INVASIVE WOODY PLANT ECOLOGY AND MANAGEMENT

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ENVIRON 436: Woody Plants

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December 17th, 2020

INTRODUCTION

Invasive species are recognized as one of the most important threats to biodiversity and native ecosystem functioning worldwide (Wilcove, 1998), making awareness and knowledge of invasive species integral to ecological restoration and natural resources management. Invasive species often impact their introduced environments on numerous ecological scales because they are imbued with traits that allow them to directly or indirectly outcompete native species. *Rhamnus cathartica* and *Lonicera maackii* are two invasive woody shrubs common in Michigan and distributed across North America. In the face of these prolific species, land managers have been working to understand the ways *R. cathartica* and *L. maackii* impact native ecosystems and the methods that are best used to reduce their distribution and abundance, thus aiding in restoring native ecosystem functioning. Management methods to date have often relied on a combination of mechanical (with an emphasis on prescribed burns) and chemical controls.

Rhamnus cathartica, or common buckthorn, is a shrub or small tree that was first introduced to North America from Europe and western Asia during the 19th century (Godwin, 1943; Mascaro and Schnitzer 2007). It is now very invasive in Ontario, Canada, the midwest states, and from Colorado to Nova Scotia, Canada (Kurylo *et al*., 2007). Studies find that this species was brought to North America for a variety of uses: originally perhaps for medicinal purposes but also potentially for ornamental, hedge, and/or shelterbelt purposes (Kurylo *et al*., 2012). It spread from New England to the west and north likely through commerce (Leslie 1864) and fruit and seed-eating animals that spread buckthorn's seeds from homesteads to new ecosystems (Kurylo et al., 2012).

Lonicera maackii, commonly known as Maack's Honeysuckle or Amur Honeysuckle, was introduced to the United States in 1898 when it was imported to the New York Botanical Garden from East Asia ("*Lonicera maackii* (Amur honeysuckle)", 2019). By the early 1900s, L. maackii was utilized for soil stabilization by the USDA and sold widely in nurseries. The first record of naturalized populations came in the 1920s, though reports substantially increased from the 1950s to the 1970s (Luken and Thieret, 1996). *L. maackii* is now present in 36 states and considered invasive in 16, including Michigan ("*Lonicera maackii* (Amur honeysuckle)", 2019).

The purpose of this paper is to examine the ecology and management of *R. cathartica* and *L. maackii*. The key questions to be addressed are: what traits allow these invasive species to be successful in their invaded environments, what is the impact of their invasion on native ecosystems, and what management strategies have proved most successful.

LITERATURE SURVEY METHODS

The studies and reviews utilized for this paper were found using the Google Scholar search engine and database. The authors accumulated sources via tracking references cited in review papers. Individual searches supplemented this method, using keyword searches that used exclusively the latin name of both species to ensure accuracy across sources paired with relevant words such as “invasive,” “ecosystem impacts,” and “management”. This paper is the culmination of numerous review papers, databases, and experimental studies.

DISCUSSION

There is a wide body of scientific literature dedicated to uncovering the environmental and physiological factors that allow non-native species to establish themselves as an invasive species. In a meta-analysis of 117 field and experimental-garden studies, Van Kleunen et al. (2010) concluded that invasive plant species generally have higher values of performance-related traits characterizing physiology, shoot allocation, leaf-area allocation, growth rate, size, and fitness than non-invasive plant species. Such traits inform invasion theories such as the enemy release hypothesis and novel weapons hypothesis, which respectively posit that non-native species are not subject to their native predators in invaded environments, and that non-native species are likely to have traits allowing them to outcompete native species unaccustomed to such strategies. It follows that our study species, *R. cathartica* and *L. maackii*, being classified as invasive species in numerous locations, also exhibit their own combinations of these traits. Both species are the subjects of extensive efforts to determine the most effective measures for invasive species management. Such efforts suggest early detection of invasive species is an integral, proactive approach to management; early detection, such as satellite imaging, allows for eradication of non-native populations before they become too widespread to control (Moody & Mack, 1988). After a population becomes established, it is usually more difficult to successfully slow the spread of invasion. Methods for managing these populations of invasive species often follow an integrated pest management (IPM) approach, utilizing biological, mechanical, and chemical methods to ensure successful eradication of individuals.

Rhamnus cathartica

The invasive *Rhamnus cathartica* is a shrub brought to North America that can grow in dense monospecific thickets with few other species in proximity, therefore dominating the understory (Archibold *et al*. 1997). This ability to take over habitats is one of *R. cathartica*’s many traits that make it extremely invasive. Its physiological adaptations, seed adaptations and dispersal methods, nitrogen fixation, and symbiotic relationship with invasive earthworms allow this species to dominate novel ecosystems.

Physiology and Ecological Adaptations

R. cathartica can act as a fairly generalist species, which allows it to persist in a variety of environments. It is able to survive drought and flood conditions (Stewart and Graves 2004), and this generalist nature may explain its invasive success (Seltzner and Eddy 2003). Further, the phototrophic adaptability of *R. cathartica* may also explain its invasibility. It can tolerate shady conditions (Archibold et al. 1997) but will quickly take advantage of sunlight gaps in forests and grow quickly (Knight *et al*., 2007). Therefore, when there are gaps in the canopy due to windfall or other events, *R. cathartica* may be the first species to colonize this new gap.

R. cathartica is a species with a fast growth rate as well. According to a study by Harrington et al. (1989), *R. cathartica* grew faster than the other shrub species including *Lonicera* x *bella*, *Prunus serotina*, and *Cornus racemosa*. Additionally, this study showed that *R. cathartica* had the highest percent nitrogen in its leaves during the growing season compared to other shrub species. Higher nitrogen levels are correlated with higher rates of photosynthesis and carbon gain, which helps to explain *R. cathartica*'s more rapid growth.

The phenology of *R. cathartica* also helps to explain its vigorous invasibility. According to Schuster et al. (2020), buckthorn growth and survival correlates more with spring and autumn light availability than summer. Other studies, like Knight et al., 2007, also found that buckthorn has a longer leaf-out phenology than native species in its range, and therefore, can avoid shading and assimilate carbon to grow and survive. *R. cathartica* is able to produce higher levels of photosynthetic carbon when overstories above it are not fully leaved (Harrington et al. 1989). This light availability in spring and autumn, in turn, is the largest factor influencing the degree of buckthorn invasion in an area. Ecosystems with evergreen canopies negate the ecological advantage that *R. cathartica* has by early leaf-out and late leaf-fall, unlike deciduous canopies. (Fridley, 2012). Thus, some forests can more effectively resist buckthorn because they are shaded in the spring and autumn, even though buckthorn can be somewhat shade-tolerant.

Fruit development, seed dispersal, and germination in *R. cathartica* give additional insight to its invasibility. A study from 1936 by Godwin described fruit production by *R. cathartica* as "very prolific" and a study by Archibold et al. in 1997 described it as "aggressive." Therefore, *R. cathartica* is producing many drupes that are then able to be dispersed and drive up buckthorn populations in other areas. Birds are the main dispersers of *R. cathartica* (Sherburne 1972; Archibold et al. 1997) and due to the laxative chemical anthraquinone in the drupes, birds will disperse seeds locally due to the rapid cathartic release (Seltzner and Eddy 2003). This is significant because *R. cathartica* seedlings are especially successful near mature conspecifics (Knight 2006). There have been observations of greater densities of *R. cathartica* seedlings under conspecifics in Europe and North America (Kollman and Grubb 1999; Leitner 1985). The evolved adaptations of *R. cathartica* and its ecological interactions explain why it is such a formidable invasive species.

Effects on Native Flora and Fauna

The dense thickets of a successful *R. cathartica* invasion can generate a multitude of issues for native plants and wildlife. Thickets can reduce the amount of sunlight that reaches the forest floor, and ultimately this can limit light that penetrates to shorter vegetation (Leitner 1985) and subsequently reduce herbaceous plant cover in areas with high *R. cathartica* density (Alsum 2003). Sunlight is often a limiting factor for plant growth, and *R. cathartica* is limiting sunlight allocation to native species.

Further, the presence of *R. cathartica* and the soil and other environmental conditions the species creates may lead to further invasion by other nonnative species. According to Alsum (2003) more weedy and exotic species were found in plots planted with *R. cathartica*, including increased *Lonicera* spp. coverage and lower overall richness of herbaceous species. However, this effect in the study may be entangled with effects from shade and competition for resources. Yet, other studies that focused on the *removal* of *R. cathartica* from an area may substantiate

Alsum's claim. When *R. cathartica* was cut and treated with herbicide in a study by Boudreau and Wilson (1992) native plants reappeared, but not without some other invasive species also cropping up.

Wildlife can be impacted by *R. cathartica* invasions. Birds may be detrimentally affected, like in the study by Schmidt and Whelan (1999), which found that birds that nest in invasive shrubs are more likely to be predated upon compared to birds nesting in native shrubs. Buckthorn invaded sites in a study by Vernon et al. (2014) changed habitat use and wildlife presence by white-tailed deer, coyotes, opossums, and raccoons. This study showed that some mesocarnivores may pass more through buckthorn invaded sites because of easily accessible bird eggs as stated in the previous study. Earthworms are also more prevalent in buckthorn invaded sites (Heneghan et al. 2006) and are an opportunistic food source for opossums and racoons.

R. cathartica has the ability to change soil chemistry and moisture, and therefore, alter entire ecosystems. As mentioned previously, this species has a high concentration of nitrogen in the leaves, therefore, leaf litter surrounding stands of *R. cathartica* will also be high in nitrogen. The nitrogen concentration levels can be 1.1–1.9% in senesced leaves (Kennedy 2000) and 2.2% N in leaf litter (Heneghan et al. 2002). This litter decomposes rapidly and mixing *R. cathartica* litter with native tree leaf litter causes the native litter to decompose rapidly as well (Heneghan et al. 2002). When leaf litter decomposes rapidly the forest floor can transform into bare soil underneath stands of *R. cathartica* (Kollmann and Grubb, 1999), which is problematic for native species because *R. cathartica* has higher seedling emergence rates in bare soil conditions (Gill and Marks 1991).

Given the soil conditions that *R. cathartica* prefers, this species has an interesting symbiotic relationship with invasive species of earthworms in its North American range. Earthworms feed on and reduce leaf litter, ultimately affecting soil chemistry and cycles similar to *R. cathartica* (Bohlen et al. 2004; Hale et al. 2005). Leaf litter that is high in nitrogen is especially attractive to earthworms (Hendriksen 1990) and could increase earthworm populations. Therefore, we see that *R. cathartica* leaf litter, with high nitrogen content, is preferable to earthworms (Hendriksen 1990) and in turn, earthworms create more bare soil that is advantageous for *R. cathartica* seedling emergence (Gill and Marks, 1991). Thus, a positive feedback loop between *R. cathartica* and earthworms encourages the growth of each invasive species' population.

An important ecosystem that suffers from the domination of *R. cathartica* are oak openings or oak savannas. They are a "globally rare ecosystem" found in southeast Michigan and northwest Ohio (Becker et al., 2013). A study by Becker et al. in 2013 utilized Landsat imagery to analyze land surface phenologies of buckthorn populations in oak openings using a multi-year data set. Field measurements were also taken to verify remotely sensed buckthorn species thickets. Thickets of *R. cathartica* were found throughout the oak opening region, especially in areas that receive drainage from agricultural plots. The data collected also showed where removal methods worked and reduced buckthorn populations in an area. The management tools and techniques for *R. cathartica* in oak openings and other native ecosystems are important to know as this species continues to spread.

Management Methods and Success

The spread of *R. cathartica* must be slowed and can be done through a variety of management methods. Management efforts can be organized by federal, state, and local agencies or private organizations. Often, the extent of management can overwhelm these organizations and the use of volunteers becomes necessary. A report by John Moriarity as part of a symposium on *R. cathartica* at the University of Minnesota in 2005 describes several conventional management methods and is a good starting point for discussing this subject.

Mechanical management of buckthorn can involve hand-pulling for small saplings, a good exercise for smaller areas and when children and volunteers are involved. Root wrenches can also be used on larger buckthorn individuals but is a slow process also not suited for large areas and can cause soil disturbance.

Chemical treatment is effective against *R. cathartica*, especially when boles are cut or girdled. Stump treating by resource managers using glyphosate or Triclopyr is common, works well for larger stumps, and can be done over larger areas than mechanical techniques. Moriarty notes that they have used this method to "treat over 300 acres in Ramsey County Parks." Archibold et al. (1997) also supports glyphosate as an effective herbicide to treat *R. cathartica*, describing how only 6% of the stumps treated with Round-up in their study resprouted, and these sprouts were much weaker.

Looking further into chemical applications to *R. cathartica*, stump treating and basal bark treatment are still slower techniques compared to foliar spraying. The former two treatments require targeted application or mechanical processes, whereas foliar spraying can treat even larger areas (Schuster et al. 2020). However, foliar spraying can affect non-target species; such is the case for fosamine ammonium (Krenite). This chemical has high efficacy against *R. cathartica* according to Schuster et al. (2020), but it negatively impacts native forb cover if foliar spraying is not carefully planned. The label for this herbicide recommends use 2 months before leaf senescence, which is tricky to plan around as this is when many native plants are still fully leaved. Due to the risks of foliar spraying, Luken et al. (1994) suggests that foliar spraying be conducted after initial brush management (as listed in mechanical management and the beginning of this paragraph) and that restoration seeding of native plants be delayed one growing season for positive long-term effects.

Fire is a physical tool used by resource managers to reduce *R. cathartica* coverage in native ecosystems. A single prescribed burn may not be very effective against *R. cathartica* thickets, but several successive burns can reduce density (Archibold et al. 1997), and is especially effective against seedlings. The Archibold et al. study (1997) also highlights how fires that occur after herbicide applications can be useful. Additionally, prescribed burns are useful in areas that are adapted to fire, like oak forests (Kline 1981), meaning native plants are adapted to and resistant to fire and will not be harmed by a prescribed burn. These burns are generally conducted between March and May when there are low carbohydrate levels which reduces re-sprouting vigor (Gale 2000). Unfortunately, in forested areas heavily populated by *R. cathartica* there may be less leaf litter, and leaf litter is a necessity to move fire to different areas, rendering fire less effective (Gale 2000).

Lonicera maackii

Like *R. cathartica*, *Lonicera maackii* exhibits a number of advantageous physiological and life-history traits that allow it to become a highly-successful invasive shrub, particularly in the forests of eastern North America (McNeish & McEwan, 2016).

Physiology and Ecological Adaptations

L. maackii's suite of traits increases its invasion potential throughout all life stages, beginning with seed dispersal. *L. maackii* seeds are produced in substantial quantities by large fruiting events, and the seeds contained in these berries are capable of long distance dispersal via abiotic vectors (stream corridors) and biotic vectors (native bird and white-tailed deer which act as true dispersers, eating only the fruit and defecating the seeds). The reproductive morphology of *L. maackii* makes dispersal by birds and mammals prominent, as seeds are packaged in berries--meaning a completely soft (and desirable) pericarp. In fact, Castellano and Gorchov 2013 found that 68% of *L. maackii* seeds were still viable after passing through the intestinal system of white-tailed deer, which specifically supports dispersal to edge habitats, or areas where one habitat meets another. This effect is compounded by the fact that, similar to many other invasive plant species, the phenology of *L. maackii* differs from native species in the invaded habitat (McNeish & McEwan, 2016). In comparison with native species, *L. maackii* has a longer growing season, with leaf development occurring two to three weeks earlier in the spring and leaf abscission occurring well into the winter owing to the freeze-resistance of the leaves (McEwan et al., 2009a). This often results in *L. maackii* being a reliable food source during months wherein native plants are dormant. Not only are seeds widely distributed, they are capable of germinating in a wide range of light, temperature, and soil conditions (McNeish & McEwan, 2016). These traits provide *L. maackii* the many advantages of dispersal including encountering favorable habitats and promoting gene flow, allowing it to establish quickly and widely in their introduced environments.

After germination, *L. maackii* shrubs continue to exhibit the environmental plasticity shown by its seeds; individuals can thrive in a variety of environmental conditions, including the darker and disturbed areas where native species have trouble establishing. Luken et al. 1997 found that while shrubs produced significantly more fruit in high sun environments, they can utilize a range of light levels more effectively than native species. Rapid growth further favors the establishment of *L. maackii* stands. As an immature shrub it rapidly produces many stem shoots, later shifting resource allocation to height and reproduction, leading to the formation of dense thickets (Deering & Vankat, 1999). Further contributing to dense stands is *L. maackii*'s ability to resprout upright stems when they are clipped or otherwise damaged (Deering & Vankat, 1999).

This combination of dispersal ability, environmental plasticity, and phenology gives *L. maackii* the ability to outcompete native plant species, rapidly colonizing both ideal environments and diverse or disturbed habitats where native species struggle to establish. Thus, *L. maackii* is able to quickly reach invasion status in introduced habitats. The ecological impact of this invasion increases with population density and stretches across numerous ecological scales.

Effects on Native Flora and Fauna

L. maackii impacts its invaded environments on almost every level from soil to bird community composition via both chemical and physical pathways. Interactions between *L. maackii* and native flora and fauna run the gamut from direct to indirect and individual to ecosystem level. Susceptible habitats can include riparian areas, where distribution of seeds from stream corridors allows for seedling establishment, and forest understories are prairies, where species depend on light availability for growth. This section will explore these individually, though it is integral to consider the way these effects work together to cumulatively alter the invaded environment.

L. maackii alters soil composition as leaf-litter breakdown is five times as fast as many native plant species and has greater nitrogen and less lignin, supporting microbial communities distinguishable from those produced by native plants (Arthur et al., 2012).

Perhaps the most visible impacts of *L. maackii* invasion occurs between *L. maackii* and native plant species. There is direct competition between these groups as *L. maackii* can be allelopathic, producing secondary metabolites in leaves, roots, and shoots that reduce the germination of native herbaceous species (McNeish & McEwan, 2016). Studies have shown that these secondary metabolites inhibit germination of native species like jewelweed, tall thimbleweed, and four grass and forb species (Dorning & Cipollini 2006, McEwan et al. 2010). Moreover, there is abundant indirect competition between these groups. Dense stands of *L. maackii* lead to a reduction in light reaching the understory, thus reducing the abundance and richness of native plant species growing below their arching branches. Empirical evidence suggests that forests invaded by this shrub have significantly less herb fecundity, fitness, and growth (Gould & Gorchov, 2000). Native tree sapling abundance also decreases under *L. maackii* invasion, decreasing the recruitment of secondary forests (White et al., 2014). These interactions are predicted to alter species composition in invaded forests, which ultimately impacts community structure, function, and successional trajectories (Hartman & McCarthy, 2008).

The chemicals and allelopathy that impact soils and native plants also impact amphibian communities, showcased by the changes in development and behaviors in American Toads connected to leaf litter and soil contaminated with *L. maackii* secondary metabolite leachate (Hickman & Watling, 2014). Amphibian communities are also impacted by physical habitat alteration, exhibiting reduced diversity in habitats where temperature and humidity were decreased due to shading from *L. maackii* (Watling et al. 2011c). Additionally, dense *L. maackii* thickets have differential impacts on arthropod communities. For example, McKinney and Goodell 2010 found that the presence of *L. maackii* reduces pollination visits to spotted geranium, while Goodell et al. 2010 found that the presence of *L. maackii* increases pollination visits to the largeleaf waterleaf. Empirical studies have shown that some arthropod guilds, such as ground spiders, increase in abundance in *L. maackii* plots, while others decrease (McNeish & McEWan, 2016). It is important to note that Acari (mites and ticks) are one of the groups that demonstrate increased abundance in *L. maackii* plots (Christopher & Cameron, 2012). This evidence, along with results from Shewhart el al. 2014 that show increased mosquito egg survivorship in *L. maackii* stands, suggests that *L. maackii* may impact mosquito and tick populations-ultimately affecting the incidence of human disease (McNeish & McEwan, 2016). Moreover, the extensive branching in dense *L. maackii* thickets impacts avian community composition in two major ways. First, the increased habitat leads to *L. maackii* invaded forests having increased densities of understory bird species and decreased densities of upper-canopy birds (McCusker et al., 2010). Second, the bushy growth pattern has been connected with increased perching sites for brown-headed cowbirds, leading to increased brood parasitism and reduced annual bird reproduction (Rodewald et al., 2010). Not only do these thickets alter native habitats, the fruit does not offer a significant source of nutrition for birds and mammals (McNeish & McEwan, 2016).

The combination of these interactions is representative of the larger scale alterations in ecosystem function and processes that are facilitated by the invasion of *L. maackii*. Taken together, it has been shown that *L. maackii* alters invaded ecosystems at every level: nutrient cycling, soil microbial communities, plant species growth and composition, animal species richness and abundance, and possibly vector-borne disease incidence in the cases of disease-carrying ticks and mosquitos. These findings support the hypothesis that the effects of *L. maackii* are complex and vary across ecosystems and ecological scales (McNeish & McEwan, 2016). The scope of *L. maackii* impacts leads to an increased need to understand its spread and management.

Management Methods and Success

L. maackii management methods follow the general guidelines utilized for the management of many invasive species. Researchers have found that remote-sensing images are especially beneficial for early detection of *L. maackii* populations in a cost-effective manner (Huang & Asner, 2009), and the extended leaf phenology differs from most native plants, allowing for detection in the early spring and late fall using image differencing of satellite images (Wilfong et al., 2009). These methods, when used in tandem with ground observations, create a cost-effective early detection plan likely to reduce time and resources required for management later on.

Many studies have been conducted in order to identify the most effective *L. maackii* management strategies. Similar to the Integrated Pest Management system mentioned earlier, studies have shown that the largest reductions in *L. maackii* individuals occur when mechanical management methods are combined with chemical management methods. Most methods begin with the mechanical process of stem cutting followed by pesticide application. Schulz et al. (2012) found that seasonal stem cutting followed by stem application of 18% glyphosate was up to 29% more effective (56% vs. 75-85%) than stem cutting followed by foliar pesticide application. This result was confirmed by Rathfon and Ruble, who upon testing four removal methods, found that stump cutting coupled with chemical application was most effective against large individuals. These methods have been found to be six times more successful when employed annually until eradication than when used only once (Loeb et al., 2010). In an experimental removal/nonremoval study, Hartman and McCarthy found that three years after removal of *L. maackii,* seedling survivorship was significantly greater than in plots with *L. maackii*. These results are bolstered by Runkle et al., who found that seven to eight years after *L. maackii* removal, plant cover, tree seedling density, and plant species richness increased.

These methods are effective, but questions remain about their usefulness on large and distributed *L. maackii* populations. Wider scale management methods may need to be employed to address heavily invaded ecosystems. Prescribed fire has been used to control *L. maackii* along with other invasive species. Fire has produced limited morality on bush honeysuckle species in spring, summer, and fall season burns (Zouhar et al., 2008). Fire has seen success completely killing young *L. maackii* individuals, but after one burn will likely only top-kill adults, allowing them to resprout from their intact roots (Czarapata, 2005). Ultimately, the chosen management method is context specific, and thanks to extensive research, land managers have an arsenal of methods to choose what best fits the needs of the ecosystem.

CONCLUSION

The two species explored in this report, *Rhamnus cathartica* and *Lonicera maackii,* tend to have similar ecologies, coexist in similar spaces, and require similar management tactics.

These species pose significant problems across North America, including Michigan, and exemplify the traits essential to invasion ecology such as differential phenology and environmental plasticity. It is imperative that restoration managers understand the traits that lead to the invasion of *R. cathartica* and *L. maackii* in order to avoid new invasions and mitigate populations already existing. Without further research into management techniques, especially techniques that focus on invasion prevention, there is a slim chance of eradication of these species in North America. Prevention is the key practice going forward in order to avoid spreading management resources ever thinner to combat the spread of these woody invasive species.

ACKNOWLEDGEMENTS

The authors would like to acknowledge the extensive amount of prior research that made this piece possible--included in this overview are numerous experimental studies, databases, and review papers. Lauren Payne uniquely contributed to this review by researching the history, characteristics, ecology, and impacts of study species *Lonicera maackii*. Kellee Byard uniquely contributed through their research on the history, characteristics, ecology, and impacts of study species *Rhamnus cathartica*. In addition to this research, both authors draw from knowledge gained through the Program in the Environment and the Nature Academy Internship Program at Matthaei Botanical Gardens and Nichols Arboretum.

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FIRST DRAFT PEER REVIEW COMMENTS

The studies and reviews utilized for this paper were found using the Google Scholar search engine and database. To find a variety of sources, the authors used the "snowball" method of research: a review paper on the species was located, and the literature cited therein was used to explore the components of each species section. Individual searches were conducted to supplement this method, using keyword searches that used exclusively the latin name of both species to ensure accuracy across sources paired with relevant words such as "invasive", "ecosystem impacts", and "management". The final result is a paper written using this many review papers, this many experimental studies, and this many websites.

DISCUSSION

There is a wide body of scientific literature dedicated to uncovering the environmental and physiological factors that allow non-native species to establish themselves as an invasive species. In a meta-analysis of 117 field and experimental-garden studies, Van Kleunen et al. concluded that invasive plant species generally have higher values of performance-related traits characterizing physiology, shoot allocation, leaf-area allocation, growth rate, size, and fitness than non-invasive plant species. These traits tie into several invasion theories, such as the enemy release hypothesis and the novel weapons hypothesis. It follows that our study species, *R. cathartica* and *L. maackii*, being classified as invasive species in numerous locations, also exhibit their own combinations of these traits. They are also both the subjects of extensive efforts to determine the most effective measures for controlling invasive species. Early detection of invasive species is an integral, proactive approach to management; early detection allows for eradication of invasive populations before they become too widespread to control (Moody & Mack, 1988). After a population becomes established, it is usually more difficult to successfully slow the spread of invasion. Methods for managing populations of invasive species often follow

Daphne Onsay
6:21 PM Yesterday
I'm also confused as to what the snowball method is. Would there be a way to describe this with more detail?

Noah Clements
9:40 PM Dec 11
I'm confused by what this means exactly. A section within the literature cited or within the paper?

Noah Clements
9:43 PM Dec 11
Put commas inside quotations

Noah Clements
9:57 PM Dec 11
great job tying the discussions of each species together

slow the spread of invasion. Methods for managing populations of invasive species often follow
an integrated pest management (IPM) approach, utilizing both mechanical and chemical methods to ensure successful eradication of individuals.

Rhamnus cathartica

The invasive *Rhamnus cathartica* is a shrub brought to North America that can grow in dense monospecific thickets with few~~hardly any~~ other species in proximity, therefore dominating the understory (Archibold *et al.* 1997). This ability to take over habitats is one of *R. cathartica*'s many traits that make it extremely invasive. Its physiological adaptations, seed adaptations and dispersal methods, nitrogen fixation, and symbiotic relationship with invasive earthworms allow this species to dominate novel ecosystems.

Physiology and Ecological Adaptations

R. cathartica can act as a fairly generalist species, which allows it to persist in a variety of environments. It is able to survive drought and flood conditions (Stewart and Graves 2004), and this generalist nature may explain its invasive success (Seltzner and Eddy 2003). Further, the

species together

Noah Clements
9:55 PM Dec 11
add the year of the paper

Noah Clements
9:54 PM Dec 11
expand on these hypotheses

Daphne Onsay
6:24 PM Yesterday
What methods are used in the early detection process? Maybe expand on one example of a method used in early detection.

Noah Clements
9:55 PM Dec 11
Replace: "hardly any" with "few"

3

photrophic adaptability of *R. cathartica* may also explain its invasibility. It can tolerate shady conditions (Archibold et al. 1997) but will quickly take advantage of sunlight gaps in forests and grow quickly (Knight *et al.*, 2007). Therefore, when there are gaps in the canopy due to windfall or other events, *R. cathartica* may be the first species to colonize this new gap.

R. cathartica is a species with a fast growth rate as well. According to a study by Harrington et al. (1989), *R. cathartica* grew faster than the other shrub species including *Lonicera* x *bella*, *Prunus serotina*, and *Cornus racemosa*. Additionally, this study showed that during the growing season *R. cathartica* had the highest percent nitrogen in its leaves during the growing season compared to other shrub species. Higher nitrogen levels are~~is~~ correlated with higher rates of photosynthesis and carbon gain, which helps to explain *R. cathartica*'s more rapid growth.

The phenology of *R. cathartica* also helps to explain its vigorous invasibility. According to Schuster et al. (2020), buckthorn~~buckhorn~~ growth and survival correlates more with spring and autumn light availability than summer. This supports what is found in numerous other studies (like Knight et al., 2007) that buckthorn has a longer leaf-out phenology than native species in its range, and therefore, can avoid shading and assimilate carbon to grow and survive. *R. cathartica* is able to produce higher levels of photosynthetic carbon when overstories above it are not fully leaved (Harrington et al. 1989). This light availability in spring and autumn, in turn, is the largest factor influencing ~~influencing factor on~~ the degree of buckthorn invasion in an area. Ecosystems with evergreen canopies negate the ecological advantage that *R. cathartica* has by early leaf-out and late leaf-fall, unlike deciduous canopies. (Fridley, 2012). Thus, some forests can more effectively resist buckthorn because they are shaded in the spring and autumn, even though buckthorn can be somewhat shade-tolerant.

Fruit development, ~~and~~ seed dispersal, ~~and~~ germination in *R. cathartica* give additional insight to its invasibility. A study from 1936 by Godwin described fruit production by *R. cathartica* as "very prolific" and a study by Archibold et al. in 1997 described it as "aggressive." Therefore, *R. cathartica* is producing many drupes that are then able to be dispersed elsewhere

Daphne Onsay
6:27 PM Yesterday
How does it do this? Does it shade out natives?

Noah Clements
9:57 PM Dec 11
Replace: "a" with "a,"

Noah Clements
10:01 PM Dec 11
this phrase is repeated later in the sentence

Noah Clements
10:01 PM Dec 11
Replace: "is" with "are"

Noah Clements
10:02 PM Dec 11
Replace: "buckhorn" with "buckthorn"

3

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Daphne Onsay
6:27 PM Yesterday
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Noah Clements
9:57 PM Dec 11
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Noah Clements
10:01 PM Dec 11
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Noah Clements
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Replace: "is" with "are"

Noah Clements
10:02 PM Dec 11
Replace: "buckhorn" with "buckthorn"

and drive up buckthorn populations in other areas. Birds are the main dispersers of *R. cathartica* (Sherburne 1972; Archibold et al. 1997) and due to the laxative chemical anthraquinone in the drupes, birds will disperse seeds locally due to the rapid cathartic release (Seltzner and Eddy 2003). This is significant because *R. cathartica* seedlings are especially successful near mature conspecifics (Knight 2006). There have been observations of greater densities of *R. cathartica* seedlings under conspecifics~~conspeifics~~ in Europe and North America (Kollman and Grubb 1999; Leitner 1985). When examining all evolved adaptations of *R. cathartica* and its ecological interactions it rationalizes why it is such a formidable invasive species.

Effects on Native Flora and Fauna

The dense thickets of a successful *R. cathartica* invasion can generate a multitude of issues for native plants and wildlife. Thickets can reduce the amount of sunlight that reaches the forest floor, and ultimately this can limit light that penetrates to shorter vegetation (Leitner 1985) and subsequently reduce herbaceous plant cover in areas with high *R. cathartica* density (Alsum 2003). Sunlight is often a limiting factor for plant growth, and *R. cathartica* is limiting sunlight allocation to native species.

Further, the presence of *R. cathartica* and the soil and other environmental conditions the species creates may lead to further invasion by other nonnative species. According to Alsum (2003) more weedy and exotic species were found in plots planted with *R. cathartica*~~their plots~~

Noah Clements
10:02 PM Dec 11
wording of this sentence is awkward

Noah Clements
10:03 PM Dec 11
Replace: "influencing factor on" with "factor influencing"

Noah Clements
10:05 PM Dec 11
remove period

Noah Clements
10:07 PM Dec 11
Replace: "and" with ","

~~with *R. cathartica* planted~~, including increased *Lonicera* spp. coverage and lower overall richness of herbaceous species. However, this effect in the study may be entangled with effects from shade and competition for resources. Yet, other studies that focused on the *removal* of *R. cathartica* from an area may substantiate Alsum's claim. When *R. cathartica* was cut and treated with herbicide in a study by Boudreau and Wilson (1992) native plants reappeared, but not without some other invasive species also cropping up.

Wildlife can be impacted by *R. cathartica* invasions. Birds may be detrimentally affected, like in the study by Schmidt and Whelan (1999), which found that birds that nest in invasive shrubs are more likely to be predated upon compared to birds nesting in native shrubs. Buckthorn invaded sites in a study by Vernon et al. (2014) changed habitat use and wildlife presence by white-tailed deer, coyotes, opossums, and racoons. This study showed that some mesocarnivores may pass more through buckthorn invaded sites because of easily accessible bird eggs as stated in the previous study. Earthworms are also more prevalent in buckthorn invaded sites (Heneghan et al. 2006) and are a opportunistic food source for opossums and racoons.

R. cathartica has the ability to change soil chemistry and moisture, and therefore, alter entire ecosystems. As mentioned previously, this species has a high concentration of nitrogen in the leaves, therefore, leaf litter~~little~~ surrounding stands of *R. cathartica* will also be high in nitrogen. The nitrogen concentration levels can be 1.1–1.9% in senesced leaves (Kennedy 2000) and 2.2% N in leaf litter (Heneghan et al. 2002). This litter decomposes rapidly and mixing *R. cathartica* litter with native tree leaf litter causes the native litter to decompose rapidly as well (Heneghan et al. 2002). When leaf litter decomposes rapidly the forest floor can transform into bare soil underneath stands of *R. cathartica* (Kollmann and Grubb, 1999), which is problematic for native species because *R. cathartica* has higher seedling emergence rates in bare soil conditions (Gill and Marks 1991).

Given the soil conditions that *R. cathartica* prefers, this species has an interesting symbiotic relationship with invasive species of earthworms in its North American range. Earthworms feed on and reduce leaf litter, ultimately affecting soil chemistry and cycles similar to *R. cathartica* (Bohlen et al. 2004; Hale et al. 2005). Leaf litter that is high in nitrogen is

Noah Clements
10:11 PM Dec 11
Delete "elsewhere" since you use "other areas" at the end of the sentence

Noah Clements
10:09 PM Dec 11
is this due to allelopathy?

Noah Clements
10:04 PM Dec 11
Replace: "conspecfics" with "conspecifics"

Noah Clements
10:12 PM Dec 11
maybe reword this

Noah Clements
10:14 PM Dec 11
might help to include some stats

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An important ecosystem that suffers from the domination of *R. cathartica* are oak openings or oak savannahs. They are a "globally rare ecosystem" found in southeast Michigan and northwest Ohio (Becker et al., 2013). A study by Becker et al. in 2013 utilized Landsat imagery to analyze land surface phenologies of buckthorn populations in oak openings using a multi-year data set. Field measurements were also taken to verify remotely sensed buckthorn species thickets. Thickets of *R. cathartica* were found throughout the oak opening region, especially in areas that receive drainage from agricultural plots. The data collected also showed where removal methods worked and reduced buckthorn populations in an area. The management tools and techniques for *R. cathartica* in oak openings and other native ecosystems are important to know as this species continues to spread.

10:14 PM Dec 11
might help to include some stats

Noah Clements
10:16 PM Dec 11
Replace: "their plots with *R. cathartica* planted" with "plots planted with *R. cathartica*"

Noah Clements
10:15 PM Dec 11
Add: ","

Noah Clements
10:15 PM Dec 11
Add: "which"

Noah Clements
10:17 PM Dec 11
raccoons

Management Methods and Success

The spread of R. cathartica must be slowed and can be done through a variety of management methods. Management efforts can be organized by federal, state, and local agencies or private organizations. Often, the extent of management can overwhelm these organizations and the use of volunteers becomes necessary. A report by John Moriarity as part of a symposium on R. cathartica at the University of Minnesota in 2005 describes several conventional management methods and is a good starting point for discussing this subject.

Mechanical management of buckthorn can involve hand-pulling for small saplings, a good exercise for smaller areas and when children and volunteers are involved. Root wrenches can also be used on larger buckthorn individuals but is a slow process also not suited for large areas and can cause soil disturbance.

Chemical treatment is effective against R. cathartica, especially when boles are cut or girdled. Stump treating by resource managers using glyphosate or Triclopyr is common, works well for larger stumps, and can be done over larger areas than mechanical techniques. Moriarty notes that they have used this method to "treat over 300 acres in Ramsey County Parks." Archibold et al. (1997) also supports glyphosate as an effective herbicide to treat R. cathartica, describing how only 6% of the stumps treated with Round-up in their study resprouted, and these sprouts were much weaker.

Looking further into chemical applications to R. cathartica, stump treating and basal bark treatment are still slower techniques compared to foliar spraying. The former two treatments require targeted application or mechanical processes, whereas foliar spraying can treat even larger areas (Schuster et al. 2020). However, foliar spraying can affect non-target species; such is the case for fosamine ammonium (Krenite). This chemical has high efficacy against R. cathartica according to Schuster et al. (2020), but it negatively impacts native forb cover if foliar spraying is not carefully planned. The label for this herbicide recommends use 2 months before leaf

an

Noah Clements
10:18 PM Dec 11
Replace: "litte" with "litter"

Noah Clements
10:19 PM Dec 11
I believe this can lead to reduced ability to burn

Noah Clements
10:20 PM Dec 11
I appreciate the interplay between invasives

Noah Clements
10:22 PM Dec 11
use italics in this section

season for positive long-term effects.

Fire is a physical tool used by resource managers to reduce R. cathartica coverage in native ecosystems. A single prescribed burn may not be very effective against R. cathartica thickets, but several successive burns can reduce density (Archibold et al. 1997), and is especially effective against seedlings. The Archibold et al. study (1997) also highlights how fires that occur after herbicide applications can be useful. Additionally, prescribed burns are useful in areas that are adapted to fire (Kline 1981), meaning native plants are adapted to and resistant to fire and will not be harmed by a prescribed burn. These burns are generally conducted between March and May when there are low carbohydrate levels which reduces re-sprouting vigor (Gale 2000). Unfortunately, in forested areas heavily populated by R. cathartica there may be less leaf litter, and leaf litter is a necessity to move fire to different areas, ~~and therefore~~ rendering fire less effective (Gale 2000).

Lonicera maackii

Noah Clements
10:27 PM Dec 11
what kinds of ecosystems?

Noah Clements
10:27 PM Dec 11
Replace: "and therefore" with ","

Physiology and Ecological Adaptations

L. maackii have large fruiting events, and the seeds contained in these berries are not only capable of dispersing long distances, they can germinate in a wide range of light, temperature, and soil conditions (McNeish & McEwan, 2016). Seeds are dispersed through stream corridors and native bird and white-tailed deer defecation. In fact, Castellano and Gorchov found that 68% of *L. maackii* seeds were still viable after passing through the intestinal system of white-tailed deer, specifically supporting dispersal to edge habitats. These dispersal mechanisms allow *L. maackii* populations to quickly distribute across a new environment, and facilitation by white-tailed deer increases introduction to easily invaded edge habitats.

After germination, *L. maackii* exhibits rapid growth and environmental plasticity. As an immature shrub, it begins by rapidly producing many stem shoots, later shifting resource allocation to height and reproduction, leading to the formation of dense thickets (Deering & Vankat, 1999). Further contributing to dense stands of *L. maackii* is its ability to resprout upright stems when they are clipped (Deering & Vankat, 1999). Environmental plasticity allows this species to thrive in a variety of environmental conditions, including the darker and disturbed areas where native species have trouble establishing. Luken et al. found that while shrubs produced significantly more fruit in high sun environments, they can utilize a range of light levels more effectively than native species.

Similar to many other invasive plant species, *L. maackii* has a phenology that differs from native species in the invaded habitat (McNeish & McEwan, 2016). In comparison with native species, *L. maackii* has a longer growing season, with leaf development occurring two to three weeks earlier in the spring and leaf abscission occurring well into the winter owing to the freeze-resistance of the leaves (McEwan et al., 2009a).

The combination of growth characteristics and phenology gives *L. maackii* the ability to outcompete native plant species in ideal conditions, and long-distance dispersal mechanisms along with environmental plasticity allow it to colonize diverse and disturbed habitats where native species struggle to establish. Thus, *L. maackii* can quickly reach invasion status in introduced habitats. The influence of these traits does not stop there, however. *L. maackii's* impact on native flora and fauna increases with population density, and the effects stretch across numerous ecological scales.

Noah Clements
10:29 PM Dec 11
define

Noah Clements
10:34 PM Dec 11
is this also why buckthorn has a longer growing season?

suggests that forests invaded by this shrub have significantly less herb fecundity, fitness, and growth (Gould & Gorchov, 2000). Native tree sapling abundance also decreases under *L. maackii* invasion, decreasing the recruitment of secondary forests (White et al., 2014). These interactions are predicted to alter species composition in invaded forests, which ultimately impacts community structure, function, and successional trajectories (Hartman & McCarthy, 2008).

L. maackii interacts with native fauna in a wide variety of ways. To begin, numerous studies have examined the impacts of *L. maackii* invasion on insect communities, with differential results. For example, McKinney and Goodell found that the presence of *L. maackii* reduces pollination visits to spotted geranium, while Goodell et al. found that the presence of *L. maackii* increases pollination visits to the largeleaf waterleaf. Similar conclusions have been made in regards to arthropod communities, wherein empirical studies have found that some arthropod guilds increase in abundance in *L. maackii* plots, while others decrease (McNeish & McEWan, 2016). It is important to note that Acari (mites and ticks) are one of the groups that demonstrate increased abundance in *L. maackii* plots (Christopher & Cameron, 2012). This evidence, along with results from Shewhart el al. showing increased mosquito egg survivorship in *L. maackii* stands, suggest that this species may impact mosquito and tick populations-ultimately affecting the incidence of human disease (McNeish & McEwan, 2016). Looking deeper into habitat impacts, the extensive branching in dense *L. maackii* thickets impacts avian species in two major ways. First, the increased habitat leads to *L. maackii* invaded forests having increased densities of understory bird species and decreased densities of upper-canopy birds (McCusker et al., 2010). Second, the bushy growth pattern has been connected with increased perching sites for brown-headed cowbirds, leading to increased brood parasitism and reduced annual bird reproduction (Rodewald et al., 2010). Not only do these thickets alter native habitats, the fruit does not offer a significant source of nutrition for birds and mammals (McNeish & McEwan, 2016). Amphibian communities are also impacted by the physical habitat alteration, exhibiting reduced diversity in habitats where temperature and humidity were decreased due to shading from *L. maackii* (Watling et al. 2011c). Habitats can be altered chemically as well as physically, and this is showcased by the changes in development and behaviors in American Toads connected to leaf litter and soil contaminated with *L. maackii* secondary metabolite leachate (Hickman & Watling, 2014). These chemical interactions go

altered chemically as well as physically, and this is showcased by the changes in development and behaviors in American Toads connected to leaf litter and soil contaminated with *L. maackii* secondary metabolite leachate (Hickman & Watling, 2014). These chemical interactions go

beyond their impacts on amphibians, possibly altering ecosystem processes and functioning at the very base: microbial communities. *L. maackii* alters soil composition as leaf-litter breakdown is five times as fast as many native plant species and has greater nitrogen and less lignin, supporting ~~distinguishable~~ microbial communities distinguishable from those produced by native plants (Arthur et al., 2012).

The combination of these interactions is representative of the larger scale alterations in ecosystem function and processes that are~~is~~ facilitated by the invasion of *L. maackii*. Taken together, it has been shown that *L. maackii* alters invaded ecosystems at every level: nutrient cycling, soil microbial communities, plant species growth and composition, animal species richness and abundance, and possibly vector-borne disease incidence. These findings support the hypothesis that the effects of *L. maackii* are complex and vary across ecosystems and ecological scales (McNeish & McEwan, 2016). The scope of *L. maackii* impacts leads to an increased need to understand its spread and management.

Noah Clements
10:43 PM Dec 11
maybe add stats

Noah Clements
10:44 PM Dec 11
Arthropods include insects, along with spiders and crustaceans

Noah Clements
10:45 PM Dec 11
does diversity increase or decrease?

Noah Clements
10:46 PM Dec 11
I know that house wrens prefer brushy areas. Though native, these birds are very common and aggressive and will remove eggs of other species like bluebirds and chickadees

Noah Clements
10:47 PM Dec 11
This would flow better if reworded or separated into 2 sentences

Noah Clements
10:48 PM Dec 11
Delete: "distinguishable"

Noah Clements
10:48 PM Dec 11
Replace: "is" with "are"

studies have shown that the largest reductions in *L. maackii* individuals occur when mechanical management methods are combined with chemical management methods. Most methods begin with the mechanical process of stem cutting followed by pesticide application. Schulz et al. found that seasonal stem followed by stem application of 18% glyphosate was up to 29% more effective (56% vs. 75-85%) than stem cutting followed by foliar pesticide application. This result was confirmed by Rathfon and Ruble, who upon testing four removal methods, found that stump cutting coupled with chemical application was most effective against large individuals. These methods have been found to be six times more successful when employed annually until eradication than when used only once (Loeb et al., 2010). In an experimental removal/nonremoval study, Hartman and McCarthy found that three years after removal of *L. maackii*, seedling survivorship was significantly greater than in plots with *L. maackii*. These results are bolstered by Runkle et al., who found that seven to eight years after *L. maackii* removal, plant cover, tree seedling density, and species richness increased.

These methods are effective, but questions remain about their usefulness on large and distributed *L. maackii* populations. Wider scale management methods may need to be employed to address heavily invaded ecosystems. Prescribed fire has been used to control *L. maackii* along with other invasive species. Fire has produced limited mortality on bush honeysuckle species in spring, summer, and fall season burns (Zouhar et al., 2008). Fire has seen success completely killing young *L. maackii* individuals, but after one burn will likely only top-kill adults, allowing them to resprout from their intact roots (Czarapata, 2005). Ultimately, the chosen management method is context specific, and thanks to extensive research, land managers have an arsenal of methods to choose what best fits the needs of the ecosystem.

CONCLUSION

ACKNOWLEDGEMENTS

Noah Clements
10:51 PM Dec 11
seasonal stem?

Noah Clements
10:52 PM Dec 11
are there any studies on benefits for fauna?

Noah Clements
10:55 PM Dec 11
is fire hindered by honeysuckle leaves? Do they decompose quickly like buckthorn?