:111–115. JSTOR. Retrieved from http://www.jstor.org/stable/10.2307/4032689.

Kowarik, I. 1995. Time lags in biological invasions with regard to success and failure of alien species BT  - Plant invasions: General aspects and special problems. in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant invasions: General aspects and special problems. SPB Adademic Publishing, Amsterdam. Retrieved from http://scholar.google.com/scholar?q=related:crNh5qomdlsJ:scholar.google.com/&hl=en&num=30&as\_sdt=0,5.

Larkin, D. J. 2011. Lengths and correlates of lag phases in upper-Midwest plant invasions. Biological Invasions **14**:827–838. Retrieved March 12, 2013, from http://www.springerlink.com/index/10.1007/s10530-011-0119-3.

Lavoie, C. 2012. Biological collections in an ever changing world: Herbaria as tools for biogeographical and environmental studies. Perspectives in Plant Ecology, Evolution and Systematics **15**:68–76. Elsevier GmbH. Retrieved January 31, 2013, from http://linkinghub.elsevier.com/retrieve/pii/S1433831912000595.

Merow, C., N. LaFleur, J. A. Silander Jr, A. M. Wilson, and M. Rubega. 2011. Developing Dynamic Mechanistic Species Distribution Models: Predicting Bird-Mediated Spread of Invasive Plants across Northeastern North America. The American Naturalist **178**:30–43. University of Chicago PressChicago, IL. Retrieved from http://www.jstor.org/stable/info/10.1086/660295.

Miller, R. J., A. D. Carroll, T. P. Wilson, and J. Shaw. 2009. Spatiotemporal Analysis of Three Common Wetland Invasive Plant Species Using Herbarium Specimens and Geographic Information Systems. Castanea **74**:133–145. Retrieved from http://www.bioone.org/doi/abs/10.2179/08-001.1.

Newbold, T. 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. Progress in Physical Geography **34**:3–22. Retrieved from http://ppg.sagepub.com/cgi/doi/10.1177/0309133309355630.

Pysek, P., and P. E. Hulme. 2005. Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience **12**:302–315. BioOne. Retrieved from http://www.bioone.org/doi/abs/10.2980/i1195-6860-12-3-302.1.

Pysek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. Journal of Biogeography **20**:413–420. Retrieved April 28, 2013, from http://www.jstor.org/stable/10.2307/2845589.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, and N. C. Ellstrand. 2001. The Population Biology of Invasive Specie. Annual Review of Ecology and Systematics **32**:305–332. JSTOR. Retrieved from http://www.jstor.org/stable/10.2307/2678643.

Salo, L. F. 2005. Red brome (Bromus rubens subsp. madritensis) in North America: possible modes for early introductions, subsequent spread. Biological Invasions **7**:165–180. Retrieved from http://www.springerlink.com/index/10.1007/s10530-004-8979-4.

Sherff, E. E. 1912. Range extenstions of Rhamnus frangula and Sporobolus asperifolius.

Taft, J. B., and M. K. Solecki. 1990. Vascular flora of the wetland and prairie communities of Gavin Bog and Prairie Nature Preserve, Lake County, Illinois. Rhodora **92**:142–165. New England Botanical Club. Retrieved from http://cat.inist.fr/?aModele=afficheN&cpsidt=19723966.