

Diminished Plant Richness and Abundance Below *Lonicera maackii*, an Invasive Shrub

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ABSTRACT.—The Asian shrub *Lonicera maackii* (Amur honeysuckle) is now common in many secondary forests in southwestern Ohio and adjacent states. We found lower species richness and abundance in plots (0.5 m²) placed below crowns of *L. maackii* than in plots placed away: all species (53% lower richness and 63% lower cover), tree seedlings with canopy potential (–41% richness and –68% density) and seed + bud bank (–34% richness and –33% density). Moreover, most individual taxa had lower abundance below *L. maackii*: 86% of herbs, 100% of trees and 56% of seed + bud bank taxa. In addition, richness of all species and richness and density of tree seedlings decreased in forests with longer residence time of *L. maackii*.

INTRODUCTION

Invasion of exotic plants occurs naturally; however, in historical time there has been a rapid acceleration in the number and rate of these invasions (Mooney and Drake, 1986; Drake *et al.*, 1989; Cowie and Werner, 1993). This has been attributed to increased human dispersal of exotic species and to expansion of disturbed habitats associated with rapid growth of the human population (Elton, 1958; Coblentz, 1990; Westman, 1990).

Many factors influence the success of invading plant species. Most studies have focused on understanding the life histories and physiological traits of exotic species (*e.g.*, Mooney *et al.*, 1986; Orians, 1986; Crawley, 1987; Simberloff, 1986; Lodge, 1993). Successful invaders are often characterized by high net primary production, phenotypic plasticity, rapid growth rates, high fecundity, long-range seed dispersal and resistance to pathogens and pests (Bazzaz, 1986). Disturbance is thought to be important in opening communities to invasion (Baker, 1986; Hobbs, 1989; D'Antonio, 1993; Robertson *et al.*, 1994; Medley, 1997). Therefore, early to mid-successional communities may be more invasible than late-successional communities (Rejmánek, 1989).

Plant invasions pose serious problems for natural and managed ecosystems worldwide (Coblentz, 1990; Westman, 1990; Hobbs and Humphries, 1995). Introduction of invasive plant species may change ecosystem structure and function (Bazzaz, 1986), including alterations in species composition, succession, net primary production, biomass and nutrient cycling (Vitousek, 1986, 1990; Walker and Vitousek, 1991). Invasive species may also deplete available resources (Bazzaz, 1986). Other studies have shown changes at the landscape (Bock and Bock, 1992), community (Bossard, 1991; Hutchinson and Vankat, 1997) and population levels (Dillenberg *et al.*, 1993; Equihua and Usher, 1993).

Although most research on invasive species has concentrated on herbs, exotic shrubs

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are also common invaders (Hobbs and Mooney, 1986; Luken, 1988; Midgley *et al.*, 1992; Moll and Trinder-Smith, 1992). When these shrubs form dense thickets, native woody and herbaceous species can be negatively affected (Hutchinson and Vankat, 1997; Luken *et al.*, 1997; Trisel, 1997; Gould and Gorchoy, 2000).

Eurasian exotics account for over 80% of invading plant species worldwide (di Castri, 1989). One of these is the shrub *Lonicera maackii* (Rupr.) Maxim. (Amur honeysuckle), which, over the last few decades, has become the most abundant shrub in many forests in southwestern Ohio and adjacent states (Luken and Goessling, 1995; Hutchinson and Vankat, 1997, 1998; Luken *et al.*, 1997). In many of these forests, dense thickets of *L. maackii* have replaced relatively open understories that, according to early descriptions of these forests (*cf.*, Braun, 1916), apparently had no abundant native shrubs. Thus, *L. maackii* has been an addition rather than a replacement in these forests, an inference supported by observations over the past three decades (J. Vankat, pers. obs.).

Hutchinson and Vankat (1997) reported a negative correlation between *Lonicera maackii* cover and tree seedling richness, tree seedling density and herb cover (results that parallel Woods' (1993) finding for *L. tatarica*, an invasive shrub in some Vermont forests). In addition, Gould and Gorchoy (2000), Miller (2001) and Trisel (1997) experimentally showed that *L. maackii* negatively impacted selected species of common forest annuals, herbaceous perennials and tree seedlings, respectively. Nevertheless, the effects of *L. maackii* on herbs and tree seedlings have not been well documented. Hutchinson and Vankat (1997) did not sample individual herb species, and Trisel (1997), Gould and Gorchoy (2000) and Miller (2001) examined a total of only 10 species.

Our research focused on examining possible effects of *Lonicera maackii* on other species by examining spatial distributions within forest stands. Because native shrubs are uncommon in forests of southwestern Ohio, we chose to sample below vs. away from crowns of *L. maackii* individuals (rather than below *L. maackii* vs. native shrubs). Our primary objective was to test the hypothesis of lower species richness and abundance below crowns of *L. maackii*. In addition, we test the hypothesis that apparent effects of *L. maackii* increase with longer *L. maackii* residence time.

METHODS

Species description.—*Lonicera maackii* is an upright deciduous shrub that reaches 4–5 m height in North America (Dirr, 1990). It is most common and successful in disturbed plant communities or along forest edges where light availability is high (Luken and Matimiro, 1991; Luken *et al.*, 1995; Hutchinson and Vankat, 1997). *Lonicera maackii* is subject to little herbivory and is in leaf through more of the growing season than any native woody deciduous species (Trisel, 1997). Several sprouts form at its base (Deering and Vankat, 1999), creating dense growth that greatly reduces light (Luken, 1988). *Lonicera maackii* produces large quantities of red fruit which are dispersed by birds (Ingold and Craycraft, 1983), especially European starlings (*Sturnus vulgaris*; J. Vankat, pers. obs.).

Lonicera maackii is native to northeastern Asia and has been planted as an ornamental in North America (Pringle, 1973; Luken and Thieret, 1995). It was introduced to North America in the 1850s (Dirr, 1990). In Ohio, it was first reported in Hamilton County (Braun, 1961) and was recently found in 34 other counties (Trisel, 1997). It was first planted in the Oxford, Ohio area around 1960 (Hutchinson and Vankat, 1998).

Data collection.—We divided the 93 stands used by Hutchinson and Vankat (1997) in the Oxford, Ohio area into three groups according to approximate date of colonization by *Lonicera maackii* (*see* Deering and Vankat, 1999). Five stands were selected from the most recent third (stems of largest shrubs sampled were ≤ 10 y) and five from the oldest

third (stems were ≥ 16 y). Criteria for stand selection were relatively flat topography, total tree basal area of 25–35 m²/ha, closed tree canopy and *L. maackii* cover of $\leq 50\%$. Most stands were in upland areas.

In each stand we randomly selected 20 *Lonicera maackii* shrubs (crown diameter ≥ 1.0 m) along a 50 m line transect centrally located by Hutchinson and Vankat (1997). Below 15 of the 20 shrubs, we sampled herbs and woody plants throughout the growing season using a doughnut shaped plot delimited by circular frames. The diameter of the inner ring (*i.e.*, the doughnut hole which contained the base of the shrub and was not sampled) was 25.0 cm; the diameter of the outer ring was 83.6 cm, giving a 0.5 m² sampling area. Each of these 15 plots was paired with a circular plot of 0.5 m² area placed in the nearest area ≥ 2 m from the crown of any *L. maackii* and other woody plant > 1 m height. This placement of “away” plots ruled out potential variation caused by different tree species. In each of the 300 plots, M. Collier visually estimated the cover of herbaceous and woody species (individuals ≤ 1 m height) every second or third week from May through September 1995 using these cover classes: < 1 , 1–5, 6–10, 11–20, 21–40, 41–60, 61–80 and 81–100%. In addition, trees ≤ 1 m height were counted by species. Nomenclature follows Gleason and Cronquist (1991).

The other five *Lonicera maackii* shrubs selected in each stand were used as sites for sampling the seeds and vegetative buds in the soil, again with samples below paired with samples away from the crowns of *L. maackii* shrubs. We randomly extracted one cylindrical soil core of 15 cm depth and 10 cm diameter from each 0.5 m² plot in early April 1995, before the start of the growing season. Each of the 100 samples was sieved through a 0.6 cm mesh screen to remove rocks and debris and then spread over 2 cm of vermiculite in plastic flats and placed in an empty room of a greenhouse. The soil samples included not only seeds, but also vegetative buds and hereafter is referred to as the seed + bud bank. We placed five additional flats containing only vermiculite in the greenhouse to detect possible seed contamination. The greenhouse thermostat was set at 21 C during the day and 18 C at night, but actual temperatures fluctuated more widely. Fluorescent lights provided a minimum 8 h photoperiod per day. We watered all flats regularly and counted (and removed) young plants (seedlings from seeds and sprouts from vegetative buds) by species on alternate weeks through December 1995. Data from these samples are presented in units of individuals/m² of soil surface sampled.

Data analysis.—All analyses were done on untransformed data using SAS (Statistical Analysis System) version 6.08. Because stands differed in composition and structure and because we sampled several times throughout the growing season, we used repeated measures analyses of variance (ANOVA; SAS procedure GLM; SAS, 1995). We examined relationships among the dependent variables of total species richness and cover, species richness and density of tree seedlings with canopy potential and cover of individual species (categorical variable), and the following independent variables: SAMPLING DATE (9 dates; within subject effect), PLOT TYPE (below vs. away from *Lonicera maackii*; within subject effect), HISTORY (stands with short vs. long *L. maackii* residence times; between subject effect) and STAND (10 stands; between subject effect nested in HISTORY). Post-hoc *t*-based multiple comparisons were performed to determine which means were significantly different (SAS procedure GLM; SAS, 1995). All mean cover values were calculated using cover class midpoints. Bonferroni adjustments were made to the alpha level of 0.05 in order to control the experiment-wise error rate (Type I error).

We also grouped sampling dates and compared mean cover and richness of spring (May), early summer (June through mid-July) and late summer (late-July through September) species using Bonferroni (Dunn) *t* tests. This analysis was restricted to the 103

herb taxa exhibiting SAMPLING DATE \times PLOT TYPE interactions in order to avoid taxa present throughout the growing season. Species were grouped into seasonal categories based on dates that species' cover values were recorded in the field.

For the seed + bud bank, we determined relationships between the dependent variables of species richness and density and the independent variables of PLOT TYPE, HISTORY and STAND. As above, STAND was analyzed only as a between subject effect nested in HISTORY.

RESULTS

All species combined.—Mean species richness for all species was 53% lower in plots below crowns of *Lonicera maackii* (4.5 ± 0.1 taxa vs. 9.6 ± 0.3 taxa away from crowns) across all sampling dates combined ($F\{8, 1324\} = 3.06$, $Pr > F = 0.0020$) and was significantly lower on each of the nine sampling dates (Fig. 1a). Mean richness below and away was highest in the spring (6.5 taxa below vs. 10.3 taxa away) and declined steadily to early fall (3.4 ± 0.1 taxa below vs. 6.9 ± 0.1 taxa away). Nine taxa (5%) were sampled only below and 48 taxa (29%) were sampled only away from *L. maackii*.

Mean cover for all species was 63% lower below *Lonicera maackii* (4.6% vs. 12.4% away) across all sampling dates combined ($F\{8, 1035\} = 3.96$, $Pr > F = 0.0008$) and was lower for each of the nine sampling dates (Fig. 1b). Cover increased from spring (2% below vs. 5% away) to peak in midsummer (7% below vs. 22% away), when the difference was largest.

Considering only herb species, 75 of the 140 taxa sampled (54%) exhibited significant PLOT TYPE differences in cover and had lower cover below *Lonicera maackii* (this and other lists of taxa are in Collier, 1997). These taxa combine with others that showed a significant interaction effect involving PLOT TYPE (*e.g.*, HISTORY \times PLOT TYPE and SAMPLING DATE \times PLOT TYPE) to give a total of 120 taxa (86%) with significantly lower cover below *L. maackii*, compared to 14 (10%) with significantly higher cover and 6 (4%) with no significant differences in cover. Also, far fewer herb taxa were sampled only below than only away from *L. maackii* (9 below, 38 away). Comparisons were also made to determine if *L. maackii* presence had more impact on common or uncommon herbs (defined as sampled in ≥ 5 stands and ≤ 2 stands, respectively). Lower cover below *L. maackii* was found for 19 of 21 (90%) common and 75 of 90 (83%) uncommon taxa (1 common and 13 uncommon taxa had higher cover below *L. maackii*).

Comparisons were also made to determine if *Lonicera maackii* affects growth of early and late summer species more than spring species. When herb taxa were divided into three growth periods, mean richness was significantly lower below *L. maackii* in spring ($F\{2, 879\} = 19.21$, $Pr > F = 0.0001$), early summer ($F\{2, 568\} = 23.14$, $Pr > F = 0.0001$) and late summer ($F\{2, 239\} = 26.79$, $Pr > F = 0.0001$), with the differences being somewhat less in spring (Fig. 1c). Moreover, mean species richness below *L. maackii* declined from spring to early summer to late summer, whereas richness away did not decline until late summer. Mean herb cover was also significantly less below *L. maackii* in spring ($F\{2, 879\} = 5.70$, $Pr > F = 0.0041$), early summer ($F\{2, 568\} = 12.31$, $Pr > F = 0.0001$) and late summer ($F\{2, 239\} = 15.09$, $Pr > F = 0.0001$), with differences less in spring (Fig. 1d). There were no significant differences among growth periods below *L. maackii* (all 0.1% cover), but cover away from *L. maackii* was significantly lower in spring (1.3%) than in early summer (3.0%) and late summer (3.1%).

For tree seedlings (≤ 1 m height), 17 of the 22 taxa sampled (77%) showed significant PLOT TYPE differences in cover and had lower cover below *Lonicera maackii*. When these taxa are combined with others that showed a significant interaction effect involving PLOT

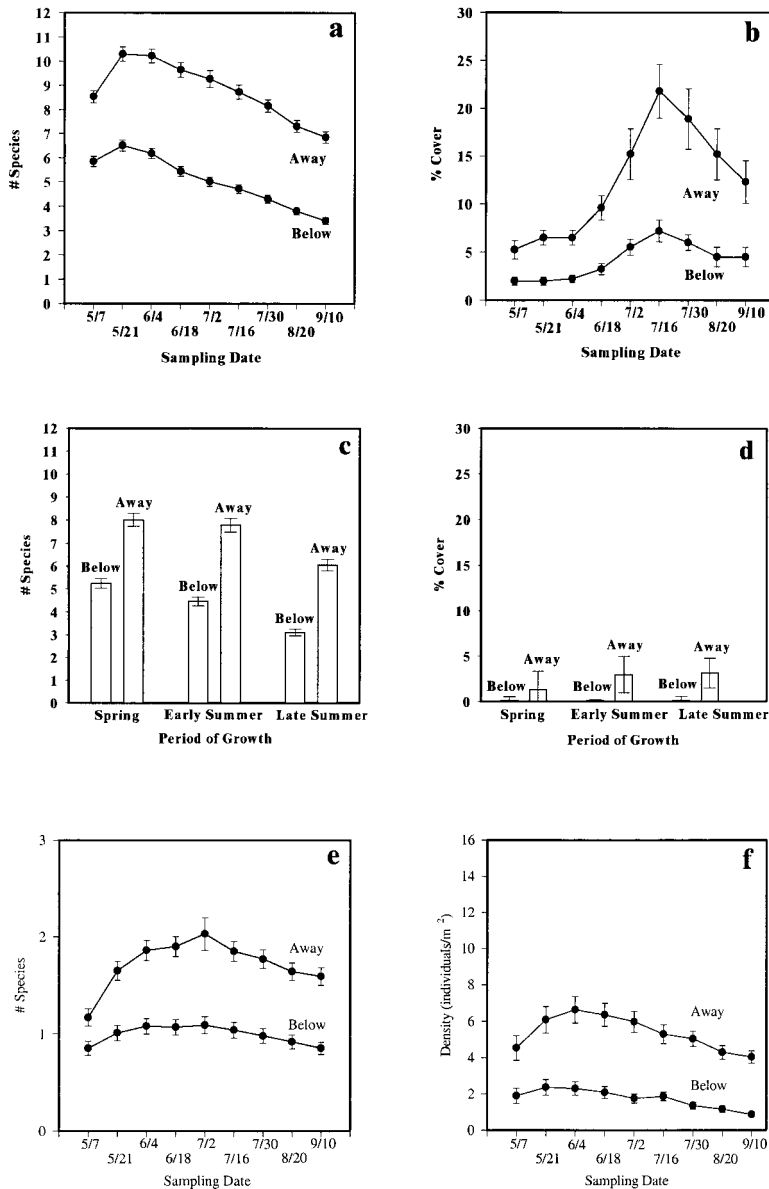


FIG. 1.—Mean species richness and cover of plants below and away from crowns of *Lonicera maackii* for (a and b) nine sampling dates during the 1995 growing season and for (c and d) spring (May), early summer (June through mid-July) and late summer (late-July through September) taxa (based on a subset of 103 herb taxa). Also shown are mean species richness (e) and density (f) of the tree seedling taxa with canopy potential below and away from crowns of *L. maackii* for nine sampling dates during the 1995 growing season. Bars represent standard errors

TYPE, all 22 tree taxa (including 8 common and 8 uncommon taxa) differed in cover and had lower values below *L. maackii*. In addition, no taxa were sampled only below, but 10 (45%) were sampled only away from *L. maackii*.

Stands with longer *Lonicera maackii* residence times had lower mean species richness for below and away plots combined ($F\{1, 140\} = 152.95$, $Pr > F = 0.0001$, 7.3 ± 0.1 taxa vs. 6.3 ± 0.1 taxa) as well as for plots below ($F\{1, 140\} = 11.98$, $Pr > F = 0.0007$, 5.3 ± 0.1 taxa vs. 4.6 ± 0.1 taxa) and away ($F\{1, 140\} = 23.61$, $Pr > F = 0.0001$, 9.2 ± 0.1 taxa vs. 7.9 ± 0.1 taxa) from *Lonicera maackii*. In contrast, there were no significant differences in mean cover for different residence times for below and away plots combined ($F\{1, 8\} = 0.68$, $Pr > F = 0.4333$, $8.6 \pm 1.7\%$ vs. $8.0 \pm 1.5\%$) or for plots below ($F\{1, 4\} = 0.55$, $Pr > F = 0.2475$, $4.0 \pm 0.9\%$ vs. $4.3 \pm 0.8\%$) or away ($F\{1, 4\} = 0.07$, $Pr > F = 0.3170$, $13.1 \pm 2.6\%$ vs. $11.6 \pm 2.1\%$) from *L. maackii*. Also, 61 of the 168 taxa (36%) showed significant HISTORY differences in cover and had lower cover in stands with longer *L. maackii* residence. These taxa plus others that showed significant PLOT TYPE \times HISTORY interaction effects give a total of 118 taxa (70%) with lower cover with longer presence of *L. maackii*, compared to 10 (6%) with greater cover and 40 (24%) with no differences in cover.

Tree seedlings of taxa with canopy potential.—Mean tree seedling richness (for taxa with the potential to reach canopy height) was 41% lower in plots below *Lonicera maackii* (1.0 ± 0.1 taxa vs. 1.7 ± 0.1 taxa away) across all sampling dates combined ($F\{1, 140\} = 48.45$, $Pr > F = 0.0001$) and was also significantly lower for each individual sampling date (Fig. 1e). Mean tree seedling richness below *L. maackii* remained around 1.0 taxa throughout the growing season, but away from *L. maackii* it increased from 1.2 taxa in the spring to 2.0 taxa in midsummer.

Mean tree seedling density was 68% lower below *Lonicera maackii* crowns (1.7 ± 0.1 individuals/m² vs. 5.3 ± 0.1 individuals/m² away) across all nine sampling dates combined ($F\{1, 1285\} = 692.23$, $Pr > F = 0.0001$) and was lower for each sampling date (Fig. 1f). Density below *L. maackii* declined from 2.4 individuals/m² in early spring to 0.9 in late summer; away from *L. maackii*, it increased from 4.5 in early spring to peak at 6.6 in late spring and declined to 4.0 in late summer.

Of the 16 tree seedlings of taxa with canopy potential, 13 (81%) showed significant PLOT TYPE differences in density and had lower density below *Lonicera maackii*. When combined with other taxa that showed a significant interaction effect involving PLOT TYPE, all 16 taxa (13 common and 3 uncommon taxa) showed lower density below *L. maackii*. In addition, no taxa were sampled only below, but 7 (44%) were sampled only away from *L. maackii*.

Stands with longer *Lonicera maackii* residence time had lower mean tree richness for below and away plots combined ($F\{1, 140\} = 61.71$, $Pr > F = 0.0001$, 1.8 ± 0.1 taxa vs. 1.0 ± 0.1 taxa) as well as below ($F\{1, 140\} = 42.74$, $Pr > F = 0.0001$, 1.4 ± 0.1 taxa vs. 0.6 ± 0.1 taxa) and away ($F\{1, 140\} = 21.47$, $Pr > F = 0.0001$, 2.1 ± 0.1 taxa vs. 1.4 ± 0.1 taxa) from *L. maackii*. Mean tree seedling density showed parallel results for below and away plots combined ($F\{1, 1285\} = 244.53$, $Pr > F = 0.0001$, 4.9 ± 0.2 individuals/m² vs. 2.2 ± 0.1 individuals/m²) as well as in plots below ($F\{1, 1285\} = 135.03$, $Pr > F = 0.0001$, 1.4 ± 0.1 individuals/m² vs. 0.8 ± 0.1 individuals/m²) and away ($F\{1, 1285\} = 173.63$, $Pr > F = 0.0001$, 3.6 ± 0.3 individuals/m² vs. 2.1 ± 0.1 individuals/m²) from *L. maackii*. In addition, 9 of the 16 taxa (56%) had significant HISTORY differences in density and had lower density with longer *L. maackii* residence. These taxa combine with others that showed a significant PLOT TYPE \times HISTORY interaction effect to give a total

of 11 taxa (69%) with lower density with longer *L. maackii* residence; no taxa exhibited the opposite trend, but 5 taxa revealed no difference in density.

Seed + bud bank.—Mean seed + bud bank richness was 34% lower ($F\{1, 40\} = 23.59$, $Pr > F = 0.0001$) in samples below *Lonicera maackii* (5.7 ± 0.1 taxa vs. 8.6 ± 0.2 taxa away). In addition, mean density was 33% lower ($F\{1, 40\} = 17.34$, $Pr > F = 0.0001$) in plots below (5.0 ± 0.1 individuals/m² vs. 7.5 ± 0.3 individuals/m² away).

Of 98 taxa sampled, 45 (46%) showed significant PLOT TYPE differences in density and had lower density below *Lonicera maackii*. Combined with others that showed a significant interaction effect involving PLOT TYPE, a total of 55 taxa (56%) had lower density below *L. maackii*, compared to 7 taxa (7%) with higher density and 36 taxa (37%) with no differences in density. Also, 18 taxa (18%) were found only in samples under *L. maackii* and 31 (32%) were found only in samples away from *L. maackii*. In addition, lower density below *L. maackii* was found for 10 of 14 (71%) common and 67 of 70 (96%) uncommon taxa (4 common and 3 uncommon taxa showed higher density under *L. maackii*).

Stands with short and long *Lonicera maackii* residence time had no significant differences in mean richness for below and away plots combined ($F\{1, 40\} = 0.16$, $Pr > F = 0.6919$, 7.5 ± 0.6 taxa vs. 6.8 ± 0.5 taxa) or in plots below ($F\{1, 40\} = 0.20$, $Pr > F = 0.4144$, 5.9 ± 0.5 taxa vs. 5.4 ± 0.5 taxa) or away ($F\{1, 40\} = 1.98$, $Pr > F = 0.1670$, 9.0 ± 0.8 taxa vs. 8.1 ± 0.4 taxa) from *L. maackii*. Similarly, there were no significant differences in mean density for below and away plots combined ($F\{1, 40\} = 0.08$, $Pr > F = 0.7831$, 6.7 ± 0.3 individuals/m² vs. 5.9 ± 0.1 individuals/m²) or in plots below ($F\{1, 40\} = 0.15$, $Pr > F = 0.7058$, 5.2 ± 0.1 individuals/m² vs. 4.8 ± 0.1 individuals/m²) or away ($F\{1, 40\} = 3.82$, $Pr > F = 0.0578$, 8.1 ± 0.3 individuals/m² vs. 6.9 ± 0.1 individuals/m²) from *L. maackii*. However, the trend in each of these data sets is for decreases with longer *L. maackii* residence. Moreover, all three soil cores that produced no plants were collected below shrubs with longer *L. maackii* residence. Also, 32 of the 98 taxa sampled (33%) showed significant HISTORY differences and had lower density with longer *L. maackii* residence. Combined with other taxa that showed a significant interaction effect involving HISTORY, a total of 42 (43%) had lower density with longer presence of *L. maackii*, compared to 7 (7%) with greater density and 49 (50%) with no differences in density.

DISCUSSION

Our results support the hypothesis of lower species richness and abundance below crowns of *Lonicera maackii* individuals. Although this finding could be explained by *L. maackii* establishing primarily in microsites of low richness and abundance, we suggest that this invasive shrub has actually diminished plant richness and abundance in secondary forests of southwestern Ohio. This interpretation is supported by experimental research (see Trisel, 1997; Gould and Gorcho, 2000).

Herbs have been reported as diminished by shrub invaders of grasslands in California (Hobbs and Mooney, 1986) as well as forests of Vermont (Woods, 1993) and southwestern Ohio (Hutchinson and Vankat, 1997; Gould and Gorcho, 2000). Tree seedlings were also reduced by exotic shrubs in tropical Australia (Braithwaite *et al.*, 1989) and forests of Vermont (Woods, 1993) and southwestern Ohio (Hutchinson and Vankat, 1997; Trisel, 1997). No previous studies examined the effects of invasive shrubs on seed + bud banks.

A seemingly important question for interpreting our results is whether native shrub species have similar effects as *Lonicera maackii*. For example, Hobbs and Mooney (1986) in California, Niering *et al.* (1986) in Connecticut and Huenneke (1983) in New York

have reported impacts of native shrubs on other species. However, native shrubs generally have been uncommon in southwestern Ohio forests. Braun (1916, 1950) provided the first thorough descriptions of these forests and mentioned shrubs only in association with forest ponds. Moreover, native shrubs in Ohio are uncommon today in most secondary forests not yet invaded by *L. maackii* (J. Vankat, pers. obs.). Therefore, the negative effects we report for *L. maackii* are a recent phenomenon in forests of southwestern Ohio, regardless of whether native shrub species have similar impacts.

Past studies have indicated several possible mechanisms for the negative effects of *Lonicera maackii*. Trisel (1997) reported reduced seedling survival for four tree species as a result of competition for light from *L. maackii*. He also documented that *L. maackii* is the first deciduous woody species to expand its leaves in spring in southwestern Ohio and the last to lose leaves in fall. Therefore, not only does *L. maackii* reduce light levels (Luken, 1988), but it does so throughout the growing season (*see also* Barnes, 1972; Harrington *et al.*, 1989; Woods, 1993). In addition, the extensive shallow root system of *L. maackii* may reduce availability of nutrients and water in the upper soil. Trisel (1997) implicated root competition in reduced survival in seedlings of two of four tree species and also reported evidence of alleopathy, as *L. maackii* leaf extract negatively affected seed germination and seedling growth in some species.

Although most taxa were negatively affected by *Lonicera maackii*, some were positively affected and a few were unaffected. Presumably, this variation is due at least in part to differences in species' life histories. Of the nine species unaffected by the presence of *L. maackii*, one is a sprawling species (*Amphicarpa bracteata*) and three are vines (*Lonicera japonica*, *Parthenocissus quinquefolia* and *Toxicodendron radicans*), one of which (*T. radicans*) can grow into the crowns of *L. maackii* where it presumably has access to more light. Niering *et al.* (1986) reported a similar observation for *L. japonica* which wrapped around root suckers of *Viburnum lentago* shrubs in Connecticut. Vines also may have less root competition with *L. maackii* by being rooted away from the shrubs. Woods (1993) also found that some vines or sprawling species (*Rubus* sp., *P. quinquefolia* and *A. bracteata*) were not suppressed by *Lonicera tatarica* in Vermont forests. Nevertheless, not all vines are unaffected by *L. maackii*, as both *Convolvulus* sp. and *Vitis aestivalis* had lower cover under *L. maackii* in our study.

Woods (1993) also reported that evergreen species were unaffected by *Lonicera tatarica*. This growth form is uncommon in southwestern Ohio forests, although *L. japonica*, one of the vines unaffected by *L. maackii*, is evergreen. Evergreen species may have the advantage of photosynthesizing when *L. maackii* shrubs are leafless.

Although previous studies have not examined the effects of exotic shrubs on seed + bud banks, the presence of such effects is not surprising. Not only do our results for the species aboveground portend this, but Gould and Gorchov (2000) found reduced fecundity below *Lonicera maackii* for all three native forest annuals that they studied.

Our second hypothesis addressed the question of whether the apparent effects of *Lonicera maackii* increase with longer *L. maackii* residence time. Here, our results were more mixed. Richness of all species combined and richness and density of tree seedlings were lower with longer residence, as hypothesized. In contrast, cover of all species combined and richness and density of the seed + bud bank were not significantly different, although most trends in these data sets support the hypothesis, as did 118 of the total 168 taxa (70%) investigated and 42 of 98 taxa (43%) in the seed + bud bank. Moreover, it is possible that some effects of *L. maackii* occur primarily in the early years after colonization and, therefore, may not have been observed in our study.

Because *Lonicera maackii* dramatically increases in both density and cover following

colonization (Hutchinson and Vankat, 1997; Deering and Vankat, 1999), the effects we observed at the scale of single shrubs (0.5 m²) should become increasingly apparent at the scale of forest stands. In fact, several findings of this study indicate that effects of *L. maackii* will become more severe in the future. For example, the finding that many effects of *L. maackii* increase through time, both below and away from shrub crowns, and the fact that *L. maackii* is a relatively recent invader, indicate that herbs and tree seedlings may become even more depleted in the future. Also, the finding that *L. maackii* appears detrimental to 98% of the uncommon taxa indicates that increased *L. maackii* density, cover and residence time has the potential to cause local extinctions of plant populations. Moreover, the finding of impacts on seed + bud banks suggests that, even if *L. maackii* is extirpated, many herb layer populations will require years to recover. This reinforces the importance of proactive rather than reactive strategies for controlling *L. maackii* (as espoused by Deering and Vankat, 1999; *see also* Hobbs and Humphries, 1995). In addition, the effects of *L. maackii* on seedlings of canopy tree species indicates that patterns of forest succession may be altered (*see also* Hutchinson and Vankat, 1997; Fike and Niering, 1999). For example, early successional tree species may persist in the canopy if regeneration of mid and late successional species is inhibited. Moreover, as older canopy individuals die, closed-canopy forests may change to open-canopy woodlands or even to *L. maackii* dominated shrublands. Such changes in composition and structure will not only greatly alter ecological processes but also substantially decrease the economic value of forested land.

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