

## THE DISTRIBUTIONS OF TWO INVASIVE HONEYSUCKLE SPECIES (*LONICERA MAACKII* AND *LONICERA JAPONICA*) IN EASTERN OKLAHOMA

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### ABSTRACT

Concerns about spreading non-native invasive plant species have increased in recent decades following their harmful impacts on ecosystems. Their encroachment, aided by survival and reproductive advantages, can negatively impact ecosystems and biodiversity. These effects often lead to larger long-term issues and can be difficult and expensive to manage. *Lonicera maackii* (Rupr.) Herder and *L. japonica* Thunb. are invasive honeysuckle species that can outcompete, inhibit, and reduce the populations of native species, thus threatening biodiversity in invaded regions. Both species have formed naturalized populations throughout much of the eastern United States, including Oklahoma. Both species reproduce quickly, grow prolifically, face less environmental resistance, and tolerate a wider range of environmental conditions than most native plant species. This study, based on field surveys and herbarium records, presents new information on the distribution of *L. maackii* and *L. japonica* in eastern Oklahoma. Surveys were conducted in parks and public recreation areas of all 47 counties of eastern Oklahoma. By combining herbarium data and field surveys, we found that *L. maackii* occurs in fewer counties than expected and *L. japonica* is present in nearly all counties surveyed. The results also revealed a strong positive relationship between the presence of *L. maackii* and the population size of towns. We also found a weak and non-significant relationship between the occurrence of *L. maackii* and the number of non-native species in a county.

## INTRODUCTION

Invasive species are a significant threat to Oklahoma's ecosystems, as they negatively impact native plants and animals. A non-native species is considered invasive when it threatens the health and safety of the environment, economy, or human population of its invaded region (Iannone et al. 2020). As non-native species naturalize outside of their native ranges, they are often unrestrained by competing species and environmental limitations (Keane and Crawley 2002). These advantages allow them to grow quickly, spread rapidly, and outcompete native species for resources (McEwan et al. 2010). This unchecked growth and reduced vigor of surrounding vegetation can disrupt natural processes, disturb native habitats, and decrease native biodiversity, creating a cascading negative effect on ecosystem function (Vilà et al. 2011). These impacts can be worsened when multiple non-native species invade a region (Vujanović et al. 2022). This study evaluates the extent of the spread of two species of non-native and invasive honeysuckles found in Oklahoma, *Lonicera maackii* (Rupr.) Herder and *L. japonica* Thunb. (Caprifoliaceae).

*Lonicera japonica*, commonly known as Japanese honeysuckle, was introduced to the United States in the early 1800s, while *L. maackii*, commonly known as Amur honeysuckle, followed in the late 1890s (Luken and Thieret 1995; Lemke et al. 2011). Both species are native to eastern Asia, including China, Korea, and Japan, and were introduced to New York with the intention of use as ornamentals, in erosion control, and as food sources for wildlife (Luken and Thieret 1996). Horticulture and habitat improvement efforts played a large role in the early spread of *L. maackii* and *L. japonica*, as planting the two species was encouraged. However, both species quickly escaped and formed naturalized populations outside of cultivated areas (Luken and

Thieret 1996; Lemke et al. 2011; Keil and Hickman 2014).

In North America, *L. maackii* grows in both open and forested areas in urban and suburban regions (Luken and Thieret 1995). Multiple factors contribute to *L. maackii*'s ability to outcompete native species. This densely branched shrub exhibits leaf emergence in early spring and drops its leaves later than most native species, allowing extended photosynthetic periods and herbivory avoidance during early leaf development. This advantage allows *L. maackii* to block sunlight and crowd out surrounding understory plants (McEwan et al. 2009). Another factor contributing to the invasive potential of this species is its allelopathy, a form of chemical inhibition, to stunt the growth of surrounding plants (McEwan et al. 2010). The chemical signals accumulate in the soil and come from every part of the plant, including leaves and berries that drop to the ground. As a result, the performance of native species can be lowered, often by inhibiting the growth of native seedlings (McEwan et al. 2010).

*Lonicera maackii* causes issues for the habitats it invades by competing with native species for resources and space (McEwan et al. 2009). When *L. maackii* invades a habitat, it is followed by decreased native species performance and lowered habitat diversity, which can negatively impact other organisms (Cipollini et al. 2009). Invaded habitats can experience lowered bird diversity, as birds that nest in *L. maackii* increase, while the abundance of bird species that prefer other nesting sites decreases (Lynch 2016). *Lonicera maackii* presence can also increase risks of mortality and predation on birds that nest in these shrubs, as they do not provide the same protective structure that many native shrubs do (Schmidt and Whelan 1999; Borgmann and Rodewald 2004). The bright red berries of *L. maackii* are attractive to native bird species, but do not provide adequate nutrition (Ingold and Craycraft 1983).

*Lonicera maackii* presence as a food source also creates a preferred habitat for white-tailed deer (*Odocoileus virginianus*), resulting in greater deer activity. White-tailed deer act as hosts for disease-carrying tick species, which increases a habitat's tick load and poses an added risk to human populations (Allan et al. 2010).

*Lonicera japonica* is adaptable to a wide array of habitats, soil types, and environmental conditions, but typically grows in shaded areas. In North America, it is mostly restricted to areas with higher temperatures and rainfall (Schierenbeck 2004; Lemke et al. 2011). *Lonicera japonica* has advantages contributing to its extensive spread and ability to outcompete native species. As with *L. maackii*, its leaves emerge in early spring and often last through the winter, an advantage over surrounding plants in photosynthetic opportunity and herbivory avoidance (Schierenbeck 2004; Lieurance and Cipollini 2012). This vine creates thick blankets of foliage on the ground and upon supporting plants. *Lonicera japonica* also propagates via adventitious growth, further contributing to extensive and prolific expansion (Wang et al. 2015).

*Lonicera japonica* causes damage to invaded regions by wrapping around supporting plants and shading foliage. As this plant grows quickly, covers large areas, and grows densely on other plants, it accesses more water and nutrients from the soil and blocks light availability, thus decreasing native species' access to adequate resources (Schierenbeck 2004; Wang et al. 2015). *Lonicera japonica* has also been found to alter the architecture of host plants, increasing the proportion of stems to leaves (Friedland and Smith 1982). These factors can inhibit the growth and productivity of native plants, posing a threat to the biodiversity of an invaded region (Wang et al. 2015).

Both honeysuckle species are found in eastern Oklahoma, where forested areas with higher temperatures and rainfall

provide suitable habitat. They are not found as frequently in western Oklahoma, where the landscape shifts to drier grasslands (Keil and Hickman 2014). *Lonicera japonica* is widespread throughout eastern Oklahoma, with recent literature showing a distribution over 77% of the 47 counties (Keil and Hickman 2014). Compared to the many studies of the distribution and ecology of *L. japonica*, much less is known about the distribution of *L. maackii*, especially in Oklahoma. However, herbarium records obtained from the Texas and Oklahoma Consortium of Herbaria (TORCH) database (<https://portal.torcherbaria.org>; data retrieved 4 October 2023) indicate that *L. maackii* is seemingly less widespread.

Because non-native species are often underrepresented in herbaria, this study aims to complement published information and herbarium records with new survey data on the distribution of both honeysuckle species in Oklahoma. Specifically, the goal of this research is to document the occurrence of *L. maackii* and *L. japonica* throughout eastern Oklahoma at the county level, determine if there is a pattern of co-occurrence with other invasive species, and explore factors contributing to their distribution. This project will test the following hypotheses: 1) based on herbarium records, observations from iNaturalist (<https://www.inaturalist.org/>), and the possibility of its presence being under-reported, we predict *L. maackii* will be recorded in 50% of all counties surveyed; 2) based on herbarium records, iNaturalist observations, and published distribution maps (Keil and Hickman 2014), we predict *L. japonica* will be recorded in 90% of counties surveyed; 3) there will be a significantly positive relationship between the occurrence of *L. maackii* and the population sizes of towns; and 4) there will be a significantly positive relationship between the occurrence of *L. maackii* and the number of non-native species per county.



Figure 1 *Lonicera maackii*, habit; plants are about 1.5 m tall; photo taken at Sanborn Lake, Stillwater, Oklahoma by Sarah Short (May 9, 2023).



Figure 3 *Lonicera maackii*, flowers in May; photo taken at Sanborn Lake, Stillwater, Oklahoma by Sarah Short (May 9, 2023).



Figure 2 *L. maackii*, leaves and immature berries in May; photo taken at Sutton Wilderness Trail, Norman, Oklahoma by Sarah Short (May 16, 2023).

## METHODS

### Study Species

*Lonicera maackii* is a shrub that can grow as tall as 5 m (Figure 1). The leaves are ovate or lanceolate and their tips are acuminate (Figure 2). The leaves are also pubescent and oppositely arranged with entire margins. The flowers, which can open from April to June, grow in pairs on pedicels shorter than the leaf petioles, and have white corollas (Figure 3). When immature, the berries are green (Figure 2). In the fall, the berries ripen and become bright red (Haddock and Freeman 2019).

*Lonicera japonica* is a vine that can grow up to 10 m long. The oppositely arranged leaves are pubescent and oval shaped (Figure 4). The margins of the leaves are typically entire but can occasionally be lobed or serrate. The flowers grow in pairs and have white and yellow corollas that are open from April to July (Figure 5) and that are larger than those of *L. maackii*. The flowers also have a strong sweet scent. The berries

are green when immature (Figure 6) and are black when ripe (Haddock and Freeman 2019).



Figure 4 *Lonicera japonica*, habit; photo taken at Pennington Creek Dam, Tishomingo, Oklahoma by Sarah Short (June 15, 2023).



Figure 5 *Lonicera japonica*, flowers in June; photo taken at Lewis V. Bond Memorial Park, Coalgate, Oklahoma by Sarah Short (June 20, 2023).



Figure 6 *Lonicera japonica*, immature berries in July; photo taken at Osage Nation Heritage Trail, Pawhuska, Oklahoma by Sarah Short (July 23, 2023).

### Field Sites

The field work consisted of a survey for the presence of *L. maackii* and *L. japonica* in all 47 counties east of Oklahoma County's western border, which is at an approximate longitude of 98°W. Surveys were conducted in the largest town of each county, with two exceptions: Osage County and McCurtain County. In these counties, the second largest town was selected to locate a suitable survey site. When selecting survey sites, the following factors were considered: public accessibility, site size, and potentially suitable habitat for both species (wooded areas or forest edges). Potential sites were evaluated prior to collection, using available maps and images from Google Maps and Google Earth

(<https://www.google.com/maps>;  
<https://earth.google.com/web/>).

Observations of *L. maackii* and *L. japonica* from iNaturalist (<https://www.inaturalist.org/>) were also

viewed prior to collection. Due to potential misidentification and the possibility of inaccurate observation data in iNaturalist, these occurrence records were not used in the final analysis of species presence at county level. However, these observations were used as a tool to guide the selection of survey sites during the beginning stages of research. In some cases, a selected site was considered unsuitable when visited, and a replacement site was selected within the same town. In very few cases of survey within smaller towns, more than one park

was surveyed (see Table 1). Within each selected town, at least one public park was surveyed.

The locations were selected to encompass a variety of natural and managed environments, including state parks, local parks, lakes, and walking trails. When selecting the locations, efforts were made to avoid locations that contained cultivated individuals of either honeysuckle species. Surveys took place from May to August of 2023.

Table 1 List of survey sites selected within one town of each county

County	Town	Survey Site	Entrance Lat/Long
Adair	Stillwell	Adair Park	35°49'56"N 94°37'28"W
Atoka	Atoka	Boggy Depot State Park	34°19'06"N 96°18'26"W
Bryan	Durant	Lake Durant Park	34°05'03"N 96°23'56"W
Carter	Ardmore	Ardmore Regional Park	34°12'26"N 97°09'30"W
Cherokee	Tahlequah	Sequoyah City Park	35°54'48"N 94°58'02"W
Choctaw	Hugo	Hugo Lake Campground	34°01'18"N 95°25'26"W
Cleveland	Norman	Sutton Wilderness Trail Park	35°14'33"N 97°25'27"W
Coal	Coalgate	Lewis V. Bond Memorial Park	34°31'20"N 96°13'08"W
Craig	Vinita	Vinita Lake Park North Park	36°40'40"N 95°07'12"W 36°38'33"N 95°09'17"W
Creek	Sapulpa	Kelly Lane Park	35°59'03"N 96°06'33"W
Delaware	Grove	Grove Springs Park	36°35'40"N 94°46'30"W
Garvin	Pauls Valley	Nature Park	34°43'54"N 97°13'14"W
Haskell	Stigler	Lake John Wells Park	35°14'05"N 95°05'43"W
Hughes	Holdenville	Stroup Park	35°05'11"N 96°23'43"W
Johnston	Tishomingo	Pennington Creek Park Pennington Creek Dam	34°14'03"N 96°40'59"W 34°14'32"N 96°40'54"W
Kay	Ponca City	Bois D'Arc Disc Golf Course	36°43'38"N 97°00'57"W
Latimer	Wilburton	Robber's Cave State Park Robber's Cave	34°58'48"N 95°21'35"W 35°00'21"N 95°20'15"W
LeFlore	Poteau	Bill J. Barber Park	35°03'49"N 94°37'43"W
Lincoln	Chandler	Bell Cow Lake Campground C	35°43'41"N 96°56'14"W
Logan	Guthrie	Mineral Wells Park	35°52'07"N 97°25'32"W
Love	Marietta	Shellenberger Park Memorial Park	33°56'31"N 97°07'35"W 33°56'31"N 97°07'35"W
Marshall	Madill	Madill City Lake	34°05'07"N 96°47'22"W
Mayes	Pryor	Pryor Creek Nature Trail	36°15'59"N 95°18'37"W
McClain	Newcastle	Lions Park Veterans Park	35°16'34"N 97°39'21"W 35°15'42"N 97°36'42"W
McCurtain	Broken Bow	Beavers Bend State Park	34°07'55"N 94°40'41"W
McIntosh	Checotah	Lake Eufaula State Park (Hummingbird Beach)	35°24'01"N 95°35'52"W
Murray	Sulphur	Chickasaw National Recreation Area (Travertine Creek)	34°30'13"N 96°58'13"W
Muskogee	Muskogee	Coody Creek Trail	35°44'14"N 95°22'36"W
Noble	Perry	Perry Lake	36°15'59"N 97°16'41"W
Nowata	Nowata	John H. Morgan Park	36°42'12"N 95°37'47"W
Okfuskee	Okemah	Okemah Lake	35°31'06"N 96°19'17"W
Oklahoma	Oklahoma City	Stars and Stripes Park	35°32'50"N 97°34'58"W
Okmulgee	Okmulgee	Okmulgee Lake & Recreation Area (Okmulgee Park)	35°37'14"N 96°03'50"W

Table 1 List of survey sites selected within one town of each county

County	Town	Survey Site	Entrance Lat/Long
Osage	Pawhuska	Osage Nation Heritage Trail	36°39'44"N 96°19'51"W
Ottawa	Miami	River View Park (Miami Parks and Recreation Bike Trail)	36°51'37"N 94°52'27"W
Pawnee	Cleveland	Feyodi Creek RV Park/ Disc Golf Course	36°16'38"N 96°26'21"W
Payne	Stillwater	Sanborn Lake	36°09'26"N 97°04'32"W
Pittsburg	McAlester	Mike Deak Walking Track	34°54'46"N 95°45'38"W
Pontotoc	Ada	Wintersmith Park	34°45'49"N 96°39'07"W
Pottawatomie	Shawnee	Glen Collins Memorial Park & Campground	34°45'49"N 96°39'07"W
Pushmataha	Antlers	Ozzie Cobb Lake	34°14'33"N 95°23'13"W
Rogers	Claremore	Claremore Lake (South Trailhead)	36°19'44"N 95°34'34"W
Seminole	Seminole	Sportsman Lake Recreation Area	35°12'31"N 96°33'19"W
Sequoyah	Sallisaw	Sallisaw City Park	35°27'53"N 94°51'40"W
Tulsa	Tulsa	Mohawk Park	36°12'29"N 95°53'59"W
Wagoner	Coweta	Roland Park	35°57'33"N 95°39'45"W
Washington	Bartlesville	Bartlesville Trails at Lake Hudson	36°48'10"N 96°01'57"W
		Johnstone Park	36°45'16"N 95°58'34"W

At each location, the area was surveyed for the presence or absence of both honeysuckle species. When present, samples were taken to prepare herbarium vouchers, which document the morphology, habitat, surrounding plant species, and geographic coordinates associated with each specimen. Additionally, the occurrence of three other non-native invasive species of interest was noted: *Ligustrum sinense* Lour., *Pyrus calleryana* Decne., and *Nandina domestica* Thunb., which are common in Oklahoma. These species were selected because, like honeysuckle, they are often intentionally planted as ornamentals and often escape cultivation. Each sample was dried and preserved for deposition in the Oklahoma State University Herbarium. Collection data for each specimen were uploaded to the TORCH database (<https://portal.torchherbaria.org>).

All previously documented herbarium records of *L. japonica* and *L. maackii* from the 47 surveyed counties were downloaded from the TORCH database (retrieved October 4, 2023) to determine prior knowledge of presence or absence of these species at the county level. Additionally, the herbarium records of *L. sinense*, *P. calleryana*, and *N. domestica* were downloaded to observe the occurrence of other known invasive species in Oklahoma. In addition, the total numbers of non-native species per

county were obtained. Briefly, all Oklahoma records of the five invasive species of interest were downloaded and filtered to remove those with missing or erroneous coordinates. Taxonomic names were standardized against the World Flora Online Taxonomic Backbone using the R package “WorldFlora” (Kindt 2020). Remaining records were filtered for non-native species (Simpson et al. 2022; accessed via Global Biodiversity Information Facility, <https://www.gbif.org/dataset/32ad19ed-6b89-447a-9242-795c0897f345>), and intersected with shapefiles for the 47 counties to determine the number of non-native species per county.

### Data Analysis

Using the presence and absence data from field surveys and herbarium records, the spatial distributions of *L. maackii* and *L. japonica* at the county level were visualized using Microsoft Excel. The prevalence of *L. maackii* and *L. japonica* were compared using the number of counties in which each was documented. The numbers of newly documented county occurrences for each species were determined by comparison to the numbers of herbarium records. The association between town population size, obtained from the Oklahoma 2020 Census (America Counts Staff 2021) and the presence of *L. maackii* was tested using

logistic regression. Logistic regression was also used to test the association between the number of non-native species in a county and the presence of *L. maackii*. Both analyses were conducted in R, using R-Studio (RStudio Team 2020). The packages used were “ggplot2” (Wickham 2016) and “cowplot” (Wilke 2020). Regressions were considered significant if the P-value was less than 0.05.

## RESULTS

Of the 47 counties visited during the field surveys, *L. maackii* was observed in 15 counties (31.9%; Figure 7). *Lonicera japonica* was found in 38 out of 47 counties (80.9%; Figure 8). The herbarium records documented *L. maackii* in eight out of the 47 counties surveyed (17%; Figure 7). The herbarium records documented *L. japonica* in 41 out of 47 counties (87.2%; Figure 8). When combining the data from both the field surveys and the herbarium records, *L. maackii* was documented in 16 out of 47 counties (34%; Figure 7), and *L. japonica* was documented in 46 out of the 47 counties

surveyed (97.9%; Figure 8). A summary of the presence and absence of both species by county is presented in Table 2.

Using notes from the field surveys and herbarium records, the occurrence of three common, non-native invasive species was recorded by county (Table 2). *Ligustrum sinense* was present in 32 counties, *P. calleryana* was present in 13 counties, and *N. domestica* was present in seven counties. Of the 16 counties where *L. maackii* was present, *L. sinense* was present in 13, *P. calleryana* was present in four, and *N. domestica* was present in six.

There was a strong positive relationship between the population size of a town and the probability of *L. maackii* occurrence (Figure 9;  $p=0.005$ ;  $df=45$ ; deviance=41.68). However, there was only a weakly, non-significantly positive relationship between the total number of non-native species per county and the probability of *L. maackii* occurrence (Figure 10;  $p=0.082$ ;  $df=45$ ; deviance=56.96).

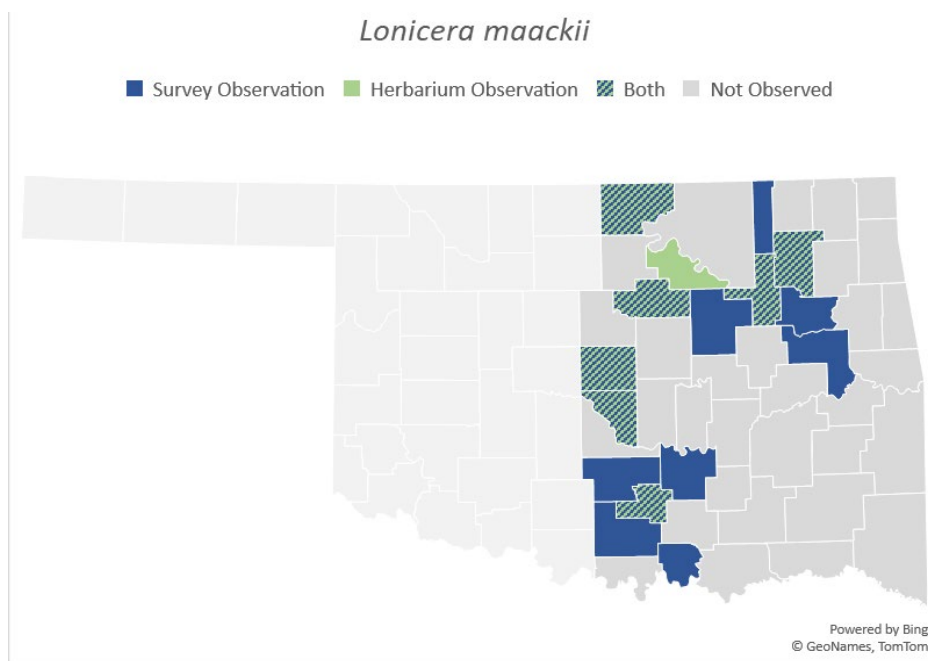


Figure 7 *Lonicera maackii* county occurrences documented by field surveys and herbarium collections



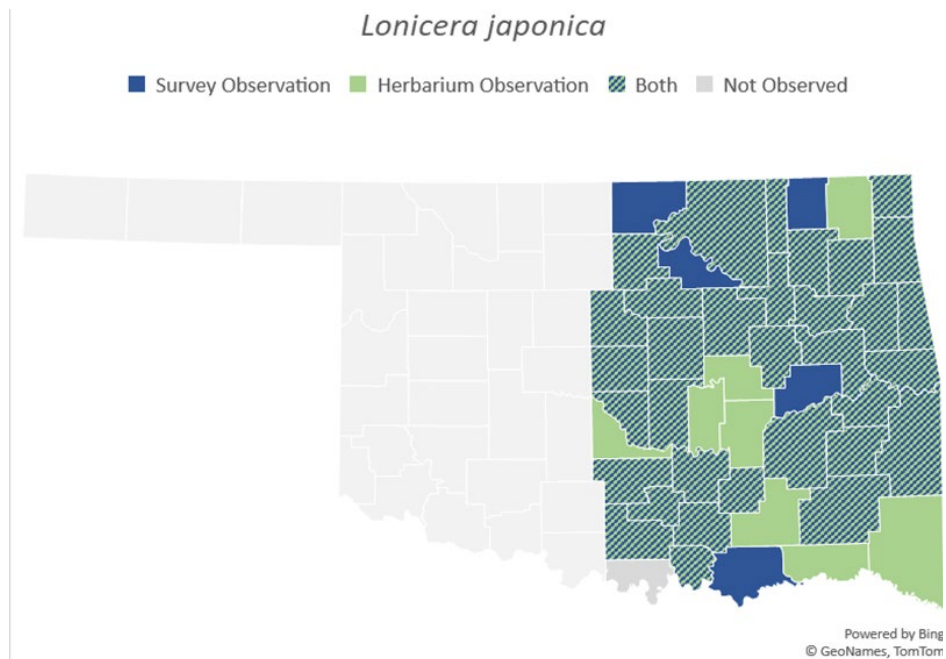


Figure 8 *Lonicera japonica* county occurrences documented by field surveys and herbarium collections

Table 2 Occurrence of invasive species associated with *Lonicera* species; X indicates the species is present.

County	<i>L. maackii</i>	<i>L. japonica</i>	<i>L. sinense</i>	<i>P. calleryana</i>	<i>N. domestica</i>
Carter	X	X	X	-	-
Cleveland	X	X	X	X	X
Creek	X	X	X	-	-
Garvin	X	X	X	-	X
Kay	X	X	-	-	-
Marshall	X	X	X	-	X
Murray	X	X	X	-	-
Muskogee	X	X	X	-	-
Oklahoma	X	X	X	X	X
Pawnee	X	X	X	-	X
Payne	X	X	X	X	X
Pontotoc	X	X	X	-	-
Rogers	X	X	X	-	-
Tulsa	X	X	X	X	-
Wagoner	X	X	-	-	-
Washington	X	X	-	-	-
Adair	-	X	X	-	-
Atoka	-	X	-	-	-
Bryan	-	X	-	X	-
Cherokee	-	X	X	X	X
Choctaw	-	X	-	-	-
Coal	-	X	X	-	-
Craig	-	X	X	-	-

Table 2 Occurrence of invasive species associated with *Lonicera* species; X indicates the species is present.

County	<i>L. maackii</i>	<i>L. japonica</i>	<i>L. sinense</i>	<i>P. calleryana</i>	<i>N. domestica</i>
Delaware	-	X	-	X	-
Haskell	-	X	X	-	-
Hughes	-	X	-	-	-
Johnston	-	X	X	-	-
Latimer	-	X	-	-	-
LeFlore	-	X	X	-	-
Lincoln	-	X	-	-	-
Logan	-	X	-	-	-
Mayes	-	X	X	X	-
McClain	-	X	-	-	-
McCurtain	-	X	X	-	-
McIntosh	-	X	X	X	-
Noble	-	X	-	-	-
Nowata	-	X	X	-	-
Okfuskee	-	X	X	-	-
Okmulgee	-	X	X	X	-
Osage	-	X	X	-	-
Ottawa	-	X	X	X	-
Pittsburg	-	X	X	X	-
Pottawatomie	-	X	-	-	-
Pushmataha	-	X	-	-	-
Seminole	-	X	X	-	-
Sequoyah	-	X	X	-	-
Love	-	-	X	X	-

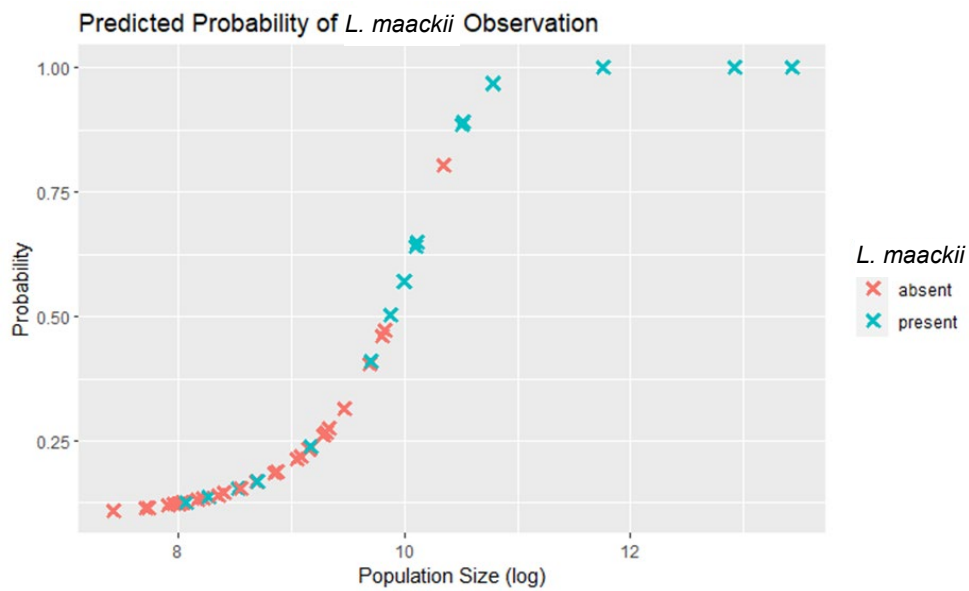


Figure 9 Probability of *L. maackii* occurrence as a function of town population size;  $p=0.005$ ;  $df=45$ ; deviance=41.68

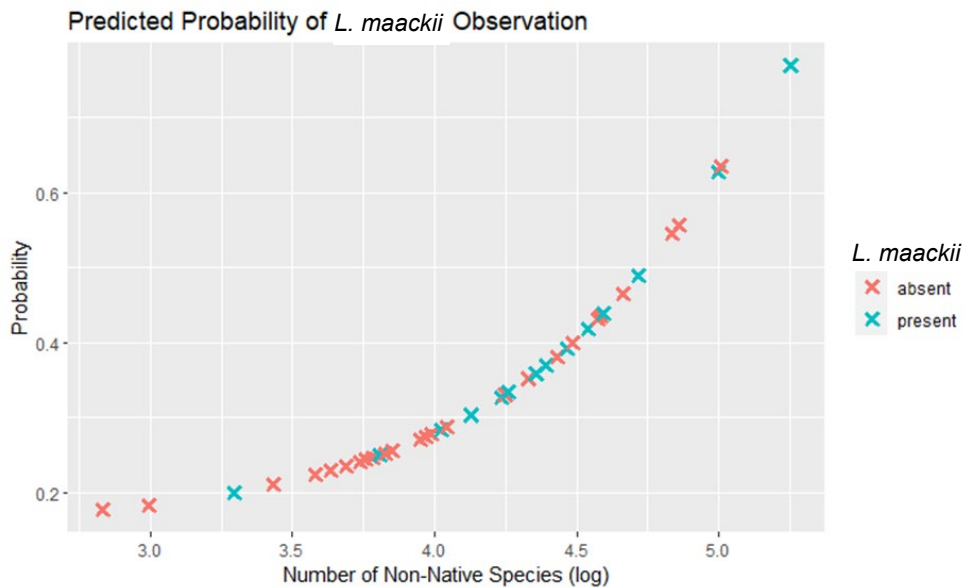


Figure 10 Probability of *L. maackii* occurrence as a function of the number of non-native species;  $p=0.082$ ;  $df=45$ ; deviance=56.96

## DISCUSSION

This study updates and expands published information on the distributions of *L. maackii* and *L. japonica* in eastern Oklahoma. The comparative prevalence of the two honeysuckle species was predicted based on the county-level distributions documented by herbarium records and in the literature (Keil and Hickman 2014). We hypothesized that *L. maackii* would be present in 50% of the counties surveyed and that *L. japonica* would be present in 90% of the counties. Field surveys found *L. maackii* in 31.9% of the eastern Oklahoma counties, while herbarium records show observations of *L. maackii* in 17.0% of counties, including one county where *L. maackii* was not observed in the field survey. When both sources of data are combined, *L. maackii* was documented in 34.0% of eastern counties. This does not support the first hypothesis. However, the new observations recorded *L. maackii* in eight counties that were not previously known from herbarium records alone. The new observations

improve our understanding of the distribution of *L. maackii* in eastern Oklahoma. Additionally, observations appeared to be concentrated around urban areas. Although *L. maackii* was found in fewer counties than expected, the persistence of *L. maackii* previously documented at the county level was confirmed, and its prevalence in eastern Oklahoma appears to have increased in recent decades. Due to this species' effects on surrounding organisms and its ability to spread by seed dispersal, its range could continue to spread into forested areas in the future if left uncontrolled (Luken and Thieret 1996). *Lonicera maackii* was expected to be less common than *L. japonica* due to the previous knowledge that *L. japonica* was widespread and frequent (Keil and Hickman 2014).

Field surveys found *L. japonica* in 80.9% of eastern Oklahoma counties, and herbarium records show the presence of *L. japonica* in 87.2% of counties, including seven counties where *L. japonica* was not

observed in the field survey. The field surveys also documented *L. japonica* in five counties that were not recorded in herbarium data. When combining both sources of data, *L. japonica* has been documented in 97.9% of eastern Oklahoma counties, with Love County being the only one without evidence of occurrence. This number supports the second hypothesis, that *L. japonica* would be found in at least 90% of counties. These records provide evidence for *L. japonica* being widespread and extremely common, and the field surveys confirm what was already expected for this well documented invasive species (Keil and Hickman 2014).

Human activity contributes considerably to the establishment and effects of invasive species. Like many invasive plant species, *L. maackii* and *L. japonica* were intentionally planted. When invasives are deliberately introduced, they can spread and form naturalized populations in the surrounding areas. In the case of these human-introduced honeysuckles, seeds can be dispersed by birds and deer, aiding in their rapid spread outside of their intended area (Castellano and Gorchoy 2013). Intentional planting isn't the only human activity that results in non-native species invasion, as the spread of urban areas is associated with increased activities that indirectly influence the potential of a habitat to be invaded. Habitat disturbances that result from urbanization can leave ecosystems more vulnerable to invasion by non-native species. Urban structures, such as roads and buildings, can alter habitats, decrease the sizes of forested areas, and result in habitat fragmentation. These structures also increase the amount of surface area that is impervious to rainwater. Additionally, urban areas and residential structures result in increased fire suppression (Nowacki and Abrams 2008). As a result, these changes heavily contribute to a cycle of changes to other environmental factors, including soil composition and quality, nutrient

availability, light, and temperature (Flory and Clay 2009). The impacts of these factors can decrease a habitat's resistance to invasion by reducing performance of native species, providing opportunity for invasives to outcompete native plants (Flory and Clay 2009).

Considering urbanization as a factor that may increase the likelihood of *L. maackii* occurrence, we hypothesized that there would be a significant relationship between *L. maackii* occurrence and the population sizes of towns. *Lonicera maackii* was found mostly in towns with populations above 15,000 people (Table 3), which supports the prediction that this species would be present in urban and suburban areas with higher populations. Outlier occurrences were observed in towns below 15,000 people, such as Madill (population 3,914), in Marshall County. There were also cities above 15,000 people where *L. maackii* was not observed, such as Shawnee (population 31,377), in Pottawatomie County. Despite these outliers, the presence of *L. maackii* was well predicted by town or city size, and there was a significant positive relationship (Figure 9). Because of the role of horticulture in the early introduction of *L. maackii* and the presence of many landscaped areas near parks, it makes sense that *L. maackii* would be more likely to be concentrated in these areas with higher populations.

*Lonicera maackii* has been observed to be associated with disturbed habitats in these larger towns, as well as with other invasive species. The presence of *L. maackii* has even been suggested to promote greater abundance and diversity of invasive plants in some regions, as well as greater ecological effects through their presence (Culley et al. 2016). Of the three additional non-native species that were recorded in each county by herbarium records and field observations, *Ligustrum sinense* was the most common, with presence in 32 counties.

Table 3 *L. maackii* presence compared to population size; X indicates *L. maackii* is present.

Town	Population by Town	<i>L. maackii</i>
Oklahoma City	681,054	X
Tulsa	413,066	X
Norman	128,026	X
Stillwater	48,394	X
Bartlesville	37,290	X
Muskogee	36,878	X
Shawnee	31,377	-
Ardmore	24,725	X
Ponca City	24,424	X
Sapulpa	21,929	X
Claremore	19,580	X
Durant	18,589	-
McAlester	18,171	-
Ada	16,481	X
Tahlequah	16,209	-
Towns with population below 15,000		
Coweta	9,654	X
Pauls Valley	5,992	X
Sulphur	5,065	X
Madill	3,914	X
Cleveland	3,205	X

The other species were less common, as *Pyrus calleryana* was found in 13 counties, and *Nandina domestica* was found in six counties. *Ligustrum sinense* occurred in 13 counties where *L. maackii* was present, *P. calleryana* occurred in four, and *N. domestica* occurred in six. This pattern of abundance follows expectations, as *L. sinense* is a widely distributed and well documented invasive shrub that shares similar habitat preferences to honeysuckles (Kuebbing et al. 2014). When *L. maackii* occurs in conjunction with *L. sinense*, they have been found to drastically alter the composition and properties of soil and further exacerbate the invasion of other non-native species (Kuebbing et al. 2014). Both *P. calleryana* and *N. domestica* are considerably less

documented than *L. sinense*, so it was expected to find them less frequently.

We hypothesized that the number of non-native species was predictive of the presence of *L. maackii*. Overall, there was a non-significant relationship between the number of non-native species per county and the probability of *L. maackii* occurrence (Figure 10), which did not support the fourth hypothesis, though the trend was in the predicted direction. It is possible that a stronger relationship would have been found if the number of non-native species were recorded per town surveyed rather than county, which would be at a more comparable scale.

The county level presence of the two honeysuckle species was surely

underestimated through field observation due to the limitations of one person surveying a large region. Because of time constraints, survey site size, and public accessibility, the survey was quite limited for the extent of the study area. Because the survey was limited to public recreation areas in one town per county, naturalized honeysuckle populations could have been present, but undocumented, outside of the sites surveyed. Naturalized populations on private lands, highways, and roadsides were not considered. Additionally, very large parks were limited to certain portions for survey, such as campsites and walking trails.

Suitable survey sites were not found in all counties. Although research was done prior to visits to find appropriate sites, some selected parks did not have as much natural habitat as expected. Two notable cases are Vinita, in Craig County, and Marietta, in Love County. In both cases, several locations were visited, but each site was highly landscaped and did not have suitable habitat for either species.

Further surveys are needed to better document the distributions of these species in Oklahoma. In addition to more surveys across the eastern part of the state, surveys at a smaller scale could be informative. For example, performing more extensive surveys for individual towns could document not only the presence of these species, but also the abundance.

The results of this study also raise questions for future research. Despite the similarities between these two honeysuckle species, *L. japonica* has a much wider distribution in Oklahoma than *L. maackii*. Both species spread via effective seed dispersal and use their phenology to gain a competitive advantage. However, perhaps *L. japonica*'s capability of adventitious propagation or longer flowering period contributes to its wider distribution. Another factor to consider would be that *L. japonica* was introduced to the United States around 100 years earlier than

*L. maackii*. With the large difference in time frame, could it be possible for the latter to become just as extensive over time, or would *L. maackii* remain more limited? If it is possible for *L. maackii* to become as extensive as *L. japonica*, it also raises concerns as to whether invasive species management practices would be able to get ahead of the spread of *L. maackii* and prevent it from worsening, given what we now know about *L. japonica*.

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