Long-Distance Dispersal and Diffusion in the Invasion of *Lonicera maackii*

David L. Gorchov, Steven M. Castellano, and Douglas A. Noe*

To investigate the relative importance of long-distance dispersal vs. diffusion in the invasion of a nonnative plant, we used age structure to infer the contribution to recruitment of external propagule rain vs. within-population reproduction. We quantified the age structure of 14 populations of Amur honeysuckle in a landscape where it recently invaded, in Darke County, OH. We sampled the largest honeysuckle individuals in each population (woodlots), and aged these by counting annual rings in stem cross sections. Individuals in the oldest four 1-yr age classes are assumed to be from external recruitment, given the minimum age at which shrubs reproduce. We used these recruitment rates to model external recruitment over the next 5 yr and used observed age structures to estimate total recruitment. We used the difference between total and external recruitment to infer the rate of internal recruitment. Our findings indicate that recruitment from within the population is of about the same magnitude as immigration in the fifth to seventh year after population establishment, but by years 8 to 9 internal recruitment dominates. At the landscape scale, the temporal-spatial pattern of population establishment supports a stratified dispersal model, with the earliest populations establishing in widely spaced woodlots, about 4 km from existing populations, and these serving as "nascent foci" for diffusion to nearby woodlots. Understanding the relative importance of long-distance dispersal vs. diffusion will inform management, e.g., whether it is more effective to scout for isolated shrubs or remove reproducing shrubs at the edge of invaded areas.

Nomenclature: Amur honeysuckle, *Lonicera maackii* (Rupr.) Herder.

Key words: Age structure, Amur honeysuckle, colonization, immigration, invasive species, nascent foci, stratified dispersal.

A fundamental question in invasion biology is the importance of diffusion vs. long-distance dispersal to expansion of the invaded range. Mack (1985) stressed how foci of isolated populations would have greater spatial spread than a single diffusing population, and that the number of foci is more important than their individual size. Moody and Mack (1988) coined the term *nascent foci* and emphasized the importance of eradicating these in the control of plant invasions. Hengeveld (1989) coined the term *stratified diffusion* for this combination of neighborhood diffusion and "jump" or long-distance dispersal. Shigesada et al. (1995) provided a general mathematical model for stratified diffusion. Although the concept of nascent foci [sensu Moody and Mack (1988)] is compelling, how can we determine if new populations function as nascent foci in an invasion? One necessary criterion is that the population is growing because of within-population recruitment, rather than continued immigration. How quickly does internal recruitment dominate population growth, and how can we measure this?

Although a record of spatial spread over time would provide direct evidence of the pattern of invasion, such a record is not available for most invasive species. But in cases where individual organisms can be aged, age structures of populations can be used to infer spatio-temporal processes (Dietz 2002). Dietz (2002) showed how age structure across a single stand can be used to infer whether the population invaded as an advancing front, colonized multiple sites more or less simultaneously (diffuse, in his terminology), or a mixture of the two. Similarly, Zhao et al. (2013) used age structure of an invasive shrub to reconstruct the temporal and spatial pattern of invasion within a forest stand. We extend this within-stand approach to an among-stand analysis, and use age structure to reconstruct the pattern of invasion in a landscape and to infer the relative importance of long-distance dispersal and short-distance diffusion.

In systems where expansion of the invaded area is dominated by populations that are founded by rare long-distance dispersal events, populations would typically be

DOI: 10.1614/IPSM-D-13-00105.1

* First author: Professor, Department of Biology; second author: Graduate Student, Department of Botany; third author: Associate Professor, Department of Statistics, Miami University, Oxford, OH 45056. Corresponding author's E-mail: GorchoDL@miamioh.edu

Management Implications

The relative importance of diffusion (expanding front) vs. long-distance dispersal can inform management of invasive species. If diffusion dominates, it will be most efficient to monitor for, and eradicate, new patches on the edges of existing patches. If long-distance dispersal dominates, one should scout for, and eradicate, initial colonists in previously uncolonized patches (Moody and Mack 1988). Furthermore, removing reproductive individuals at the edge of the current range would slow the spread of diffusing populations, but have little effect if long-distance dispersal dominates.

We assessed the relative importance of diffusion vs. long-distance dispersal in the invasion of Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder] in forested patches in an agricultural landscape in southwest Ohio. We examined the age structures of woodlot populations, used these to estimate the importance of immigration vs. within-population recruitment, and examined the temporal-spatial pattern of population initiation.

Our findings indicate that long-distance dispersal dominates early in the invasion, and new populations grow slowly, until the original colonists begin reproducing. Thus, efforts to slow the spread of *L. maackii* should involve scouting for colonists in woodlots up to 4–5 km from existing populations. Fortunately, this is feasible, as even small honeysuckle shrubs are easily spotted during early spring and late fall, when native deciduous woody plants are not in leaf. These searches could be as infrequent as every 3 yr, given the lack of reproduction in the youngest age classes.

founded by one or a few individuals, and would not increase in density until those founders began to reproduce. An age structure of such a population would therefore be expected to show discontinuities in the older age classes (Figure 1). Conversely, in systems where invasions proceed primarily by diffusion, early population growth would be caused primarily by continued arrival of new recruits (immigration) from nearby seed sources. In that case, a more continuous age distribution would be expected.

Our objective was to use age structure to infer the spatio-temporal pattern of invasion of a partly self-compatible shrub, *Lonicera maackii*. We used the minimum reproductive age to define the duration of the period when all recruits could be assumed to be immigrants, and from this estimated immigration rates. We used this immigration rate to estimate the proportion of recruits in subsequent years that could be attributed to immigration or internal recruitment. We also used the ages of the oldest *L. maackii* individual in each stand to reconstruct the landscape level spatial pattern of invasion, including minimum dispersal distances.

Materials and Methods

Study Species. Amur honeysuckle, *Lonicera maackii* (Caprifoliaceae), is an upright, deciduous shrub native to northeast Asia that is a major forest invader in eastern North America. *Lonicera maackii* was introduced to North America in 1898 and marketed for its high flower and fruit production, as well as its ability to prevent erosion (Luken and Thieret 1995). Over the past century it has escaped its horticultural confines and invaded forests and successional areas in at least 24 different states, including Ohio (Luken and Thieret 1995; Trisel and Gorchov 1994). *Lonicera maackii* negatively affects growth and fecundity of forest annuals and perennials (Gould and Gorchov 2000; Miller and Gorchov 2004) and tree seedling recruitment (Gorchov and Trisel 2003; Hartman and McCarthy 2004), with impacts on forest floor diversity and composition (Hutchinson and Vankat 1997; Collier et al. 2002; Hartman and McCarthy 2008). *Lonicera maackii* also reduces nesting success of native birds (Schmidt and Whelan 1999; Rodewald et al. 2010) and larval survival of amphibians (Watling et al., 2011).

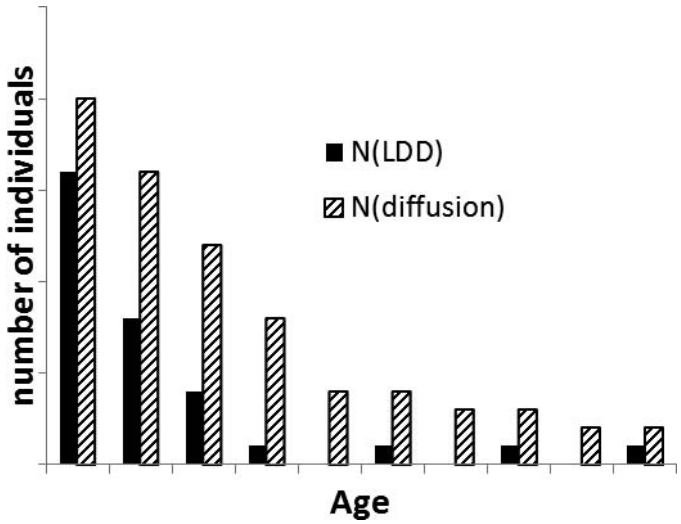

Figure 1. Hypothetical age distributions expected in a system where populations are founded by rare, long-distance dispersal events (LDD) vs. a system where new populations continually add recruits because of diffusion from nearby propagule sources.

Several aspects of *L. maackii* demography are directly relevant to this study. Under woodlot conditions, shrubs begin to reproduce as young as 3 yr old, with older shrubs more likely to reproduce (Deering and Vankat 1999; see also Figure 2). This shrub does not reproduce clonally and is primarily outcrossing, but there is some self-compatibility (Goodell and Iler 2007; Barriball et al. in press), so a single individual could initiate a population. Seeds are dispersed by birds (Bartuszevige and Gorchov 2006) and white-tailed deer (Castellano and Gorchov 2013). Seedlings establish in sun or shade (Luken and Goessling 1995).

Age-Dependent Fecundity. To determine the age at which *L. maackii* begins to reproduce, we analyzed age and fruit count data collected over several years by classes at the

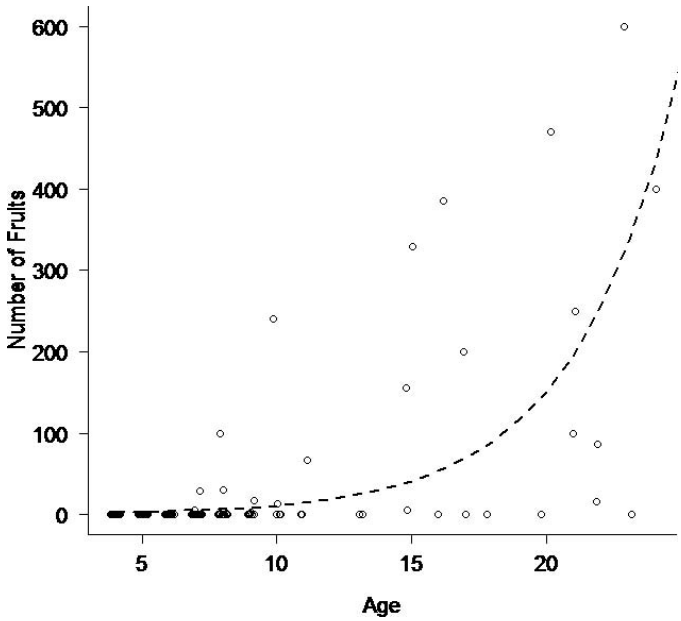

Figure 2. Scatter plot of the number of fruits vs. shrub age based on annual rings for 317 shrubs near Oxford, Butler County, OH. The line shows the Poisson regression fitted to these data ($P < 0.001$, McFadden's pseudo-$R^2 = 0.59$).

Miami University Ecology Research Center, 50 km (30 miles) south of the main study area described below. A total of 317 shrubs were aged by counting annual rings in the largest stems and roots, approximately equal numbers in woodlot edges and interiors. Field work was done after fruit maturation and before dispersal, enabling fruits to be counted, or estimated if > 100. To determine how reproduction depends on age, we fitted a Poisson regression to the fruit count vs. age data.

Study Area. We chose a 20-km^2 area where *L. maackii* has only invaded recently (< 20 yr) in southern Darke County, OH (Figure 3). Within the study landscape *L. maackii* shrubs occur in woodlots in a matrix of row crop agriculture. Woodlots ranged in size from 1.1 to 14.5 hectares. Although some woodlots were nearly adjacent, others were separated by agricultural fields, up to 1.1 km from the closest study woodlot.

All woodlots in the study area should be invasible by this shade-tolerant shrub (Luken et al. 1997), based on the finding of Bartuszevige et al. (2006) and Gorchov et al. (2014) that presence and percent cover of *L. maackii* in woodlots in this region were statistically dependent only on features of the surrounding landscape, and not on stand characteristics such as woodlot area or stand basal area.

Sampling of *L. maackii* Populations. We considered each woodlot to be a separate population of *L. maackii*. The Universal Transverse Mercator (UTM) coordinates (NAD (North American Datum) 1983 UTM Zone 16N) were determined for the center point of each woodlot. We determined the age structure of each population by counting annual rings in stems. For populations with < 30 individuals, we sampled every individual. For populations with > 30 individuals, we sampled the largest 30 individuals, based primarily on height. Height is strongly correlated with age in this species (Deering and Vankat 1999). We were able to find every *L. maackii* individual in these woodlots in spring or fall by taking advantage of the extended leaf phenology of this invasive shrub; *L. maackii* leafs out earlier in the spring (McEwan et al. 2009) and retains its leaves later in the fall (Wilfong et al. 2009; Johnston et al. 2012) than native deciduous trees and shrubs in our area. Most populations were sampled in fall 2010 or spring 2011, with a few sampled fall 2011 or spring 2012.

Aging *L. maackii* Individuals. For each individual shrub we recorded height, number of stems originating from the burl, diameter of the three largest stems, and for several populations, GPS coordinates (with a Trimble Geo-Explorer GPS [Trimble Navigation Limited, Sunnyvale, CA] receiver with submeter accuracy). We then collected the basal portion of the largest stems (1–4 stems per shrub). We used a mitre saw to make a clean cut of each of these stem portions, and the cross-sectional surface of each of these stem portions was then scanned with a flatbed scanner. The images were then processed with 'Image J' software to enhance contrast, facilitating detection of annual rings. Two individuals independently counted rings of each stem. There were high correlations in ring counts among observers, with the mean difference between observers of < 0.5 rings. For each stem we determined the mean of individual observers' ring counts. To assign an age to each shrub, we used the highest mean ring count among its stems, rounded up to the next integer. In the case of shrubs sampled in fall 2011 or spring 2012, we subtracted 1 to obtain the plant's age the previous year. We assigned an age to each population as equivalent to the age of the oldest individual (Table 1).

For each population we constructed an age distribution. For those populations where we sampled only the largest 30 shrubs, rather than all individuals, we assumed that the youngest three age classes were incompletely censused. For the purpose of modeling internal and external recruitment, we used only the oldest 9 age classes. That is, we only modeled the contributions of internal and external recruitment for the first 9 yr of each population. Thus the data used in these analyses came from the completely sampled populations ≥ 9 years in age and incompletely sampled populations ≥ 12 years in age. A total of 14 populations met the criteria, and were used in the model.

These age structures were used to reconstruct the number of individuals in each population at specific points

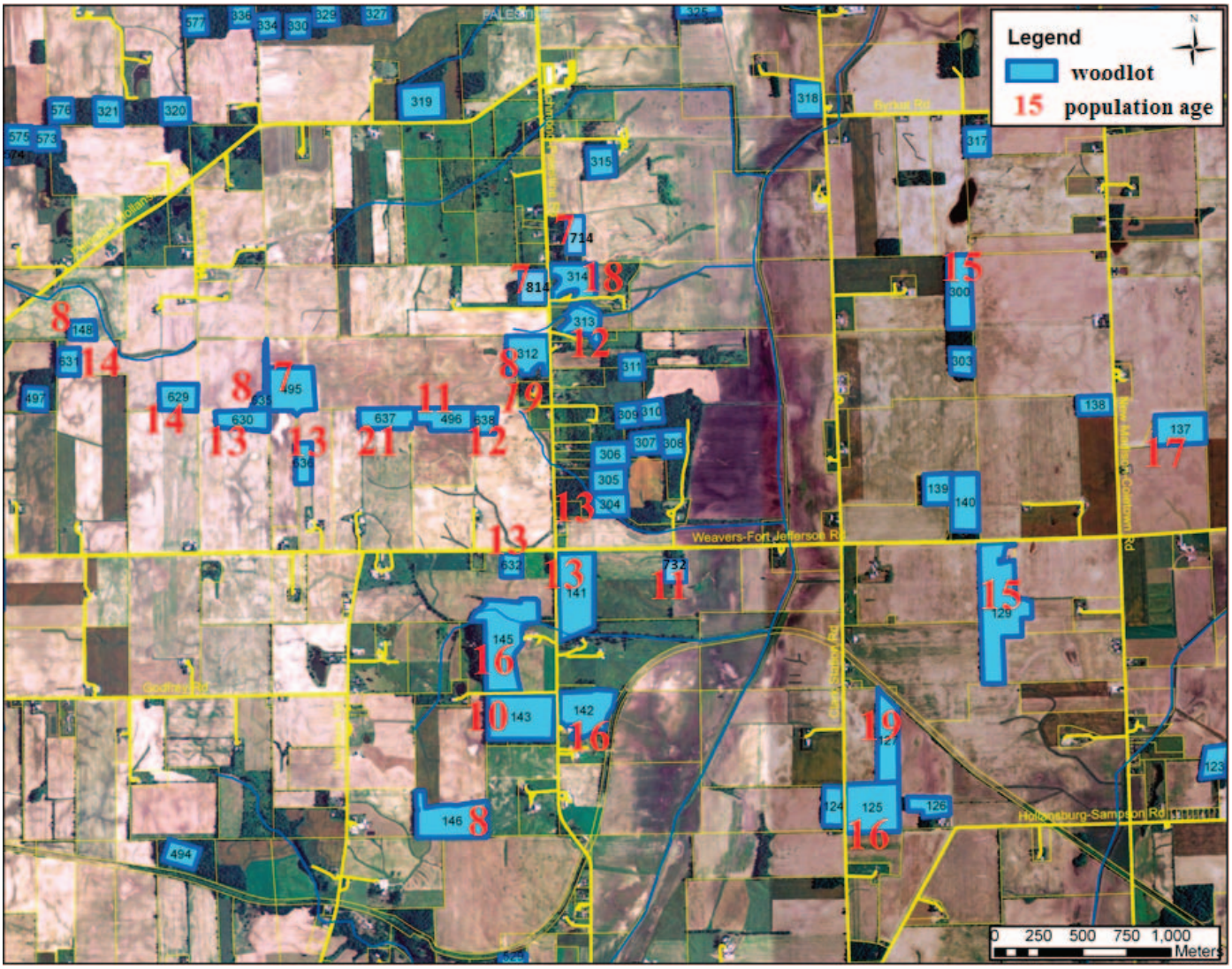

Figure 3. Map of the study woodlots in south-central Darke County, OH, showing the woodlots where Amur honeysuckle shrubs were sampled for age distributions, numbered as per Table 1. Numbers in red indicate the age of the oldest Amur honeysuckle shrub in each of the woodlots, as of 2010. The red 19 in italics south of woodlot 312 is the age of an isolated large Amur honeysuckle shrub (3756). The village of Palestine appears at the top of the figure. The westernmost and easternmost woodlots are separated by 6.3 km; the north–south extent is 3.3 km.

in the past. The implicit assumption is that there is no mortality—that all individuals alive in an earlier year are still alive at the sampling date. This same assumption is implicit in other studies that have inferred population growth from age structure (e.g., Dietz 2002; Zhao et al. 2013). This assumption is reasonable for *L. maackii* because individual shrubs, once established, have very high survivorship. This is evidenced by the high survival of *L. maackii* individuals in forest stands throughout Ohio (K. Knight, unpubl. data); 103 out of 104 shrubs > 1 m height in 2008 were still alive 2 yr later (annualized survival rate of 99.5%), as were 56 of 60 shrubs 0.5 to 1 m height (annualized survival 97%).

Immigration vs. Internal Recruitment. We used two algebraic models to estimate the proportion of recruits from internal vs. external sources based on the assumptions that recruitment rate from external sources (X) was constant over time, and any additional recruitment was attributable to recruitment from reproduction within each population (Y). We assumed that shrubs do not reproduce in their first 3 yr, based on the Deering and Vankat (1999) finding that < 5% of 3-yr-olds were reproductive and our finding (Figure 2) that none of the 231 shrubs aged 0 to 5 bore fruits. Based on this assumption, we estimated the external annual recruitment rate (immigration rate) for each population as the observed number of shrubs in the

Table 1. For each Amur honeysuckle population (woodlot) sampled in Darke County, OH, the number of shrubs sampled and aged, the age of the oldest shrub, the number of recruits established in the first 3 yr of each population (= number of individuals in the oldest three age classes), and the immigration rate (immigration rate = mean number of recruits for the first 3 yr). Populations in bold are those in which sampling was complete for the oldest nine age classes, enabling estimation of immigration vs. internal recruitment in years 4 through 9 (Table 2). The bottom row reports mean values across all 28 populations. Additionally, the largest individual in woodlot 126 was 12 yr old, and an isolated large shrub just south of woodlot 312 was 19 yr old.

Population no.	Shrubs aged	Oldest (yr)	Number of recruits, years 1–3	Immigration rate (ind/yr)
125	94	16	1	0.33
127	36	19	3	1.00
129	20	15	1	0.33
137	36	17	6	2.00
141	30	13	1	0.33
142	44	16	1	0.33
143	29	10	6	2.00
145	26	16	2	0.67
146	19	8	1	0.33
148	2	8	1	0.33
300	40	15	1	0.33
304	30	13	1	0.33
312	38	8	8	2.67
313	37	12	7	2.33
314	32	18	5	1.67
495	4	7	4	1.33
496	10	11	2	0.67
629	12	14	1	0.33
630	3	13	2	0.67
631	3	14	1	0.33
632	30	13	2	0.67
635	3	8	2	0.67
636	13	13	2	0.67
637	28	21	1	0.33
638	11	12	1	0.33
714	30	7	3	1.00
732	3	11	1	0.33
814	25	7	9	3.00
Total	688		76	25.33
Mean across populations			2.62	0.87
Additional samples				
126	1	12		
3756	1	19		

three oldest age classes divided by three (Table 1). In the first model we assumed that each population retained this same immigration rate, and that any additional individuals in younger age classes were caused by internal recruitment (Table 2). In the second model we assumed that all populations shared a global immigration rate, and estimated this as the mean of the individual population immigration rates. To parameterize this global immigration rate we also included data from 14 additional populations where we were confident the oldest three age classes were complete.

A uniform immigration rate would not be a reasonable assumption if the immigration rate increased over time, i.e., populations establishing later experience a higher immigration rate because of the higher density of reproductive shrubs in the landscape. To test this assumption, we regressed immigration rate vs. establishment year for all 28 populations.

To explore landscape scale invasion patterns, we plotted the age of the oldest individual shrub in each woodlot (population) on a map of the study landscape. We also constructed a bubble plot to show the population size (number of shrubs) in each population at three points in time (1997, 8 yr after the oldest individual in the landscape was established, 2002, and 2007). This population size was inferred from the age structure, assuming that individuals age $\geq x$ were the only ones alive in the population x yr ago.

Dispersal Distances. To estimate the minimum distances that seeds dispersed to establish new populations, we determined, for each of the study populations, the closest potential source population. To be a potential source, a population had to be $\geq$ 4 yr older than the target population. Distances were calculated as the linear distance between woodlot centers. If an edge of the 20-km^2 study area was closer than a potential source, e.g., for the oldest populations, the distance from the woodlot center to this edge was used as the minimum dispersal distance.

Results and Discussion

Age-Dependent Fecundity. Of the 317 sampled shrubs, aged 0 to 42 yr old, 25 bore fruits, with the youngest fruiting plants of age 6 (Figure 2). Both the proportion of individuals fruiting, and the number of fruits per reproductive shrub, were positively correlated with age.

Age Distributions in a Recently Invaded Landscape. Annual rings were counted for a total of > 1200 stems, from 689 individual shrubs in 29 populations, plus one isolated shrub. The population ages, based on oldest individual, ranged from 7 to 21 yr old (Table 1). Age distributions of most, but not all, populations showed discontinuities in the oldest age classes (Figure 4), similar to that expected for a system where long-distance dispersal dominates (Figure 1). Populations generally have few

Table 2. Estimates of proportions of recruitment attributable to immigration for each population (Population) of Amur honeysuckle for which sampling was complete for the oldest nine age classes. Population age and sample size are given in Table 1, where these populations are marked in bold. For each population we report the number of recruits established in the fourth year (= number of individuals in fourth oldest age class), in years 5 to 7, and in years 8 to 9, and the proportion of these recruits attributed to immigration according to two methods: (1) assuming each population had a constant immigration rate (Table 1, last column), and (2) assuming a single constant (uniform, global) immigration rate across all populations (Table 1, last row, last column).

				Percentage of recruits attributed to immigration			
	Number of recruits			Based on population's immigration rate		Based on uniform global immigration rate	
Population no.	Year 4	Year 5–7	Year 8–9	Year 5–7	Year 8–9	Year 5–7	Year 8–9
125	1	9	18	0.11	0.04	0.29	0.10
127	1	8	5	0.38	0.40	0.33	0.35
129	0	2	5	0.50	0.13	1.31	0.35
137	0	5	11	1.20	0.36	0.52	0.16
141	1	7	12	0.14	0.06	0.37	0.15
142	1	3	6	0.33	0.11	0.87	0.29
145	0	4	10	0.50	0.13	0.66	0.17
300	2	12	20	0.08	0.03	0.22	0.09
314	1	4	12	1.25	0.28	0.66	0.15
496	2	5	1	0.40	1.33	0.52	1.75
629	1	3	2	0.33	0.33	0.87	0.87
630	0	0	0				
636	1	5	4	0.40	0.33	0.52	0.44
637	0	1	0	1.00		2.62	
Total	11	68	106	0.43	0.18	0.54	0.23

individuals in the oldest age classes, and more individuals in younger age classes, young enough to be offspring of the original colonists.

Immigration Rates. For the 28 populations with complete census data for the oldest three age classes, the immigration, or recruitment, rate averaged 0.87 ind/yr (range 0.33 to 2.67, Table 1). We expected immigration rates to increase over time, as more populations fill the landscape and each increases in abundance. However, the regression of recruitment rate on establishment year was not significant ($F = 2.61$, df = 1,26, $P = 0.12$, Figure 5), justifying the use of a constant global immigration rate. Our finding that immigration rate was not significantly higher for populations that were founded later in the invasion process suggests that factors other than propagule pressure, or more precisely, propagule rain (Lockwood et al. 2009), influence the early growth of new populations.

Immigration vs. Internal Recruitment. *Assuming Constant Immigration Rate for Each Population.* Under the assumption that each population has a constant immigration rate, then, during the fifth-to-seventh years after population founding events, an average of 43% of new recruits are attributed to immigration (Table 2), with the balance attributed to reproduction from within the population. For three of the populations immigration accounted for more recruits than within-population recruitment, for eight populations within-population recruitment was greater, and for the remaining three populations the inferred contributions were equal (or there were no recruits during this period). For the eighth-to-ninth years after establishment, internal recruitment predominated for nearly all populations; immigration accounted for most individuals in only one of the populations (Table 2). On average, immigration accounted for only 18% of recruits in years 8 to 9.

Assuming Uniform Immigration Rate. Under the assumption of a uniform immigration rate, immigration accounted for an average of 54% of recruits in years 5 to 7 and 23% of recruits in years 8 to 9 (Table 2). Immigration accounted for most of the year 5 to 7 recruits in 9 of 13 populations, but for most of the year 8 to 9 recruits in only two populations.

If mortality of established shrubs is important, then our present-day counts underestimate the number of individuals that established in previous years. Thus our estimate of immigration rate, based on the number of individuals in the oldest age classes, may be low, which would result

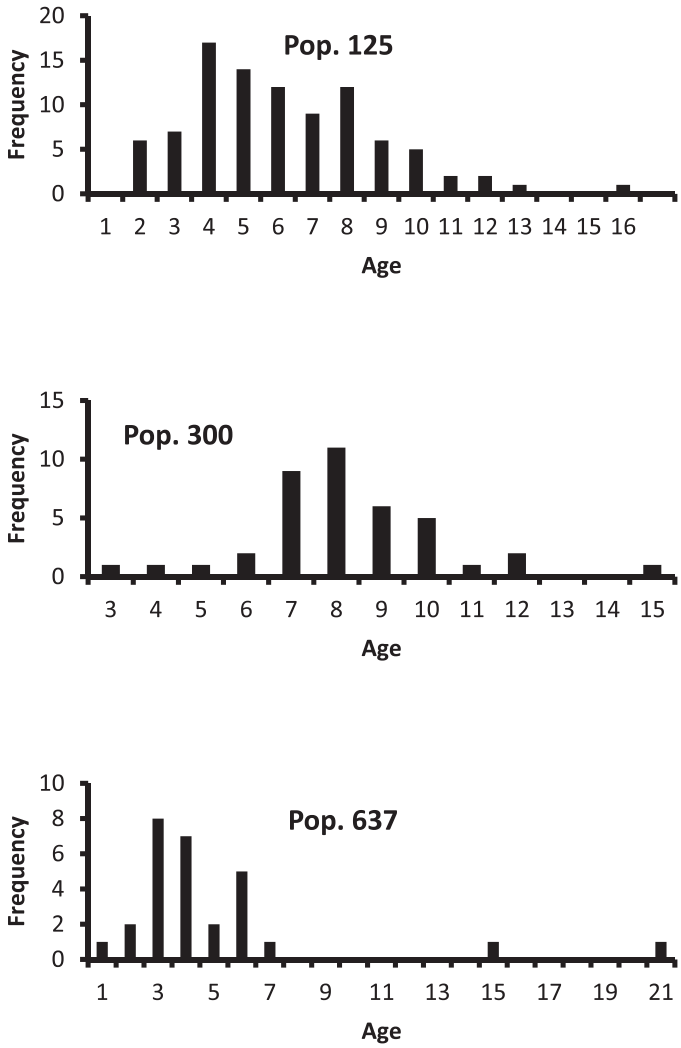

Figure 4. Age distributions of some representative Amur honeysuckle populations, showing discontinuities in recruitment in the early years of each population. Woodlot 125 had the largest sample of aged shrubs ($N = 94$). Woodlot 300 had the largest number of shrubs in the oldest nine age classes ($N = 35$). Woodlot 637 had the oldest shrub in the study (21 yr old). In each case, the low counts of individuals in the youngest age classes are caused by undersampling, as only the largest individual shrubs in each population were sampled.

in our underestimating the contribution of subsequent immigration to recruitment. We suspect this is not a major problem, as *L. maackii* individuals have extremely high survival after their first few years, as evidenced by the data referenced earlier.

Landscape Scale Spatiotemporal Patterns. At the level of the entire landscape, there was no spatial association of the oldest populations (Figure 3). A bubble plot showing the location of the populations, and the number of individuals in each, at three points in time (Figure 6), shows that the

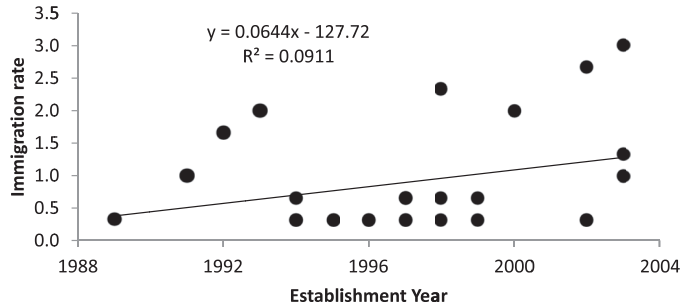

Figure 5. Regression of immigration rate vs. year of establishment for 28 populations of Amur honeysuckle in Darke County, OH. Immigration rate is the number of individuals in the oldest three age classes divided by 3. Establishment year is the birth year for the oldest individual in the population, based on stem ring counts.

oldest populations were widely spaced in the landscape. Over time, the numbers in these populations increases while new populations initiate at other locations. Neither figure shows any evidence of an invasion front, where the oldest populations would be clustered in one area, and progressively younger populations would radiate out from these.

Early in the invasion of this landscape, four of the first five populations initiated from sources that were > 4 km from any existing source of propagules (Figure 7), and they were not close to each other (Figure 3). From about 1993

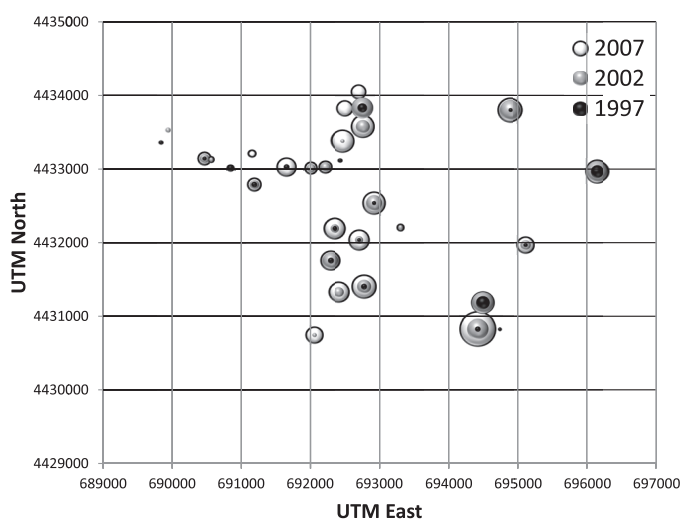

Figure 6. Bubble plot showing the relative size (number of individuals) in each of 28 populations of Amur honeysuckle in Darke County, Ohio in 3 years, based on the age structure of the population as censused in 2010 to 2011. Axes are Universal Transverse Mercator (UTM) coordinates. For each population, the bubble is centered on the center of the woodlot. The landscape is the same landscape shown in Figure 2.

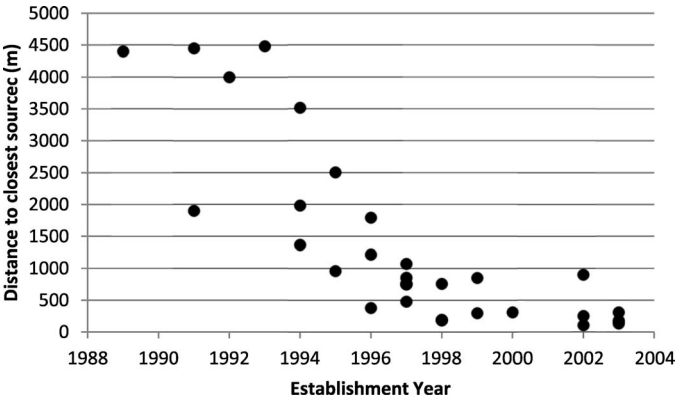

Figure 7. Scatter plot of distance to closest potential source population vs. establishment year of a population for woodlots in Darke County, Ohio. Establishment year was based on the age of the oldest individuals. The closest source was the closest population that was > 4 yr older than the target population, thus potentially had at least one reproductive shrub, except for the four oldest populations, where we used the distance to the edge of the intensively studied landscape. Distances were calculated from between geographic centers of the respective woodlots.

to 1996 (4 to 7 yr after the oldest population was founded), minimum dispersal distances declined, as woodlots 1 to 2.5 km from the oldest woodlots were colonized. From 1997 on the invasion was characterized by colonization of the remaining woodlots in the landscape, each within 1 km of a potential source.

This spatiotemporal pattern of invasion clearly supports a stratified diffusion model. Long-distance dispersal events, rather than short-distance diffusion, characterize the initial phase of the invasion. Over the next 10 yr, many additional woodlots were colonized, filling in the uninvaded habitat in between the initial foci of invasion. Fifteen years after the initial colonization, most woodlots in the study area had at least some individuals of *L. maackii*, although most populations were still quite small.

Importance of Nascent Foci. Long-distance dispersal events were relatively rare, as evidenced by the low colonization rates, which averaged less than 1 individual per year per population (Table 1, Figure 5). Nevertheless, after about 5 to 7 yr these new populations began to grow more by internal recruitment than by continued immigration, thus potentially serving as nascent foci (Moody and Mack 1988).

This switch from immigration to within-population recruitment, combined with the spatial pattern of invasion described above, indicate that the early populations function as nascent foci, accelerating the range expansion much faster than by diffusion alone (Mack 1985; Moody and Mack 1988). The relative importance of birds vs. deer in these long-distance dispersal events is not known, but could be relevant to management strategies. American Robins might be unlikely to cross fields to disperse seeds to isolated woodlots, given their affinity for forest edges and hedgerows after feeding on *L. maackii* (Bartuszevige and Gorchov 2006). White-tailed deer, on the other hand, are projected to disperse seeds several kilometers (P. Guiden, pers comm). If deer are responsible for the long-distance dispersal events, reducing deer populations may effectively slow the spread.

This demographic analysis does not permit us to assess whether the small number of individuals founding each population come from a single source population or multiple source populations, but evidence from microsatellite markers of the same *L. maackii* shrubs implicates multiple sources (O Rocha, pers. comm.). Our analyses do suggest that within-population recruitment exceeds immigration after the first 7 yr. Thus, we predict that most individuals that are not in the oldest 7 age classes can be genetically matched as offspring of the oldest individuals.

Acknowledgments

We thank numerous landowners for permission to sample their woodlots, Peter A. Frank, Sujan Khanal, Holly Andrews, and Charlotte Freeman for field work, scanning, and counting of annual rings,Rodney Kolb and the Miami University Ecology Research Center for use of a mitre saw, and Peter Guiden and Kathleen Knight for sharing unpublished data. We thank two anonymous reviewers and the Associate Editor for valuable comments that improved this manuscript. This research was funded by United States Department of Agriculture (USDA) Cooperative State Research Education and Extension Service (CSREES) National Research Initiative (NRI) Competitive Grant 2007-35320-18349, to DLG, Mary Henry, and Oscar Rocha.

Literature Cited

Barriball K, Goodell K, Rocha OJ (2014) Outcrossing rates, mating structure and pollinator communities of the invasive shrub *Lonicera maackii*: a comparison of plants in the interior and along the edge of a woodlot. Int J Plant Sci. In press

Bartuszevige AM, Gorchov DL (2006) Avian seed dispersal of an invasive shrub. Biol Invasions 8:1013–1022

Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography 29:213–222

Castellano SM, Gorchov DL (2013) White-tailed deer (*Odocoileus virginanus*) disperse seeds of the invasive shrub, Amur honeysuckle (*Lonicera maackii*). Nat Areas J 33:78–80

Collier MH, Vankat JL, Hughes MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am Midl Nat 147:60–71

Deering RH, Vankat JL (1999) Forest colonization and developmental growth of the invasive shrub *Lonicera maackii*. Am Midl Nat 141: 43–50

Dietz H (2002) Plant invasion patches—reconstructing pattern and process by means of herb-chronology. Biol Inv 4:211–222

Goodell K, Iler AM (2007) Reproduction and habitat-mediated pollinator services in the invasive shrub *Lonicera maackii*. Pages 47–57 *in* Cavender NC, ed. Ohio Invasive Plants Research Conference Proceedings. Delaware, OH: Ohio Biological Survey

Gorchov DL, Henry MC, Frank PA (2014) Invasion of an exotic shrub into forested stands in an agricultural matrix. Inv Plant Sci Manag 7: 336–344

Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol 166:13–24

Gould AMA, Gorchov DL (2000) Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. Am Midl Nat 144:36–50

Hartman KM, McCarthy BC (2004) Restoration of a forest understory after the removal of an invasive shrub, Amur Honeysuckle (*Lonicera maackii*). Restor Ecol 12:154–165

Hartman KM, McCarthy BC (2008) Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J Torrey Bot Soc 135:245–259

Hengeveld R (1989) Dynamics of biological invasions. New York, NY: Chapman and Hall

Hutchinson TF, Vankat JL (1997) Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conserv Biol 11: 1117–1124

Johnston SE, Henry MC, Gorchov DL (2012) Using Advanced Land Imager (ALI) and Landsat Thematic Mapper (TM) for the detection of the invasive shrub *Lonicera maackii* in southwestern Ohio forests. GIScience Remote Sens 49:450–462

Luken JO, Goessling N (1995) Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. Am Midl Nat 133:124–130

Luken JO, Kuddes LM, Tholemeier TC, Haller DM (1997) Comparative responses of *Lonicera maackii* (Amur honeysuckle) and *Lindera benzoin* (Spicebush) to increased light. Am Midl Nat 138: 331–343

Luken JO, Thieret JW (1995) Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae): its ascent, decline, and fall. Sida 16:479–503

Mack RN (1985) Invading plants: their potential contribution to population biology. Pages 127–142 *in* White J, ed. Studies on Plant Demography: A Festschrift for John L. Harper. Orlando, FL: Academic Press

McEwan RW, Birchfield MK, Schoergendorfer A, Arthur MA (2009) Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. J Torrey Bot Soc 136: 212–220

Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139:359–375

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. J Appl Ecol 25:1009–1021

Rodewald AD, Shustack DP, Hitchcock LE (2010) Exotic shrubs as ephemeral ecological traps for nesting birds. Biol Invasions 12:33–39

Schmidt KA, Whelan CJ (1999) Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conserv Biol 13:1502–1506

Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. Am Nat 146:229–251

Trisel DE, Gorchov DL (1994) Regional distribution, ecological impact, and leaf phenology of the invasive shrub *Lonicera maackii*. Abstract. Bull Ecol Soc Am 75(Suppl):231

Watling JI, Hickman CR, Lee E, Wang K, Orrock JL (2011) Extracts of the invasive shrub *Lonicera maackii* increase mortality and alter behavior of amphibian larvae. Oecologia 165:153–159

Wilfong B, Gorchov DL, Henry MC (2009) Detecting an invasive shrub in deciduous forest understories using remote sensing. Weed Sci 57:512–520

Zhao W, Goebel C, Cardina J (2013) Temporal and spatial pattern of a Privet (*Ligustrum vulgare*) invasion. Inv Plant Sci Manag 6:310–319

Received December 18, 2013, and approved April 30, 2014.