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# **Examining the Invasion of a Bush Honeysuckle using Climate Analysis**

An Honors Thesis submitted in partial fulfillment of the requirements for Honors  
Studies in Biology

By

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Spring 2021

Biology

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## Acknowledgements

First, I would like to thank my friends and family for the constant encouragement and support in exchange for way too much time listening to me talk about honeysuckle. I'd like to thank Nate Weston of the Beaver Watershed Alliance who first introduced me to *L. maackii* and its effects on the natural spaces in Fayetteville, AR. Dr. Jason Tullis provided access and valuable insight on the ArcGIS software that made this research possible. The Missouri Botanical Garden, Harvard Herbaria, the New York Botanical Garden, and the University of Arkansas Herbarium generously granted me access to their collections.

Thank you to the faculty and staff at the University of Arkansas Honors College for everything you do for students and for the funding which enabled this research.

I am very grateful for Dr. Andrew Alverson's generosity in granting me both laboratory space and his expertise in genomics and Dr. Wade Roberts for patiently introducing me to DNA extraction.

Finally, in my three years in Dr. Jeremy Beaulieu's laboratory I have always been welcomed as a full member of the team. Thank you for trusting me to follow my research interest down many winding roads and giving me the independence to develop my research skills. I am endlessly grateful for Dr. Beaulieu's support.

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## Abstract

Within the study of invasive plants, particular importance is placed on elucidating the mechanisms by which these plants proliferate and dominate within their introduced ranges. Several theories have been advanced to explain these invasions, each with different implications for the predicted range of invasive plants. Recent studies have provided support for the application of several invasion theories to *Lonicera maackii*, or what is more commonly referred to as bush honeysuckle. This species provides a unique opportunity to examine the efficacy of these theories in explaining the range expansion of invasive plants. *L. maackii* is endemic to eastern Asia, but it has invaded much of the eastern United States, posing a serious threat to the health of forests and other natural areas. To evaluate the application of biotic and abiotic theories of invasion for *L. maackii*, we modeled the climatic niche space of *L. maackii* in both its native and invasive ranges. We visually inspected and verified 1,046 *L. maackii* localities and 126 *L. subsessilis* localities, the sister taxon to *L. maackii*. After associating these localities with 19 climatic variables (BIOCLIM), we performed a principal component analysis (PCA) and observed a clear separation between the climatic conditions of the native East Asian *L. maackii* points and the invasive North American points. The climate niches of each population group (native *L. maackii*, invasive *L. maackii*, and *L. subsessilis*) were significantly different, suggesting that the North American population of *L. maackii* occupies a different climate niche than in its native East Asian range. This separation was consistent with the predicted versus observed probable occurrence maps of North America and East Asia which we built using Maxent. This change in *L. maackii*'s climatic niche lends support for ecological theories of invasion that feature biotic constraints on range expansion (like the Enemy Release and Novel Weapon Hypotheses) over theories relying on abiotic climatic constraints (like the Environmental Filtering Hypothesis).

## Introduction

There is growing demand for studies into the mechanisms and drivers of biological invasions, wherein species' distributions expand beyond their historical ranges (Catford et al., 2009). For most plant species, ranges are limited by species traits like dispersal ability, environmental tolerance, and body size and by biogeographic features like mountain ranges, oceans, and continental landmasses (Lowry & Lester, 2006). With the rapid proliferation of global trade over the past 500 years, many plants have overcome these biogeographic range barriers as they are transported inadvertently (as with rats on trade ships) or purposefully (as in the growing ornamental and commercial plant trade; see Prentis, 2009). When these introduced species become naturalized, they may spread rapidly and leave enormous ecological and economic damage in their wake (Catford et al., 2009).

Overcoming biogeographic obstacles and surviving the dispersal process is only the first step to naturalization: invasive plants must also face novel climate conditions and unfamiliar competing species (Richardson et al., 2000). *Lonicera maackii* is a deciduous shrub, often known as “bush honeysuckle” and “Amur Honeysuckle,” which has escaped its ancestral Eastern Asian range and spread widely across the Northeastern and Midwestern United States (Luken & Thieret, 1995). The dramatic success of *L. maackii* in naturalizing and greatly expanding its range presents a valuable opportunity to elucidate the potential drivers of biological invasion.

*L. maackii* exhibits a network of shallow roots, which not only made it an ideal plant to prevent soil erosion, but also potentially provided a competitive advantage over native plants in the acquisition of water and minerals (Gorchov & Trisel, 2003; Luken & Thieret, 1995). Between the 1960's and mid-1980's, the USDA Soil Conservation Service (SCS) facilitated the introduction of *L. maackii* five times in the name of soil stabilization and wildlife-habitat

improvement (Luken & Thieret, 1995). In the early 1960's the USDS SCS cultivated three strains of *L. maackii* selected for fruit production, retention, and maturation date to establish the creation of a cultivar known as 'Rem-Red' which was commercially marketed as a food source for birds, deer, and other wildlife (Sharp & Belcher, 1981). Importantly, white-tailed deer (*Odocoileus virginianus*) and several North American bird species consume *L. maackii* berries and pass viable seeds that may facilitate dispersal within its invasive range (Castellano & Gorchov, 2013). Additionally, its extended leaf phenology and late fruiting habit have contributed to its designation as a "handsome" plant, encouraging horticultural cultivation (Luken & Thieret, 1995). These factors have enabled repeated introductions of *L. maackii* and a subsequent rapid spread within North America. Today it is listed as a Class B noxious weed in Vermont and commercially banned in Connecticut and Massachusetts (USDA, 2021).

The dramatic success of *Lonicera maackii* in invaded habitats has created several major problems for native species. *L. maackii* reduces the survival and reproduction of several plant species and reduces the richness, diversity, and abundance of native species and their seedbanks (Dorning & Cipollini, 2006). *L. maackii* also exhibits a broad, dense canopy extending beyond the growing season of native plants which inhibits growth of shade-intolerant shrubs (Barriball et al., 2015). The plant is nutritionally poor for birds, as it produces lipid-poor fruit in late fall and winter when higher quality fruit is depleted (White & Stiles, 1992). Finally, *L. maackii* also interrupts forest succession patterns following disturbance wherein dense *L. maackii* mid-canopy domination limits the survival of tree seedlings and prevents succession (Hartman & McCarthy, 2008).

Research in invasive ecology has established several hypotheses to explain the success of non-native plants. For example, the "Novel Weapon" hypothesis proposes that invasive plants

have novel biochemical features that confer allelopathic advantage over neighboring plants (Ni et al., 2012). Alternatively, the “Empty Niche” hypothesis suggests that invasive plants more efficiently exploit resources where native species to occupy suitable niches are lacking (Shea & Chesson, 2002). Together, these hypotheses suggest biotic constraints on invasion. The “Environmental Filtering” hypothesis, however, suggests that community composition is determined by abiotic factors that filter out species poorly adapted to local conditions (Bello et al., 2012; Le Bagousse-Pinguet et al., 2017). The Environmental Filtering hypothesis postulates that invasive species must be similar to native species present in the same habitat to succeed within the similar niche spaces (Divíšek et al., 2018).

*Lonicera maackii* presents an excellent and ideal model to evaluate the application of various hypotheses on the invasion of species into novel spaces (McNeish & McEwan 2016). Previous research has shown that the leaves and roots of *L. maackii* contain secondary compounds that inhibited seed germination and growth of several native species, supporting the Novel Weapon hypothesis (Gorchov & Trisel, 2003; Dorning & Cipollini, 2006; McNeish & McEwan, 2016). The extended leaf phenology of *L. maackii* relative to native species may allow the honeysuckle to capitalize on an open canopy in both early spring and winter (McNeish & McEwan, 2016; Smith, 2014). Furthermore, the plant performs well in areas of anthropic disturbance, becoming abundant in fencerows, woodland borders, roadways, and disturbed forests (Hutchinson & Vankat, 1998; Luken & Thieret, 1995). Both the open deciduous canopy and disturbed habitat present an “empty niche” that *L. maackii* may be well suited to fill (Shea & Chesson, 2002).

Comparing *L. maackii*’s climatic niche space between its native and invasive ranges may provide insight as to whether biotic hypotheses of invasion (like Empty Niche and Novel

Weapon) or abiotic hypotheses (like Environmental Filtering) more convincingly explains this particular invasion. A climatic range expansion or shift may suggest that invasion is not so constrained by climate, but by ecological factors. Similarly, retention of the plant's climatic niche space from its native to invasive range would suggest that environmental filtering is the key driver of invasion success.

## Materials and Methods

### I. Data Preparation

Initially, 1,503 logged entries of *Lonicera maackii* were collected from GBIF (Global Biodiversity Information Facility, accessed 2018). Points were visually inspected using Google Earth and removed if (1) the point was located in or around an herbarium or botanical museum, (2) the point was located in a body of water and greater than 30 meters (the error margin of most GPS systems) from a shoreline, (3) was located in a manicured lawn or park where the plant would receive additional support (i.e. irrigation or fertilization), (4) or was located a great distance from the next nearest point, indicating a likely misidentification or mistaken plotting by the identifier. 78 points were removed in this manner. When these points were joined with the climate conditions, as outlined below, 379 points were classified as “Water Body” and were thus discarded. The points were classified as Native (n=88) or Nonnative/Invasive (n=958) by longitude, with East Asian points as native and North American Points as invasive. After culling, 1046 *L. maackii* points were useable for model building and analysis. For reference, the present study also collected 126 localities for *Lonicera subsessilis*, the sister taxon to *L. maackii* from the IUCN database (Kim et al., 2018).

These localities were then spatially joined to a 30 arc-second grid (square kilometer resolution) containing information for 19 BIOCLIM variables using the geospatial processing program ArcMap. The 19 BIOCLIM variables are derived from monthly temperature, rainfall measurements, and biologically meaningful measures over 30 years (Fick & Hijmans 2017).

## II. Niche Modeling

The climate niche spaces of the native and invasive *L. maackii* populations and the *L. subsessilis* population in Korea were quantified using Principal Component Analysis (PCA) in the statistical programming language R. PCA reduces dimensionality of the 19 BIOCLIM variables into a smaller set of orthogonal axes while preserving variation within the dataset (Ringnér, 2008). Probability ellipses were drawn around the native and invasive clusters of *L. maackii* in the principal component plots with a 95% confidence level. The three principal components accounting for the greatest amount of variation within the dataset were used to demonstrate significant climate niche differences between the native and invasive *L. maackii* and Korean *L. subsessilis* populations (Smith & Donoghue, 2010). QQ plots were used to evaluate the normality of residuals for PC1-3. A leptokurtic distribution observed in the QQ plot of residuals for PC2 suggested a violation of the normality assumption for ANOVA, necessitating the use of a non-parametric test known as the Kruskal-Wallis test. A Tukey's Honestly Significant Test (Tukey's HSD) was used to demonstrate significance in pairwise differences in the ANOVAs for PC1 and PC3. Finally, a pairwise Wilcoxon Rank Sum Test was used for post-hoc testing following the Kruskal-Wallis Test for PC2.

A machine learning technique known as maximum entropy modeling, or Maxent, was used to build probable occurrence maps of the *Lonicera* species (Philips et al., 2018). Maxent builds probable occurrence maps by comparing presence data (latitude and longitude) to all

environments available in a study region. The climate variable grids for the specified region of study are then used to predict occurrence for the specific region. Thus, areas with similar climate conditions to those of the observed localities of *L. maackii* will have higher occurrence probability scores (Phillips et al., 2006). However, Maxent requires the climatic grids, from BIOCLIM, in an ASCII text format, whereas the BIOCLIM data is available only as a raster image (i.e., TIFF format). This requires that each BIOCLIM raster image be converted using Raster to ASCII conversion tool in ArcMap. This step converts the pixel color value to an ASCII text value for every square kilometer of land on Earth. The new ASCII matrix can then be imported into Maxent for niche modeling.

Probable occurrence models in Maxent built with points in one geographic range may be projected onto a novel range. In other words, a climate niche model was built using localities in North America and projected onto East Asia, predicting a geographic distribution. The same was performed in the reverse, with the East Asian model projected onto North America. These projections were compared to the observed distributions to demonstrate the presence of a climatic niche shift between the invasive and native ranges.

**Table 1.** Description of BIOCLIM variables used and the loadings of the first three principal components from a PCA.

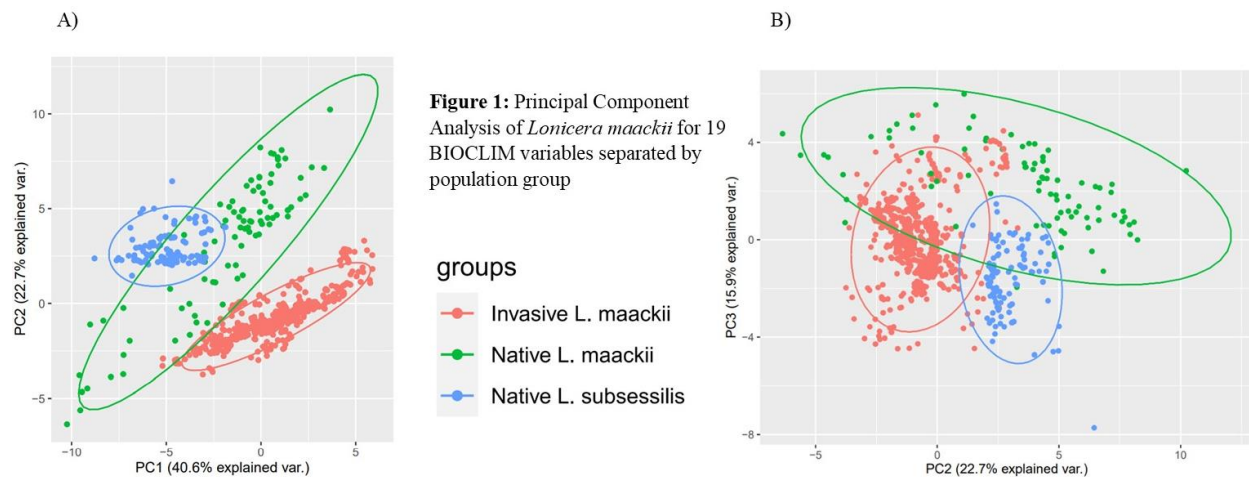
<b>Variable description</b>	<b>BIOCLIM</b>	<b>PC1 (40.6%)</b>	<b>PC2 (22.7%)</b>	<b>PC3 (15.9%)</b>
<i>Annual Mean Temp.</i>	BIO1	0.289	0.211	0.205
<i>Mean Diurnal Range</i>	BIO2	0.178	-0.190	<0.001
<i>Isothermality (BIO2/BIO7)* 100</i>	BIO3	0.268	<0.001	<0.001
<i>Temp. Seasonality</i>	BIO4	-0.222	-0.287	0.107
<i>Max Temp. of Warmest Month</i>	BIO5	0.253	<0.001	0.255
<i>Min Temp. of Coldest Month</i>	BIO6	0.265	0.308	<0.001
<i>Temp. Annual Range</i>	BIO7	-0.132	-0.330	0.112
<i>Mean Temp. of Wettest Quarter</i>	BIO8	<0.001	0.107	0.293
<i>Mean Temp. of Driest Quarter</i>	BIO9	0.266	0.142	<0.001
<i>Mean Temp. of Warmest Quarter</i>	BIO10	0.247	<0.001	0.299
<i>Mean Temp. of Coldest Quarter</i>	BIO11	0.298	0.252	0.105
<i>Annual Precip.</i>	BIO12	<0.001	0.207	-0.457
<i>Precip. of Wettest Month</i>	BIO13	-0.202	0.337	-0.160
<i>Precip. of Driest Month</i>	BIO14	0.252	-0.159	-0.334
<i>Precip. Seasonality (CV)</i>	BIO15	-0.259	0.282	0.126
<i>Precip. of Wettest Quarter</i>	BIO16	-0.201	0.338	-0.190
<i>Precip. of Driest Quarter</i>	BIO17	0.249	-0.163	-0.336
<i>Precip. of Warmest Quarter</i>	BIO18	-0.225	0.309	-0.203
<i>Precip. of Coldest Quarter</i>	BIO19	0.258	-0.141	-0.342

## Results

The PCA reduced the 19 BIOCLIM variables into a set of three new orthogonal axes which cumulatively account for 79% of the variation in the dataset. Each observation was recast and scored along these new PC axes (Figure 1). Each PC is unitless, but can be interpreted by examining the loadings, which describe the relative contribution of each input variable in the PC (Jolliffe & Cadima, 2016). For example, for PC1 maximum temperature in the warmest month, minimum temperature of the coldest month, mean temperature of the driest quarter, and mean temperature of coldest quarter all loaded positively, whereas precipitation seasonality, precipitation in the wettest quarter, and precipitation in the wettest month loaded negatively (Table 1). This suggests that PC1 represents a continuum where colder and seasonal precipitation is represented on one end and warmer persistent precipitation is represented on the other. Of the three PC axes retained there was a clear and dramatic separation between invasive and native populations of *L. maackii* in PC2 (Figure 1A), which represents a shift towards cooler, seasonal precipitation environments when compared to the generally warmer, but seasonal temperatures of their native range. There was more overlap on PC1 and PC3 generally, but 95% confidence ellipses drawn around population clusters still showed a visual separation (Figure 1A). Interestingly, native *L. maackii* was less tightly clustered than either invasive *L. maackii* or native *L. subsessilis*. Furthermore, native *L. maackii* populations occupy a climatic niche that may more closely resemble that of *L. subsessilis*, than the invasive *L. maackii* populations (Figure 1A). This suggests a dramatic shift in the climates inhabited by *L. maackii* in North America.

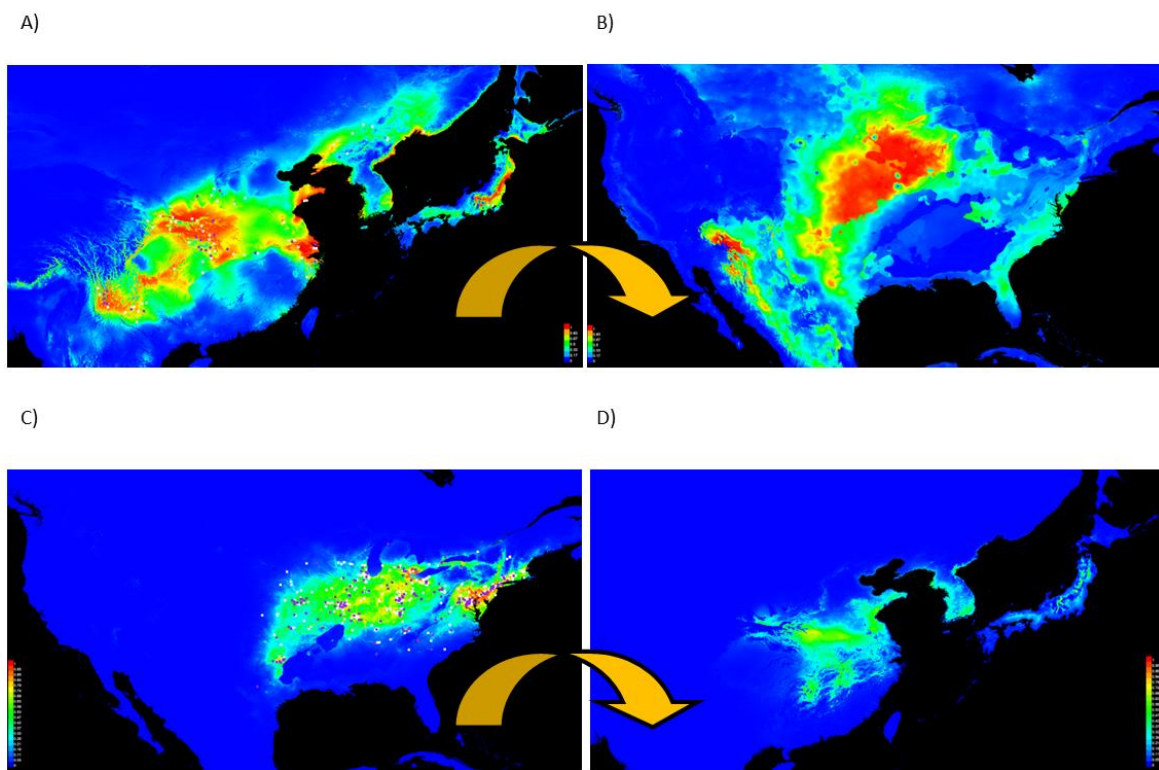
Normality of principal component residuals for ANOVA was visually determined with QQ plots. ANOVAs performed on PC1 ( $F_{1,1168} = 456.9, p < 0.001$ ) and PC3 ( $F_{1,1168} = 160.0$ ,

$p < 0.001$ ) both showed significant differences between population score means (native *L. maackii*, invasive *L. maackii*, and *L. subsessilis*). Additionally, post-hoc tests showed that each pairwise comparison in score means between population groups were significantly different along PC1 ( $p < 0.001$ ) and PC3 ( $p < 0.001$ ). For PC2, there was a detectable leptokurtic (fat-tailed) distribution, suggesting a violation of the normality assumption for ANOVA. Thus, the non-parametric Kruskal-Wallis test was used and showed a significant difference in score means between population groups on PC2 ( $H = 372.7$ ,  $p < 0.001$ ). Post-hoc pairwise comparisons between population groups demonstrated significant differences between the PC2 score means of the invasive *L. maackii* and native *L. maackii* ( $p < 0.001$ ), invasive *L. maackii* and native *L. subsessilis* ( $p < 0.001$ ), and native *L. maackii* and native *L. subsessilis* ( $p = 0.002$ ). Taken together, the mean scores for each population along all three components were significantly different, suggesting a quantitative separation in the climate niches between native and invasive *L. maackii* and its sister taxa in its native range.



When projecting the probable occurrence of the native range onto North America, and vice versa, Maxent showed a dramatic deviation between the observed range of invasive *L.*

*maackii* (Figure 2C) and the range predicted from climate conditions in its native range (Figure 2B). There was also a large deviation in the observed native range (Figure 2A) and the range predicted from climate conditions in its invasive range (Figure 2D). However, there is some overlap between the observed and predicted range in this region, particular in Central China and parts of the Korean Peninsula (Figure 2D). This projected range is dramatically narrower than its observed range (Figure 2A).



**Figure 2:** Maxent probable occurrence maps of *L. maackii* for A) native Chinese points and B) model projected onto North America. These models were also drawn from *L. maackii* from C) North America and D) projected onto China. Red coloration denotes higher probability of occurrence with blue coloration denoting a lower probability of occurrence.

## Discussion

We uncovered a visually, and statistically significant, shift between the native and invasive niche space of *Lonicera maackii* with PCA. Additionally, the native *L. maackii* niche space overlapped with that of its sister taxa, *L. subssesilis*, to a greater extent than with the invasive population. If range expansion were fully determined by abiotic factors, we would expect the native *L. maackii* population to have a climatic niche space more similar to its invasive North American population than its sister taxon. Instead, these results suggest the possibility of a climatic range expansion through a major shift in its niche requirements in North America – lending support to biotic constraints of range expansion and the Novel Weapon and Empty Niche hypotheses.

These findings were also supported through Maxent climatic niche modeling which also found a shift between the native and invasive niche spaces. When models built from one population of *L. maackii* were projected onto the range of the other population, there was a clear mismatch in both directions (native to invasive and invasive to native). There was, however, some overlap in the range between the projected range in East Asia and the observed range. As a result, we cannot rule out the possibility that founding populations come from the margins of its native range. Further study is needed to confirm that this separation is not due to selection bias wherein the North American *L. maackii* population was founded by individuals from a narrow range in East Asia with similar climatic conditions to those observed in North America. Nevertheless, both parametric and nonparametric differences showed a significant difference between all three populations among all three of the studied principal components of BIOCLIM variables. Taken together, these three forms of analysis all support the same conclusion, that

there is a difference in the climate conditions that *L. maackii* thrives under in East Asia relative to North America.

Genetic sampling and phylogenetic analysis of individuals collected from around these ranges may resolve this limitation. Leaf tissue samples, available at herbariums around the country, may provide genetic material for the construction of an intraspecific phylogeny (rooted with material from the *L. subsessilis* sister taxon) that could elucidate the invasion pattern of *L. maackii*. For example, a detailed phylogenetic hypothesis of relationships among populations may associate the invasive North American *L. maackii* populations with their native East Asian places of origin. If the invasive *L. maackii* populations are not closely related to the *L. maackii* population in a narrow margin of East Asia in which there is overlap between the observed and projected ranges by Maxent, then the climatic niche of *L. maackii* likely shifted and hypotheses of biotic constraints of invasion and range expansion may be insufficient to explain the success of *L. maackii* in North America.

Additionally, consideration of biotic constraints on range expansion of an understory shrub may be incomplete without consideration of canopy cover between native and invasive ranges. Further study on canopy cover differences (full-shade vs open-canopy), in addition to relationships among populations may provide an ecological context beyond climatic conditions.

## Conclusion

The quantification and modeling of the climatic niche space of *L. maackii* suggests that it experienced a rapid and dramatic climatic niche shift as it escaped East Asia and became naturalized in North America. Thus, climate conditions were not likely serving as strong

constraints against range expansion and invasion of *L. maackii* in novel environments as predicted by the Environmental Filtering hypothesis. These findings lend support, instead, for ecological theories of invasion driven by biotic factors. However, phylogenetic analysis may be necessary to confirm that this observed range expansion is not due to biased selection of introduced populations from small regions in China resembling the climate envelope of *L. maackii* populations in North American.

With a broader understanding of the conditions that drive the spread of invasive species, it may be possible to predict further invasions and range expansions of ecologically damaging species like *L. maackii*. Land managers may prioritize environmental intervention strategies optimized to combat the invasion patterns of *L. maackii* in sensitive habitats. Governmental organizations may be able to better predict which plants pose the greatest risk for invasion, which is a particularly valuable tool in agriculture. Our findings suggest that future study might be best directed at elucidating the biotic constraints of range expansion and invasion, particularly for understory shrubs like *L. maackii*.

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