Effects of Climate Change on the Invasive Ecology of the Amur Honeysuckle, *Lonicera maackii* (Ruprecht) Maximowicz (Caprifoliaceae), and Its Impact on Native Wildlife Species and Communities in the Midwestern and Eastern United States[1]

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Abstract: Climate change significantly impacts species composition, competition, range, and variability. Invasive species, such as the Amur honeysuckle, *Lonicera maackii* (Ruprecht) Maximowicz (Caprifoliaceae), which is native in western Asia, are rapidly expanding, and altering forest ecosystems in the United States. I attempt to provide a framework for initially understanding the effects of climate change on *L. maackii* and its relationship with the native wildlife. To assess the influence of global climate change on invasive species, such as *L. maackii*, and to help direct future research and understanding of the complexity of ecosystems with invasive species like *L. maackii*, I suggest direction for future research to address important knowledge gaps on the ecological impacts of *L. maackii.* For instance, effects of *L. maackii* on native plants have been documented to a great extent but, little is known about the influence of *L. maackii* on native wildlife species, specifically leaf-litter invertebrates, and amphibians. Studies show that the Amur honeysuckle impacts native wildlife species with pressures such as increased bird nest predation due to it being low to the ground and bushy in appearance, leading to decreased nesting success and population sinks in some bird species. The Amur honeysuckle provides cover to small mammals against predators and alters the microclimate and chemical composition of nearby waters of amphibian habitats making them more susceptible to predators. *Lonicera maackii* has both a positive and negative relationship with pollinators on crop fields. *Lonicera maackii*'s fruit also lacks nutritional substance and its effect on the ecosystem is widely unknown. I review how basic ecological principles can be used to predict the response of honeysuckle to climate change and its future impact on native wildlife.

Key Words: Climate change, invasive plant, ecology, Amur Honeysuckle, *Lonicera maackii*, Caprifoliaceae, native wildlife communities, midwest United States of America, eastern United States of America

Introduction

The effects of climate change are becoming more apparent around the world as natural disasters become more devastating and costly, snow cover decreases, and the oceans rise, warm, and become more acidic (Fant et al. 2020, Ghazali et

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al. 2018, Neumann et al. 2021, Ornes 2018, Sanderson et al. 2002). The effect of climate change on ecosystem biodiversity is increasingly threatening as well, questioning if we are in the midst of the sixth mass extinction (Barnosky et al. 2011, Pievani 2013). The negative effects of invasive species are exacerbated by climate change due to their advantageous traits that give them a competitive advantage over native plants (Bellard et al. 2013, Guiden et al. 2015, Kolbe et al. 2015). One such impact is outcompeting native species for light resources (Sena et al. 2021). However, invasive species can have both direct and indirect effects on native wildlife species (Dukes et al. 2009, Schlea and Holzmueller 2012). One impact is decrease in nesting success when Morrow's honeysuckle was used as a nesting substrate and found surrounding the nest (McChesney and Anderson 2015). Invasive species can be detrimental to their ecosystem by changing the behavior of native wildlife communities (Bates et al. 2013, Bell et al. 2021, McChesney and Anderson 2015, Sena et al. 2021, Weiskopf et al. 2020). General climate change trends include changes in species behavior, phenology, and general shifts in species range northward and higher in elevation (Chen et al. 2011, DeGaetano and Allen 2002, Körner and Basler 2010, Weiskopf et al. 2020).

Forests in the United States are seeing an unprecedented amount of change due to climate change and human pressure such as increase in droughts and wildfires, increase of invasive species and forest pests and pathogens outbreaks as well as habitat loss. Climate change, directly and indirectly, affects forest growth by changing the temperature and rainfall, and higher concentrations of carbon dioxide (EPA 2021). According to the EPA, these climate impacts, in conjunction with human pressures, enact various changes in forest ecology. With increasing temperatures comes an extension of the growing season, a decrease in precipitation leading to drought, and an increase in carbon dioxide, allowing more productivity in soils (EPA 2021). There are an estimated 5,000 invasive species established in the United States (Kerns and Guo 2012). As climate change reduces the plasticity of natural habitats, this effect is compounded by the influence of invasive species (IUCN 2021). Climate change adds to the effects invasive species have by creating new opportunities for invasive species from introduction through to spread and establishment (Bellard et al. 2013, IUCN 2021). The destruction and management of invasives incur high economic costs, which average $26 billion per year. (Crystal-Ornelas et al. 2021, USDA 2021). According to Seebens et al. (2021), North America will see a 23% increase in invasive species from 2005 to 2050. Key ecosystem functions, such as productivity, decomposition, and energy flow and nutrient cycling, are altered in the presence of invasive species and climate change further alters the biotic and abiotic conditions by facilitating the spread of invasive species (Bellard et al. 2013, Devine and Fei 2011). It is important to understand the behavior of invasive species and their interactions with the surrounding environment to protect our ecosystems.

The Amur honeysuckle, *Lonicera maackii* (Ruprecht) Herder (Caprifoliaceae), is a highly invasive bush native to northeastern Asia (Luken and Thieret 1995). *Lonicera maackii* (Figures 1-2) was initially brought to the US in 1898 by the New York Botanical Garden to be used as an ornamental and it is primarily found in the Midwest and Eastern United States (Luken and Thieret 1995). Before spreading quickly, it was used for various ecological reasons, such as wildlife cover and soil erosion control (Luken and Thieret 1995). *Lonicera maackii* leafs out weeks earlier than native plants in the spring and loses its leaves weeks later than native plants in the winter, giving it a competitive advantage for vital resources (Fridley 2012). *Lonicera maackii* forms a dense forest understory that outcompetes native plants by blocking valuable sunlight (Fridley 2012). This invasive species disrupts ecosystem functions and processes by displacing native species and altering nutrient cycling and chemistry (Devine and Fei 2011).

Figures 1 and 2. The Amur honeysuckle, *Lonicera maackii*. Photo credit: Nathan Johnson. https://theoec.org/blog/amur-honeysuckle-lonicera-maackii/.

An essential part of addressing invasive species is ensuring that they are thoroughly studied and that the impact of their presence on ecosystems is well-documented. Although effects on native flora have been documented to a great extent, little research is available regarding the direct and indirect relationships between *L. maackii* and native wildlife species. There is an extensive literature on *L. maackii*. However, gaps in our knowledge include the direct and indirect effects of *L.* maackii on pollinators, the allelopathic effects depending on the abiotic factors in the environment, how *L. maackii* impacts soil composition, how those impacts affect leaf-litter invertebrates, and how the low nutritional quality of *L. maackii's* fruits affect birds who eat its fruits.

This review analyzes *L. maackii's* invasive characteristics and their effect on the native wildlife in the Midwest and Eastern United States of America. Also, I examine how basic ecological principles predict *L. maackii's* response to climate change. Finally, I identify and discuss future research directions that will strengthen our understanding of this invasive species and direct efforts to mitigate the anticipated worsening impacts of *L. maackii* on native wildlife due to climate change.

Life-history traits of *Lonicera maackii* that facilitates its invasiveness

Dispersal mechanisms

Long-distance dispersal, propagule abundance, and propagule pressure measure of the number of individuals released into a region where they are not native are key advantageous traits of many invasive species (Carr et al. 2019, Lieurance 2016). A study on secondary wind dispersal (SWD) of seeds of the invasive tree of heaven, *Ailanthus altissima* (Miller) Swingle (Simaroubaceae), which is the main host of the invasive insect spotted lanternfly, *Lycorma delicatula* (White, 1845), show seeds dispersed at a distance of up to 456 m (Kowarik and von der Lippe, 2011). Dispersal distance also increased for *A. altissima* as the time the seed was released increased (Kowarik and von der Lippe 2011). *Lonicera maackii* is another good example of long-distance dispersal. *Lonicera maackii* produces fruit at six years, at the earliest (Gorchov et al. 2014), and consumption of *L. maackii*'s fruits occurs from November to February (Bartuszevige 2004). The fruit of *L. maackii* is extremely durable, producing seeds that germinate at various temperatures, lighting, and soil conditions (Lieurance 2016, Luken and Goessling 1995).

Most of *L. maackii*'s seeds are consumed by birds or deer that disperse the seeds by defecation (Gorchov et al. 2014, Guiden et al. 2015, Luken and Goessling 1995). *Lonicera maackii* fruit is also shown to germinate in situations where mammals step on the fruits that have fallen to the ground, releasing the seeds (Bartuszevige and Gorchov 2006). Of the seventeen species determined to consume *L. maackii* fruits in Ohio, five species were determined to be seed-dispersers including the American Robin (*Turdus migratorius*) (Figure 3), Cedar Waxwing, (*Bombycilla cedrorum*) (Figure 4), European Starling (*Sturnus vulgaris*), and Northern Mockingbird (*Mimus polyglottus*) (Bartuszevige and Gorchov 2006). The Eastern Bluebird (*Sialis sialis*) is also thought to be a seed-disperser of *L. maackii,* but the study was unable to catch any (Bartuszevige and Gorchov 2006). The five species that ate and dispersed the seeds were shown to disperse them in their habitats whether that be edge habitats or tree-fall gaps (Bartuszevige and Gorchov 2006). While birds disperse *L. maackii* seeds to nearby habitats, ungulates disperse them over long distances (Guiden et al. 2015). It is suggested that defecation of *L. maackii* seeds by ungulates may potentially link fragmented habitat patches where female white-tailed deer dispersed seeds further than 100m and rarely up to 7900m (Guiden et al. 2015).

Figures 3 and 4. Avian consumers of *Lonicera maacki* fruits. 3. American Robin, *Turdus migratorius*. 4. Cedar Waxwing, *Bombycilla cedrorum*. Photo Credit: – C Watts. https://www.flickr.com/photos/watts_photos/16900930244/in/photostream/ . Creative commons license.

Environmental plasticity and phenology

A study in deciduous forests showed that invasive shrubs grow leaves earlier and maintain leaves 4 weeks longer than native shrubs (Fridley 2012). *Lonicera maackii* is particularly threatening due to its rapid early growth, which gives it a competitive advantage over native plants when it outcompetes them for resources (Luken and Thieret 1995). *Lonicera maackii* leafs out about two to three weeks earlier in spring than natives (Fridley 2012). A study found that *L. maackii* thrives in environments with lower leaf litter (Bartuszevige et al. 2007). A Kentucky study on the relationship between *L. maackii* and flowering spring wildflowers found a relationship between high *L. maackii* abundance with lower species richness and abundance of flowering spring wildflowers (Sena et al. 2021). This relationship can be attributed to the rapid early growth of *L. maackii.* It was also found that study plots which did not contain *L. maackii*, had a 2.8-3.8 times higher abundance of flowering plants than the study plots with high *L. maackii* abundance during all four weeks of their study (Sena et al. 2021). This relationship may also be attributed to *L. maackii's* invasion success, where native plants diversity and abundance is lowest in areas with high percent cover of *L. maackii* due to competition for light resources (Culley and Cameron 2016, Luken and Thieret 1995, Shields et al. 2015). Light intensity under *L. maackii* is lower than native understories and temperature is studied to be lower under *L. maackii* during the spring season (Chen and Matter 2017).

Figure 5. Amur honeysuckle #1, *Lonicera maackii*. Photo credit: Travis Mitchell. https://radfordphenology.weebly.com.

Figure 6. Amur honeysuckle #4, *Lonicera maackii*. Photo credit: Travis Mitchell. https://radfordphenology.weebly.com.

Several studies have contributed understory success of plants to tree canopy mortality (Jain et al. 2020, Mestre et al. 2017, Pec et al. 2015, Steinke et al. 2020). One study contributed increased growth in *L. macckii* to mortality in the tree canopy layer (Bartuszevige et al. 2007), meaning *L. maackii* is most successful with more sun. *Lonicera maackii* also has a greater freeze tolerance than that of native plants (McEwan et al. 2009). This means that *L. maackii* will be able to survive more extreme temperatures than native plants giving it a competitive advantage. The freeze tolerance of *L. maackii's* leaves allows it to survive longer than native flora during periods of freezing temperatures. In the presence of 47°F, the leaves on *L. maackii* persisted through the cold (Figure 5, Figure 6). Invasive plant phenology varies in comparison with native plants. *Lonicera maackii*'s phenology is further enhanced by the properties of its surroundings.

Allelopathy

Several studies have demonstrated that certain invasive plant species produce allelochemicals that have a biochemical effect on native plants (Ens et al. 2009, Hierro and Callaway 2003). Allelopathy in plant communities is one of the contributing factors of invasive species success by suppressing seed germination, nutrient uptake, and growth in native plant species (Bauer 2012, Ens et al. 2009). There is evidence of *L. maackii's* allelopathy effects on some plants (Bauer 2012, Cipollini et al. 2008).

A methanol extraction from the leaves of *L. maackii* showed several substantive chemical compounds and methanol-water extracts that inhibited the sprouting of a target plant (Cipollini et al. 2008). Further analysis determined that the main allelopathic chemicals detected in leaf extracts were luteolin and apigenin derivatives (Cipollini et al. 2008). Although allelopathic tendencies were discovered in *L. maackii*, allelopathy itself greatly depends on abiotic factors in the environment, such as soil composition (Cheng and Cheng 2015, Scavo et al. 2019). Therefore, more research is needed to understand the relationship between *L. maackii*'s allelopathy and its impact on the spread of this invasive species.

Plant-soil feedbacks

Several studies have shown the influence of *L. maackii* on litter composition and the microbial community (Arthur et al. 2012, Hopfensperger et al. 2017, Kolbe et al. 2015, McNeish et al. 2018). A study found that the understory of *L. maackii* showed higher levels of nitrogen, a lower carbon to nitrogen ratio, lower lignin, and five times faster decomposition rates than the native trees (Arthur et al. 2012). Another study examined the impact of *L. maackii* on soil organic carbon (SOC) and N density where they found that at sites where *L. maackii* had been present the longest showed the highest SOC and N densities (Kolbe et al. 2015). This is likely due to the increased litter decomposition and alteration of soil composition.

The dense forest understory of *L. maackii* has also been shown to impact throughfall levels defined as the amount of rain that reaches the forest floor, impacting the forest floor soil composition. A study on the effect of *L. maackii* and the chemistry of throughfall, found that 28-64% of throughfall reached the *L. maackii* bushes compared to the top of the canopy (McNeish et al. 2018). The percentage that reached *L. maackii* means that there was less rainfall under the honeysuckle (McNeish et al. 2018). The study also found that total carbon, total organic carbon, and dissolved inorganic carbon were greater under *L. macckii* compared to collections from the upper tree canopies and plots without *L. maackii* (McNeish et al. 2018). Nitrogen densities were also highest in areas with *L. maackii* (Arthur et al. 2012). A study that measured ecosystem function in a restored forest found that after removing *L. maackii* and with efforts to reintroduce native species, restored sites had more available soil nitrogen and faster nitrogen mineralization rates (Hopfensperger et al. 2017). It is clear from these studies that *L. maackii* alters the soil composition of the forest understory.

Climate change data and impacts by geographical region

Studies show that future changes in the US climate are consistent with warmer overall temperatures, including shrinking snow cover, more frequent droughts, and increased winter precipitation (Hayhoe et al. 2006). According to data provided by the EPA, Climate Change in the US is associated with rising temperatures, shifts in snow and rainfall patterns, and more extreme weather events such as an increase in heatwaves (EPA 2021). Global warming is also expected to lengthen the growing season by approximately 4-6 weeks in the Eastern United States, affecting the growth patterns of all plant life (DeGaetano and Allen 2002, Dukes et al. 2009). For the purposes of this study, climate information has been narrowed to the Midwest and Northeast United States, where Amur honeysuckle primarily resides (Figure 5).

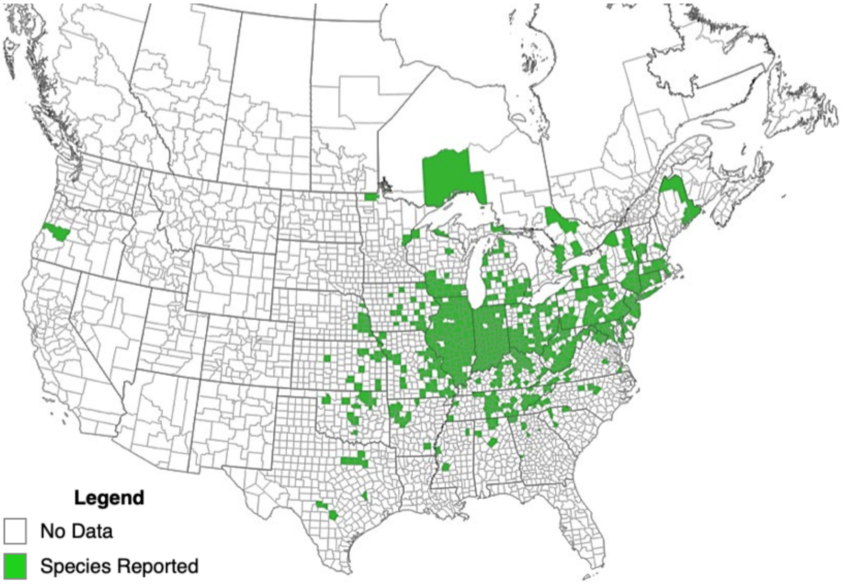

Figure 7. Amur honeysuckle, *Lonicera maackii*. Photo Credit: EDDMapS. https://www.bugwood.org/contact.cfm

The average annual temperature in the Northeast has risen by +0.08 ± 0.01° C each decade since 1900 (Hayhoe et al. 2006). In line with recent trends, winter precipitation is expected to increase by 10%-15% (DeGaetano and Allen 2002). Some reports even include summer precipitation increase, but severe droughts will likely increase in frequency due to variability in rainfall. (Dukes et al. 2009, Winkler et al. 2012). The EPA (2021) expects precipitation to have increased by almost 20% in some areas with greater increases in the East. Since 1901 temperatures across the United States have increased by 0.16°F per decade (EPA 2021). With precipitation increases in the winter and spring, summer is projected to become drier (EPA 2021). A study by Tebaldi et al. (2006) used multi-model simulations to predict that the number of frost days in the Northern Hemisphere will also continue to decrease (Tebaldi et al. 2006).

Changing climate and potential outcomes of L. maackii

The advantageous life-history traits of *L. maackii* point to it being an incredibly invasive species, able to outcompete native plants in a variety of ways (Luken and Thieret 1995). Extended leaf phenology is an important characteristic of invasive species (Fridley 2012, Smith 2013, Smith and Hall 2016). Non-native species leaf emergence is sensitive to spring temperatures and show earlier full extension of leaves (Fridley 2012). There is evidence that extended leaf phenology increases herbivore density, allowing invasive species to dominate native species, even when the invader is inferior to the native species (Smith and Hall 2016). It is suggested that species with extended leaf phenologies may be able to increase the production of allelochemicals due to increased resource acquisition in early spring (Smith 2013). It is also suggested that invasive plants may influence herbivore population dynamics by providing food at times it would be unavailable on native species (Smith 2013) With a longer growing season, according to climate experts (Degaetano and Allen 2002, EPA 2021, Hayhoe 2006, Ornes 2018), I suggest that *L. maackii* will be able to leaf out even earlier than it already does compared to native plants where *L. maackii* leaf-out is suggested to be impacted by climate and precipitation (Zohner and Renner 2014). With earlier leaf-out suggested by researchers, invasive plants like *L. maackii* will have more time to overtake the areas they are present in.

One study predicts that there will be an increase in invasive species in northeastern United States and globally, invasive species will be more susceptible to invade in the northern hemisphere compared to the southern hemisphere (Bellard et al. 2013). How will this effect on the growing pattern of plant species relate to native wildlife species? With this diminishing effect on native plants, the native wildlife species will also be directly and indirectly impacted by competition for resources (Culley and Cameron 2016, Luken and Thieret 1995, McKinney and Goodell 2011, Iler and Goodell 2011, McKinney 2010, Sena et al. 2021, Shields et al. 2015). If climate models predict that by 2050, the northeastern US will warm by 1.5°C with increased winter precipitation, then will invasive plants like Amur honeysuckle have an increased advantage? If so, how will this change affect native wildlife species? Suppose the temperature in the northeastern United States continues to warm. In that case, it can be hypothesized that *L.* maackii will move northward, deeper into Canada, and higher in elevation.

It has been studied that photoperiodism may slow range shifts in invasive species because their phenology is adapted to daylength and light availability (Bradshaw and Holzapfel 2001, Saikkonen et al. 2012). It was found that across all species and ecosystems, climate warming advanced all early season phenophases (Stuble et al. 2021).

If native plants leaf out too soon, they will be affected by spring frost which does not affect *L. maackii*. In a study on frost damage, it was found that the most vulnerably species to frost damage are those that began development earliest in spring (Augspurger 2013). The study supports the prediction that frost damage has increased in recent decades (Augspurger 2013). In spite of increased frost damage (Augspurger 2013), species in the Midwest and Eastern United States rely on phenological strategies such as cold winter chills and longer days instead of only relying on warm spring temperatures (Zohner et al. 2020). Some species, however, may profit from a warmer climate and gain competitive advantage over photoperiod-sensitive species (Körner and Basler 2010). Other factors that limit the range of *L. maackii* include land use change and human disturbance (Sala et al. 2000, Wingfield et al. 2015), changes in atmospheric CO_2 (Sala et al. 2000) or quality of old habitats deteriorating (Wingfield et al. 2015).

It is worth noting that *L. maackii*'s spread will be into areas with different forest plant communities and wildlife species. However, it is studied that certain wildlife species will also increase in range under climate change (Hitch and Leberg 2006, Kanda 2005, Myers et al. 2009, Thomas and Lennon 1999, Xu et al. 2021). Studies on *L. maackii's* life-history traits will still be applicable and important when considering new study areas. *Lonicera maackii's* life-history traits will be vital to this species adaptability and how it shifts in range due to climate change. Studies show *L. maackii* able to survive in various light levels as well, meaning as temperatures and sunlight increase due to climate change it will have an increased competitive advantage over native plants as it attempts to spread north in range (Bartuszevige et al. 2007, Luken and Thieret 1995).

Ecological role of Lonicera maackii in the midwest and eastern United States birds

Several studies have been completed regarding the direct effect of *Lonicera* spp. on nesting success (Borgmann and Rodewald 2004, McChesney and Anderson 2015, Schmidt and Whelan 1999, Wenner 2013) however, the indirect effect on native birds has been studied less extensively. The appeal of *Lonicera* spp. as a nesting substrate relates to its phenology of early leafing in spring and lack of thorns (McChesney and Anderson 2015). Even when *Lonicera* spp. is present in the surrounding environment and not used as a nesting substrate, nesting success is still decreased (McChesney and Anderson 2015). The indirect effects on native bird species due to the presence of *L. maackii* are widely understudied, however, some studies have been done, and others have been done on Morrow's honeysuckle which resides in the same genus. Because Morrow's honeysuckle is in the same genus as *L. maackii*, it has many of the same life-history traits. For this reason, impacts caused by any of the *Lonicera* spp. in relation to birds are assumed to have a similar relationship with *L. maackii*.

A study examining field sparrows, *Spizella pusilla*, and Morrow's honeysuckle, *Lonicera morrowii* A. Gray, found reproductive success of this species to not be enough to maintain a stable population (McChesney and Anderson 2015). Reproductive success was based on the density of *L. morrowii* surrounding the nests as well as the nesting substrate used (McChesney and Anderson 2015). Using a population model, they found that the reproductive success of *S. pusilla* resulted in a population sink because it was not sufficient enough to maintain a stable population (McChesney and Anderson 2015). Another study examined Gray Catbirds, *Dumetella carolinensis*, and *Lonicera* spp. (Gleditsch and Carlo 2014). However, they did not find nest predation to increase in areas with high honeysuckle abundance (Gleditsch and Carlo 2014). It is important to note that not all studies on nesting success use the same measurements. The large range in reported nesting success can also vary due to other factors such as nesting substrate, habitat quality, and early success (McChesney and Anderson 2015).

By using basic ecological concepts such as bird nesting behavior, it can be inferred that high densities of *L. maackii* in the environment surrounding bird nests play a role in predicting nesting success (McChesney and Anderson 2015). *Lonicera maackii* alters its surrounding landscape by outcompeting native plants for resources and changing soil composition (Arthur et al. 2012, Hopfensperger et al. 2017, Kolbe et al. 2015, McNeish et al. 2018). This impact can also change the quality of resources such as insects, seeds, or fruits (Gleditsch and Carlo 2014). The dense forest understory of *Lonicera* spp. can also lead to cover for predators, which increases nest predation in nests built in or around *Lonicera* spp. (McChesney and Anderson 2015).

For example, the carbohydrate-rich fruits (Figure 6) of *L. maackii* are highly attractive to birds that consume them but do not compare to the nutritional value of the lipid-rich fruits of native species (Ingold and Craycraft 1983). More studies need to be done to understand if the lack of nutrients in *L. maackii* fruit causes any change to native bird specie's diet if *L. maackii* was not in their environment and if *L. maackii* was more prevalent.

Figure 8. Amur honeysuckle, *Lonicera maackii*. Photo credit: Nathan Johnson. https://theoec.org/blog/amur-honeysuckle-lonicera-maackii/.

If climate experts agree on a warming temperature which will lead to increased range and abundance of *L. maackii* (Bellard et al. 2013), nesting success and nest predation in songbirds will also increase. It was studied that this could lead to some songbird populations becoming endangered or even extinct (McChesney and Anderson 2015). It was also studied that bird species will shift northward due to climate change (Hitch and Leberg 2006, Thomas and Lennon 1999). More research must be done on the effects of *L. maackii* and native bird species to discover if a more stringent management process of *L. maackii* needs to be done to keep bird species from becoming endangered. More research is needed regarding the fruits of *L. maackii*, particularly the nutrient difference in the fruit versus native flora. It is reasonable to assume that with climate change increasing the range of *L. maackii* and bird species, more bird species will consume the fruits. Research is needed to know what effect this will have on native bird species. Since bird species are studied to move northward in range under climate change (Hitch and Leberg 2006, Thomas and Lennon 1999), I hypothesize that there will be more bird species consuming *L. maackii*'s fruit which will lead to decreased nutritional intake and could adversely affect the density and abundance of native bird species.

Pollinators

Pollinators not only rely on flowering plant species as a source of food (nectar and pollen), but humans also increasingly rely on pollinators. About 35% or one-third of our food is pollinated by animals, most of which are bees (McGregor 1976, USDA). *Lonicera* spp. provide nectar and pollen for a variety of pollintators including *Apis mellifera, Bombus terrestris, Bombus lucorum, Bombus hortorum, Bombus pascuorum* as well as syrphid flies, wasps, and coleopterans (Jachula et al. 2019). A study in Poland found mean sugars per shrub of *L. maackii* to be 66.3g and mean pollen yield to be 110.1g (Jachula et al. 2019). Agricultural production would decrease without pollinators by 3 to 8 % (Aizen et al. 2009). As pollinators decline or become endangered, the result may be an increased demand for agricultural land (Aizen et al. 2009). As a result of pollinating insects, the quality or quantity of 39 of the 57 major crops worldwide increase (Aizen et al. 2009).

Invasive plants indirectly disrupt native plant reproduction through competition for pollination (McKinney and Goodell 2011). Other studies show an indirect relationship between pollinators and *L. maackii* (Iler and Goodell 2011; McKinney 2010). After examining the effects *of L. maackii* on a native herb (*Hydrophyllum macrophyllum*), it was found that pollinators visited *H. macrophyllum* less frequently when located in areas with some *L. maackii*; however, this did not affect the seed set of *H. macrophyllum* (Iler and Goodell

2011). Another study plot found that *H. macrophyllum* had more pollinator visits when more *L. maackii* surrounded the herb. The increased pollination led to an increase in the seed set of *H. macrophyllum* (Iler and Goodell 2011). Having *L. maackii* in the vicinity of *H. macrophyllum* lead to a mitigation of the effects of shade on pollinator visitation and an increase in seed production (Iler and Goodell 2011). Increased shade from *L. maackii* may be responsible for a negative indirect relationship between pollinator visitation and pollen deposition to native herbs in the presence of *L. maackii* (McKinney 2010). Study plots containing *L. maackii* and *H. macrophyllum* did not co-flower, and fewer pollinators visited (McKinney 2010). There were also fewer pollinator visits in another study plot containing *L. maackii* and *Geranium maculatum* (McKinney 2010). The difference between the studies is that the two plants were co-flowered in Iler and Goodell's (2011) study but not in McKinney's (2010) study. Regardless of how *L. maackii* is impacting pollinator visits to native plants during these studies it is important to note that the nature of *L. maackii* to outcompete native plants regardless of the pollinator visit data results in a long-term impact on the habitat. Therefore, those native plants may be outcompeted to the point where they are not there or not flowering and therefore unavailable to be visited by pollinators.

Edges surrounding crop fields are home to many invasive species. Invasive species can either suppress or facilitate the pollination of crops. While pollinators and their effect on native flora have been studied, less is known about the influence of pollinators on invasive species and their relationship with crops. *Lonicera maackii* is studied to suppress small-bodied bee communities while also attracting large-bodied generalist bees (Cunningham-Minnick and Peters 2020). Fewer large bees visited crops when *L. maackii* was removed; however, smaller bees visited plants surrounding *L. maackii* more often (Cunningham-Minnick and Peters 2020). After two years, it was shown that bees' abundance and species richness increased when *L. maackii* was removed (Cunningham-Minnick and Peters 2020). This study shows a direct relationship between *L. maackii* and the pollination of crops. Not only that, but an increase in crop production would decrease bee species and their resulting pollinating in wild landscapes (Klein et al. 2007). While it is true that pollinator visits to crops may temporarily decrease in response to removing invasive shrubs, it is important to acknowledge that where these invasive shrubs dominate on edges, they are also the dominant flowers on those edges. Replacing those invasive shrubs with native flowering small trees and shrubs will not only provide the pollinator services lost by removing the invasive shrubs, but also provide numerous ecological benefits to native wildlife.

Empirical studies show both direct and indirect effects on native flora and crop fields and high nutritional content of *L. maackii*'s pollen and nectar (Cunningham-Minnick and Peters 2020, Iler and Goodell 2011, Jachula et al.

2019, Klein et al. 2007, McKinney 2010, McKinney and Goodell 2011). While it is not possible to predict the direction or magnitude of the direct and indirect effects on native flora and crop production, it is clear that a changing climate will alter the interaction. While habitat loss is thought to be an important factor driving bee decline (Winfree et al. 2009) climate change in part has contributed to the decline in pollinator abundance (Potts et al. 2010, Williams et al. 2007), species distribution (Hickling et al. 2006) and species richness (Dormann et al. 2008). In a review on the role of climate change in pollinator decline it is suggested that climate change is an important driver in pollinator biodiversity loss (Vasiliev and Greenwood 2021). The effects of climate change could exacerbate a direct relationship leading to higher cultivations of large-bodied generalist bees or an indirect relationship leading to higher or lower pollinator visits to nearby plants. More research is needed to come to a comprehensive conclusion. More empirical studies are necessary to fully understand the indirect relationship between pollinators and *L. maackii*.

Small mammals

Little is known about the influence of *L. maackii* on small mammals in regard to population density, food consumption, and behavior. The bitter-tasting fruit of *L. maackii* does not deter native wildlife from consuming it (Williams et al. 1992). Deer mice (*Peromyscus maniculatus*) consume seeds from over 63% of *L. maackii* fruits, which was consistent in both a lab and field study (Williams et al. 1992). While small mammals are not deterred from consuming the fruits, it does not explain how this influences the foraging behavior of these mammals.

A study in Indiana examined how the removal of *L. maackii* influences the abundance and habitat use of white-footed mice (*Peromyscus leucopus*) (Shields et al. 2014). They found a relative increase in *P. leucopus* in sections with and without *L. maackii*, the extent of an increase in the area without was greater (Shields et al. 2014). A possible explanation for this is the increase in the cover provided by native plant species after the removal of *L. maackii* (Shields et al. 2014). Another study in Missouri examined a more comprehensive range of small mammals, which included two seed predators, mice (*Peromyscus* spp.) and squirrels (*Sciurus* spp.), as well as two mesopredators, raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) (Dutra et al. 2010). They studied the role of shelter and food on these mammals and found that removal of the cover provided by *L. maackii* in two of their study plots reduced the mammalian activity more than the removal of *L. maackii* fruits in their other two study plots (Dutra et al. 2010). Mice activity was only significant on nights with low or no cloud cover, showing the important role *L. maackii* plays in providing cover for this species (Dutra et al. 2010).

The findings of these studies are consistent with the hypothesis of others that equate higher small mammal activity to habitats that provide greater cover (Coppes et al. 2017, Hunter 2007, Mysterud and Østbye 1999). It is worth noting that Mattos and Orrock (2010) found no statistically significant differences between mice in locations with and without *L. maackii*. Increased foraging activity of small mammals in locations with high densities of *L. maackii* does not equate to higher population abundance of these species (Mattos and Orrock 2010).

It is important to acknowledge that observing trends in abundance (whether that be increases or decreases) at different levels of *L. maackii* densities does not provide a complete story in terms of long-term impacts on small mammals. While small mammals are observed in higher numbers or with higher activity in areas with more *L. maackii* (Dutra et al. 2010, Shields et al. 2014) this does not necessarily mean that this is what is best for their species in the long term. It is studied that small mammals prefer habitats of high canopy cover (Fauteux et al. 2012, Horváth et al. 2001, Zollner and Crane 2003). With invasive shrub thickets, this could actually result in ecological traps whereby animals gravitate towards those thickets for the cover but then do not meet their nutritional needs due to the overwhelmingly dominant food source being a carbohydrate-rich berry (Ingold and Craycraft 1983) from a single species of exotic shrub. More empirical studies are needed to understand if *L. maackii* influences food availability for small mammals.

A combination of land-use changes and global warming has led to increased northern and upward range as well as increased abundance of small mammals (Kanda 2005, Myers et al. 2009). Some small mammal's distribution, however, may be limited by winter temperatures (Bowman et al. 2005, Weigl 1978). Research on several small mammals shows that environmental temperatures affect species populations and distributions (Myers et al. 2009). Habitat fragmentation and urbanization of habitats as well as climate change might limit routes to suitable habitats (Francl et al. 2010). Findings of a study suggest that many species in Indiana may reach a "dead-end" as far as their migration potential goes due to habitat fragmentation and urbanization (Francl et al. 2010).

It is difficult to conclude on the effects of climate change and the interaction with small mammals and *L. maackii*. The empirical evidence in the literature shows both a direct and indirect relationship and no real evidence of which is more likely. Since *L. maackii* is shown to provide great cover for small mammals specifically *P. leucopus* (Dutra et al. 2010, Persons and Eason 2019, Shields et al. 2014), I hypothesize that with the increased northern range of *L. maackii*, small mammals will have a greater opportunity to hide from predators, leading to increased abundance in small mammals.

Ungulates

Lonicera maackii may influence herbivore population dynamics by providing food during early leaf-out when it would otherwise be unavailable (Smith 2013). *Lonicera maackii* comprises a significant amount of the white-tailed deer (*Odocoileus virginianus*) diet, where *L. maackii* made up 14-47% of their annual diet (Martinod and Gorchov 2017). Deer consumption of *L. maackii* twigs and leaves was highest in spring and summer and lowest in winter where deer browsed 0.2-6% of *L. maackii* twigs per month (Martinod and Gorchov 2017). White-tailed deer consuming the leaves and stems of *L. maackii* (Figure 9). The nutritional value of the twigs and leaves of *L. maackii* were also studied to be more nutritious than twigs of other woody species (Martinod and Gorchov 2017). Another study found that *L. maackii* was less preferred compared with other woody species (Wright et al. 2019). This study hypothesizes that there may be some threshold to where white-tailed deer prefer native species over *L. maackii* (Wright et al. 2019). This threshold is also in part due to *L. maackii's* availability earlier in spring (Wright et al. 2019).

Figure 9. Deer eating honeysuckle. Photo credit: Garrykinney https://www.dreamstime.com/stock-image-deer-eating-honeysuckle-image21271371. Creative commons license.

Ungulates alter the composition of forest litter biomass via changes in decomposition (Kasahara et al. 2016, Ramirez et al. 2020) where ungulates decreased litter depth and sapling density and diversity (Ramirez et al. 2020). Removing both deer and *L. maackii* results in an increase of forest biodiversity and abundance (Haffey and Gorchov 2019). Excluding only deer, study plots increased tree seedlings' density (Haffey and Gorchov 2019). While another study found no effect on the overall density, species richness, or diversity of tree seedlings but negative effects on the survival of underplanted seedlings by white-tailed deer due to the alteration of soil composition through feces and urine (Owings et al. 2017). They also attributed increased shade of *L. maackii* to lower survival rates of seedlings in *L. maackii*'s understory (Owings et al. 2017).

With studies showing ungulates altering forest litter biomass (Kasahara et al. 2016, Ramirez et al. 2020) and exerting pressure on forest biodiversity and abundance (Haffey and Gorchov 2019) their effect in addition to *L. maackii*'s (Owings et al. 2017) show significant changes in forest ecosystems. Climate change will further exacerbate the invasive phenology of *L. maackii* and negatively impact forest floor biodiversity and abundance. A literature review on ungulate migration found that climatic variations impact migratory patterns and species abundance of ungulates (Xu et al. 2021). They also found that migratory plasticity is common in ungulates (Xu et al. 2021) where change in distribution is primarily driven by changes in climate (Dawe and Boutin 2016). Milder winters also have the potential to affect ungulate density due to the availability of food (Weiskopf et al. 2019). I hypothesize that the increased range of *L. maackii* and the high nutritional quality of *L. maackii's* leaves and twigs will impact the ungulate communities through increased abundance. Having *L. maackii* as a food resource in early spring could possibly increase herbivore populations (Smith 2013) and therefore increase the pressures on forest ecosystems.

Leaf-litter invertebrates and pestiferous herbivorous arthropods

How the high levels of nitrogen, high total carbon and total organic carbon, lower carbon to nitrogen ratio and fast decomposition rate of *L. maackii*'s understory affects leaf-litter invertebrates and arthropod's is lesser known (Arthur et al. 2012, McNeish et al. 2018). I suggest that this has a direct effect on leaf-litter invertebrates' and arthropod abundance and species richness because of the shade provided by *L. maackii* and high decomposition rate of the understory of *L. maackii* (Arthur et al. 2012).

It was studied that *L. maackii* positively affected earthworm biomass when deer were present and negatively affected earthworms when deer were excluded (Mahon and Crist 2019). Areas with high densities of *L. maackii* contain higher levels of invasive earthworms (Lloyd and Crist 2019). It is not known however whether *L. maackii* is the main driver for earthworm density. Other factors such as tree canopy cover and soil chemistry may be important (Lloyd and Crist 2019). A study on Eurasian earthworms found that mean total earthworm biomass was

35.5% to 85.2% higher in plots with *L. maackii* in the spring as well as 13.8% to 66.0% higher earthworm density across all seasons (Pipal 2014). This may be due to the higher quality of leaf litter due to *L. macckii* but other changes in soil composition due to the shade provided by *L. maackii* may be an important factor during the summer months (Pipal 2014). *Lonicera maackii* produces litter with a lower carbon to nitrogen ratio and lower lignin than native litters (Arthur et al. 2012) which are preferential factors for invasive earthworms (Hendriksen 1990) and may promote the abundance of leaf-litter invertebrates (Pipal 2014).

A study on litter-dwelling arthropod communities found an increased abundance of Araneae in *L. maackii* absent plots and increased abundance of Acari in plots with *L. maackii* (Christopher and Cameron 2012). Lower food availability due to *L. maackii*'s allelochemicals (Cipollini et al. 2008) could have affected the abundance of prey in the litter (Christopher and Cameron 2012). Another study found lower spider diversity in their hedgerow samples and attributed this to the lower complexity at the ground layer due to *L. maackii* (Buddle et al. 2004). A study on shrub-layer insects found that cover of *L. maackii* contributed to higher species richness of Hexapoda and Coleoptera and higher abundance of Hexapoda, Diptera, Hymenoptera, and Psocoptera (Loomis and Cameron 2014). During their study, 33 families were also unique to *L. maackii* present plots (Loomis and Cameron 2014).

Lonicera maackii alters soil composition and makeup (Arthur et al. 2012, Hopfensperger et al. 2017, Kolbe et al. 2015, McNeish et al. 2018) and these studies show that *L. maackii* exerts pressure on leaf-litter invertebrates (Lloyd and Crist 2019, Mahon and Crist 2019, Pipal 2014) and arthropods (Buddle et al. 2004, Christopher and Cameron 2012). A study on leaf-litter invertebrates found that an increase in temperature reduced invertebrate abundance and richness as well as altered soil invertebrate community composition (Figueroa et al. 2021). On the other hand, changes in arthropod populations largely depend on latitudinal location where family richness declines with warming at midlatitudes and increases at high latitudes (Youngsteadt et al. 2016). I hypothesize that under climate change, earthworm biomass and arthropod abundance will increase in areas with *L. maackii* due to a decrease in soil temperature, lower carbon to nitrogen ratio, and increased decomposition under *L. maackii*. However, more empirical studies are necessary to understand the relationship between *L. maackii* and litter-dwelling invertebrates and arthropods.

Forest pests and pathogens

The EPA (2021) points to warmer temperatures in the Midwest and Eastern United States, likely leading to an increased outbreak of forest pests and pathogens. The Hemlock Wooly Adelgid (Ellison et al. 2018, Tuula et al. 2019), Spruce Budworm (Candau and Fleming 2011), Two-lined Chestnut Borer

(Lucash et al. 2018, Sallé et al. 2014, USDA 2011), Emerald Ash Borer (Hoven et al. 2017, Liang and Fei 2014) and *Armillaria* spp. (Kubiak et al. 2017) will have an increased advantage under a warmer climate. Climate change may also stress host species making them more susceptible to pathogen outbreaks (Lucash et al. 2018). If pests will profit from increasing temperatures (Kubiak et al. 2017), then forest pests will significantly impact tree canopy morbidity.

A study on forest disturbance under climate change found that the Two-lined Chestnut Borer, *Agrilus bilineatus* Weber, outbreaks occur when its host species is stressed by drought and defoliation (Lucash et al. 2018). The Emerald Ash Borer,*Agrilus planipennis*, kills ash,*Fraxinus* spp., trees, which causes extensive changes to forest composition (Hoven et al. 2017). Ash mortality has positive indirect effects on *L. maackii* growth where *L. maackii* growth was significantly greater in study sites where ash tree condition was poorer (Hoven et al. 2017). Greater *L. maackii* growth was also associated with lower woody seedling species richness and abundance (Hoven et al. 2017).

If the Hemlock Wooly Adelgid who feed on hemlock trees are more prevalent under warmer temperatures, then this will lead to decreased canopy cover (Ellison et al. 2018, Tuula et al. 2019). However, the phenology of *L. maackii* shows plasticity in various photosynthetic environments (Lieurance 2016). Considering the range of light that *L. maackii* can thrive in and the fact that studies have linked understory success of plants with tree canopy mortality (Jain et al. 2020, Mestre et al. 2017, Pec et al. 2015, Steinke et al. 2020), outbreaks of Hemlock Wooly Adelgid and Spruce Budworm due to climate change (Candau and Fleming 2011, Ellison et al. 2018, Tuula et al. 2019) will only further impact the indirect relationship between *L. maackii* and native plants.

Amphibians and aquatic macroinvertebrate

There are few empirical studies on the effects *L. maackii* has on the amphibian community. However, some general hypotheses can be made surrounding the evidence presented in the following studies. One study found that *L. maackii* altered the forest understory microclimate by lowering daily ground temperatures (Watling et al. 2011). *Lonicera maackii* was also shown to shift amphibian species composition possibly due to changes in the microclimate (Watling et al. 2011). Because amphibians rely on the abiotic conditions of their environment for survival, this alteration in understory light (Luken and Thieret 1995), and temperature (Watling et al. 2011) could have unknown effects on the amphibian community. American toad tadpoles showed risk-prone behavior due to leachates from *L. maackii* in one study (Hickman and Watling 2014). These studies show that in addition to altering soil composition and makeup (Arthur et al. 2012, Hopfensperger et al. 2017, Kolbe et al. 2015, McNeish et al. 2018), *L. maackii* can also change the chemical composition of nearby waters (Hickman and Watling 2014). In this way, these studies show that *L. maackii* chemically alters amphibian habitats, which in turn makes them more prone to predators because of their increase in risky behaviors as tadpoles.

A study on the effects of leaf leachate from *L. maackii* on an aquatic macroinvertebrate found that all organisms died when exposed to any concentration of leachate (Borth et al. 2018). They also found that mean percent survival also decreased in dilutions taken in spring (Borth et al. 2018). Another study found that overall abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT, commonly used water quality indicators) decreased in association with increasing *L. maackii* invasion intensity (Little et al. 2021). These studies suggest the indirect effect *L. maackii* has on aquatic macroinvertebrate through its production of allelochemicals (Borth et al. 2018, Little et al. 2021)

Similar to the other wildlife species, it can be said that the increased range of *L. maackii* in the presence of climate change will have an adverse effect on the amphibian community by altering the understory temperature (Watling et al. 2011) and contaminating nearby water (Hickmann and Watling 2014). Amphibians are studied to be vulnerable to future projected climatic changes where species are projected to experience range loss rather than range expansions (Lawler et al. 2010). Amphibians may decrease in abundance and species richness, but more empirical studies are needed to form conclusions on the effect of *L. maackii* and the amphibian community to understand the impact further. Coleoptera richness was found to be correlated with temperature and precipitation where composition was consistent among the years studied (Lawrence et al. 2010). Under climate change *L. maackii* will also have an increased indirect effect on aquatic macroinvertebrate due to the production of allelochemicals present in its leaves (Borth et al. 2018, Little et al. 2021).

Future Directions and Considerations

Herein, I synthesize empirical studies to provide a framework for understanding the effects of climate change on *L. maackii* and the relationship between it and native wildlife species. *Lonicera maackii* has been shown to (a) directly affect nesting success (McChesney and Anderson 2015, Schmidt and Whelan 1999, Wenner 2013) and nest predation in various bird species as well as population sink in some species, where a demographic deficit occurs in habitats of *L. maackii* (McChesney and Anderson 2015), (b) provide poor nutritional sustenance for birds (Ingold and Craycraft 1983), (c) directly and indirectly affect native plant reproduction through competition for pollination (McKinney and Goodell 2011), (d) provide cover from predation for a variety of small mammals (Dutra et al. 2010, Shields et al. 2014), (e) impact forest biodiversity and abundance (Haffey and Gorchov 2019), (f) exert pressure on forest litter composition with little effect on the arthropod community (Mahon et al. 2019) and, (g) chemically alter amphibian habitats making them more susceptible to predators (Watling et al. 2011). It is not simply an abundance of *L. maackii* that has caused these impacts but rather, climate change giving *L. maackii* yet another competitive advantage over native flora and fauna.

This discussion of *L. maackii* plasticity and changes in the Midwest and Eastern United States is essential for several reasons. With a warmer climate and increased precipitation, climate change will exert pressure on forest ecosystems. Forests in the United States comprise about one-third of the total land cover (EPA, 2021). US forests are home to a wide array of species and support various wildlife species. Our success as a nation is vital to understanding how our forests will change in the coming years due to climate change factors. Understanding the characteristics of invasive species is only the starting point in the proper management of our forests. Proper management is vital to the forest's long-term success. Having substantial research on invasion ecology will make proper management and delegation of resources easier to achieve. The latest Intergovernmental Panel on Climate Change urges us to see that we still have time to act in the face of mitigating climate catastrophes (Masson-Delmotte et al. 2021). Without increased research findings to help us mitigate and control the environmental pressures exerted by climate change, we risk rising to the 1.5° C warming threshold (Masson-Delmotte et al. 2021). It is important to identify changes within the United States forests to understand better how to properly manage our forests and prevent further degradation such as the 'sixth mass extinction' (Barnosky et al. 2011). Protection of our ecosystems that provide us clean water, provide us clean air, provide us with food and recycle nutrients with sustenance, oxygen, and various other important things are dependent on our ability to mitigate these factors.

Climate change will exacerbate the spread of *L. maackii* by increasing the range that *L. maackii* can grow in due to global temperature increases and increased winter and spring precipitation. More research will be needed to understand the impact this will have on native wildlife species; however, a few things can be hypothesized. My literature review uncovered that climate change could exacerbate *L. maackii's* pressure on wildlife species by (a) exerting pressure on the songbird populations, possibly leading to the endangerment or extinction of certain species, (b) increasing food availability to birds due to increased range which could have an adverse effect on the population abundance and species richness due to the poor nutritional value, (c) exacerbating the indirect relationship with native flora and adversely affect the pollinator community and pollination of vital crops due to increased range, (d) providing more cover for small mammals which could increase population abundance in some species due to increased range, (e) exacerbating the direct relationship with ungulates by providing a valuable food source in early-spring, (f) having an indirect effect on leaf-litter invertebrates and arthropods by influencing forest floor microclimate, (g) forest pests and pathogens creating new opportunities for *L. maackii* to become invasive, (h) decreasing abundance in amphibian population and species richness and due to increased range and, (i) declines in macroinvertebrate species due to increased range. Therefore, it can be assumed that *L. maackii* will have both direct and indirect relationships with native wildlife species due to increased climate warming and increased precipitation.

Since *L. maackii* has spread throughout most of the Midwest and the Northeast (WIGL 2021), more stringent mitigation efforts are needed to reduce its pressures on native wildlife species. Understanding the impacts *L. maackii* has on native wildlife species is a good first step in the mitigation process which is why further research is impertinent to the process. *Lonicera maackii*'s ability to thrive in various environments (Luken and Thieret 1995) enable it to invade many different habitats. Removal efforts can be done to mitigate the facilitation and spread of *L. maackii*. Removal efforts include but are not limited to removal before fruiting to avoid germination in the following season, intensive mowing every two weeks and subsequent weeks until regrowth is minimal and, applying herbicide in late fall and subsequent applications to regrowth (WIGL 2021).

Several studies have suggested both direct and indirect effects across the spectrum of wildlife species (Dutra et al. 2010, Shields et al. 2014, *Peromyscus* spp.; Haffey and Gorchov 2019, Mahon et al. 2019, *Odocoileus virginianus*; Ingold and Craycraft 1983, Wenner 2013, avian species; McChesney and Anderson 2015, *Spizella Pusilla*; McKinney and Goodell 2011, pollinator visitation; Schmidt and Whelan 1999, *Turdus migratorius*; Watling et al. 2011, amphibian species; Borth et al. 2018, aquatic macroinvertebrate species. More work is necessary to determine the direct and indirect effects on wildlife species from *L. maackii* more thoroughly. Continued studies are needed to determine how those effects will be exacerbating under changing environmental pressures. It is critical to understand these direct and indirect effects on the surrounding wildlife species for guiding future research and management efforts.

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