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Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*)

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HARTMAN, K. M. (Department of Biology, St. Andrews Presbyterian College, Laurinburg, NC 28352) AND B. C. McCARTHY (Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701). 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. 2008.—Heavy infestations of a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*) are frequently linked to poor individual performance and reduced species diversity. We used chronosequence methods and analysis of forest strata to investigate potential impacts of *L. maackii* on 1) species richness, 2) density of sub-canopy recruitment layers, 3) indicator species affinity, and 4) within- and among-strata compositional similarities. We compared sites ranging from 12 to 26 years since initial invasion as well as non-invaded, control sites. When assessing non-invaded versus long-invaded sites, we found significantly ($P \leq 0.05$) reduced densities in the herb (−57%), seedling (−58%), and sapling layers (−90%), and also reduced species richness in the seedling (−34%), and sapling (−58%), and herbaceous layers (−4%). Interestingly, the germinable seed bank density showed significant increases among non-invaded and long-invaded sites (+78%), while the species richness of the seed bank demonstrated a marked decrease (−41%). Indicator species analysis found that most species had greater frequencies and abundances in non-invaded sites, and nearly all species had greater affinities for the non-invaded sites, especially in the seedling, sapling, and seed bank layers. Responses were species-specific in the herbaceous layer. Within-layer species similarity decreased with increased time of *L. maackii* occupancy in all sub-canopy strata. This pattern was also found with reductions in between-layer compositional similarity for the long-invaded ($r = 0.16$) versus the recently-invaded ($r = 0.37$) and non-invaded ($r = 0.51$) sites. Our data suggest that in many invaded sites, habitats are experiencing wholesale alterations in species composition, structure, and successional trajectory, and invasion may also change competitive interactions in forest understories as well as alter between-layer species linkages. These results validate the candidacy of *L. maackii* sites for increased removal and restoration efforts.

Key words: biological invasion, composition, diversity, management, restoration, species richness, southwestern Ohio, succession, understory, vegetation.

Impacts of invasive species are becoming a matter of great scientific and public concern. Invasive species are not only threatening endeavors related to human sustainability such as agriculture, commerce, and human health (Sumner 2003), and they are also profoundly detrimental to natural areas, which have innate ecological value and provide free ecosystem services such as regulation of climate, regeneration of soil fertility, and decomposition of wastes (van Wilgen et al. 2004). Ecologically, invasive species are exceptionally damaging, and biological invasions have been ranked as comparable in impact to other global environmental problems (Campbell 1997).

With expansions of current invasions expected to continue, studies assessing invasive species impacts are becoming increasingly important (Parker et al. 1999). The first step towards invasive species assessment and management is to demonstrate that a species has a negative effect (Walters and McCarthy 1997); however, most ecological studies use only short-term approaches, which may not as accurately represent the levels or types of ecological changes detectable with longer-term studies (Taylor 1989). Furthermore, short-term investigations can be particularly problematic in studying long-lived trees and successional processes because both may respond slowly to certain types of changes (Davis 1989).

Generally, most long-term ecological impact studies are not designed with invasive species in mind, and specifically there is insufficient overlap of the disciplines of invasive species

ecology and succession. Davis and Guy (2001) state the lack of intersect in these research areas may be due to frequency of studying "conspicuous invaders" and the belief that invasion is a unique phenomenon requiring "special explanation," which may not be applicable to traditional successional studies. The addition of a dominant species to a natural system can profoundly affect a number of emergent properties within communities, especially biological interactions (Thompson et al. 1995); therefore, there is a possibility for highly effective invaders to strongly influence the successional dynamics of communities. Invasives can impact the both the short and long-term interactions of species as well as cause displacement of individuals; therefore they can trigger a complex set of new interactions with the invaders themselves, among existing species, and with other co-invaders (Gilliam 2007). Thus, a logical step towards understanding the long-term successional impacts of invasive species is to employ traditional ecological investigative methodologies.

The optimal approach to understanding the complex, long-term impacts of invasion on succession would be to implement well-replicated, controlled studies at sites well before and well after invasion. These types of studies are conducted infrequently, and one way to augment the difficulty in executing these types of studies is to use chronosequence methods as a substitution of space for time. Chronosequence studies extract temporal trends from a series of different aged samples (Rankin and Pickett 1989) and have been extensively used to examine the spatio-temporal dynamics of communities, particularly the processes and patterns of succession (Rankin and Pickett 1989). Thus, more extensive use of chronosequence studies in invasive ecology could lend valuable insights into long-term invasive species' impacts.

Forests are potentially useful in studying more complex, long-term invasion questions given that they are temporally and spatially dynamic, vertically stratified biotic systems. Individuals that successfully establish in lower forest strata are the recruitment capital for what may eventually become dominant canopy trees (Kozlowski 2002). Most invasive species studies are conducted from a 2-dimensional approach by studying impacts on individuals within the same stratum as the

invader, but in forests, lower layers have been known to act as ecological filters and influence the composition and abundance of recruiting strata (Cox 1999). Winnowing events do naturally occur during the development of any "ascending" forest layer (Young et al. 2001), but in heavily invaded communities, changes to any recruitment layer in a forest could instigate successional divergence. Thus comparison of sites with different invasion times could lend insight into the long-term successional impacts on pattern and process associated with particular invasions. Two requirements of investigating long-term invasive impacts are that 1) the age of the invader must be detectable, and 2) for invaded sites, the impacts of invasives must have storage effects (such as in forests with long-lived woody species), which can be measured as long-term changes in abundance, recruitment structure, or composition through time. For this experiment we sought to evaluate the possibility of using chronosequence techniques to understand the long-term storage effects of invasive species as impacts on community succession.

As a case study, we wanted to investigate Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder), a non-indigenous, aggressive shrub that is able to virtually dominate the midstory layer of forest interiors as well as successfully invade open habitats and forest edges (Luken 1988). In forests, *L. maackii* is reported to have nearly 100% midstory coverage (Luken et al. 1997) and have a net primary productivity that is equal to that of entire forests (Luken 1988). This shrub was intentionally introduced into the United States in 1898 for horticultural and conservation purposes by the U.S. Department of Agriculture (Luken and Thieret 1996), but avian dispersal (Ingold and Craycraft 1983) and *L. maackii*'s rapid individual and population growth rates have allowed it to escape to at least 26 eastern states in the U.S. (Hutchinson and Vankat 1997). In southwest Ohio where we conducted our study, *L. maackii* was introduced around 1960 (Hutchinson and Vankat 1998). Despite the fact that shrubs are reported to be historically rare in this area (Braun 1916), *L. maackii* invades intact forests quite successfully and dominates the midstory stratum of forest communities.

The long-term impacts of *Lonicera maackii* invasion on forest succession could potentially

be profound, and we wanted to utilize chronosequence techniques to test for possible consequences on the composition, abundance, structure, and recruitment processes of forest vegetation. Specifically our goals were to 1) test effects of *L. maackii* invasion using a number of univariate and multivariate techniques by comparing the abundance, diversity, and species composition at sites with different invasion chronosequence levels (non-invaded, recently-invaded, and long-invaded), 2) compare differences in patterns of species composition in relation to invasion status, 3) identify indicator species which demonstrate affinity for sites with different invasion levels, and 4) quantify patterns of between-strata compositional similarity and possible recruitment variation at sites with different levels of invasion.

Materials and Methods. The chronosequence method was used to study the long-term effects of *Lonicera maackii* on forest structure, composition, and regeneration (see Rankin and Pickett 1989). Twelve sites with various times of initial *L. maackii* establishment were sampled, as well as four non-invaded (control) sites, to investigate possible community-level changes associated with invasion. Sites were randomly selected from potential locations in secondary forest stands and were free from apparent, large-scale, post-tree-harvest disturbances such as broad windthrow, burning, or ice damage. Sites were also fairly homogenous in terms of tree composition and stand age. All non-invaded sites were within 100 m of *L. maackii* patches and were therefore likely unaffected, yet potentially invasible, by *L. maackii*. Size of forest stands were estimated from satellite images (TerraServer 2004).

All sites were located in Montgomery and Hamilton Counties in southwestern Ohio, U.S.A. The region is typified by a mosaic of agricultural land, semi-isolated forest patches and connecting corridors, rivers and streams, and urban and suburban developed areas (Davis et al. 1976). Total forested land in this region is roughly 13% (Griffith et al. 1991). Climate is continental with warm, humid summers and cold, cloudy winters. Temperatures range from a mean low in December of 0°C to a mean high in July of 25°C. Precipitation is roughly 100 cm yr^{-1} with half typically falling during the growing season

(Davis et al. 1976). Edaphic conditions naturally varied among locations, but potential sites were held to those with topographies that were flat to gently rolling and soil texture that ranged from loam to clay loam (Davis et al. 1976, Lerch et al. 1980). Soil substrate was largely glacial till with an underlying limestone substrate (Forsyth 1970).

VEGETATION SAMPLING. Composition and structure of forest strata were measured using the Point-Centered Quarter (PCQ) sampling method (Cottam and Curtis 1953). Sampled vegetation included overstory trees, saplings, shrubs, vines, tree seedlings, herbs, and seed bank as well as the *Lonicera maackii* shrub layer. At each site, fourteen PCQ points were positioned every 10 m along two parallel 60 m transects. Transects were situated 50 m apart and were located at least 50 m from forest boundaries to avoid edge effects. The nearest overstory tree to each PCQ point with diameter at breast height (DBH) ≥ 10 cm was cored using an increment borer, and trees were aged by counting annual rings and cross-dating (Phipps 1982). Tree species identities were noted, and DBHs and distances to PCQ points were used to compute overstory tree basal area, density, and composition (Krebs 1999).

The time of initial *Lonicera maackii* invasion was used as our chronosequence index, and determination of exact invasion time was possible because *L. maackii* is a semi-ring-porous woody shrub that produces visually detectable annual growth rings (Chiu 1992). The nearest *L. maackii* shrub was cut in each PCQ quadrant at 5 cm height, and annual rings were counted (n = 48 shrubs/site). Distances from *L. maackii* shrubs to PCQ points were measured and converted to densities (Krebs 1999). To assess woody plant composition and structure, densities of tree seedlings (defined as height ≤ 30 cm) and tree saplings and non-*L. maackii* shrubs (defined as height > 30 cm and DBH < 2.5 cm) were quantified in 5 m^2 circular plots in each PCQ point quadrant. Herbaceous vegetation (including vine seedlings) was estimated via visual percent cover, and *L. maackii* seedlings were assessed using count data (Daubenmire 1959). Canopy height and spread, number of stems, largest stem radius, and total stem basal area were measured on randomly selected interior shrubs of various sizes (n = 32), and

using allometric methods, biomass of *L. maackii* was best predicted by total stem basal area ($R^2 = 0.67$; $P = 0.001$).

To measure the germinable seed bank composition (Brown 1992), soil plugs were collected at each PCQ point ($n = 224$ total) with an 8 cm diameter bulb planter to a depth of 10 cm. Soil plugs were spread in flats on a vermiculite medium ($25 \times 25 \times 3$ cm). Ten seed-free flats containing vermiculite were intermixed among the array to monitor potential seed contamination, and all flats were randomized every two weeks. Germinated plants were removed upon positive identification, and trays were kept in a greenhouse from 16 May 2000 to 16 Nov 2000. At the end of this period, all germinated, unidentifiable plants were transferred to larger containers and grown for an additional six-month period until identifiable to species (or genus if species was not identifiable). Sampling of *Lonicera maackii* seedlings, herbaceous vegetation, vines, and harvesting of soil plugs was conducted from 1 May 2000 to 15 May 2000. Measurement and coring of trees occurred from 1 Sept 2000 to 1 Oct 2000, and tree seedlings, native shrubs, saplings, and *L. maackii* adults were sampled from 1 June 2000 to 31 July 2000. Fourteen tree cores, soil cores, and PCQ points were sampled at each of 16 sites ($n = 224$ total PCQ points). Gleason and Cronquist (1991) was used as the taxonomic authority for all vegetation identification. Cooperrider et al. (2001) was used to assess indigenous or non-indigenous status of species.

STATISTICAL ANALYSIS. Ordinary least squares linear regressions were used to compare differences within each stratum of forest structure among *Lonicera maackii* invasion levels. Invaded versus non-invaded sites were compared via *t*-tests in terms of canopy age, density, and basal area. Strata densities were the dependent variables and initial time of *L. maackii* invasion at each site was the predictor variable. Species richness (S) within each stratum was compared by analysis of variance among the following three *L. maackii* invasion levels: 1) non-invaded with no *L. maackii* present, 2) recently-invaded including sites with an initial time of invasion 12–17 years before sampling, and 3) long-invaded sites with an initial invasion time of 18–26 years before sampling. Percent native species for

each stratum was compared similarly via ANOVA. Assumptions of normality and equal variance were satisfied prior to *t*-tests and ANOVAs, and log normal transformations were used where appropriate (Bouzille et al. 2001). Untransformed means $\pm$ 1 SE are reported.

To compare species composition among chronosequence levels within each stratum, we performed beta-flexible hierarchical agglomerative clustering using the Bray-Curtis similarity coefficient (S_{17}, Legendre and Legendre 1998). The Bray-Curtis coefficient was used because it is less affected by outliers than other indices, preserves sensitivity in heterogeneous datasets, and is independent from joint absences. The beta-flexible clustering method was applied because it is able to control space contraction and allows elements to be better grouped than other clustering methods (McCune and Grace 2002). Percent cover (%; herbs and vines), density (numbers per m^2; seedlings, saplings, and seed bank), and basal area (m^2 per ha; overstory trees) were used to construct similarity hemi-matrices. A natural weighting procedure was performed prior to calculating similarity matrices by dividing raw measurements by sample unit totals, and this standardizes for both differences in site productivity and scale of measurement (Mielke 1984).

Multivariate response permutation procedures (MRPP, Berry et al. 1983) were performed following cluster analysis as a nonparametric way to test for overall differences in species composition between 1) invasion chronosequence levels and 2) non-invaded versus invaded groups. MRPP tests were performed using data from each forest stratum, and Bonferroni adjustments were made to account for multiple statistical comparisons (Bouzille et al. 2001).

To test understory species composition within invasion chronosequence levels (i.e., group affinity), an indicator species analysis was performed (Dufrene and Legendre 1997). This procedure uses each species' frequency and abundance within a group (invasion chronosequence level) to calculate importance values (IVs). IVs range from 0 (no group affinity) to 100 (perfect indication, Dufrene and Legendre 1997). Species with large IVs have both large frequency and abundance values and are classified as having a statistically significant affinity for a group. Rare

species have small IVs and are not statistically significant (McCune and Grace 2002).

To test compositional similarity between forest successional layers and among invasion chronosequence levels, cross-strata congruence analyses were performed (Su et al. 2004). We used standardized PCQ point abundance values to calculate Bray-Curtis similarities between pairs of vegetation strata at all PCQ points. We summarized Bray-Curtis similarities between all biologically possible pair-wise combinations of recruitment strata for each invasion level as a matrix for each, and Mantel tests were used to compare matrices to examine between-strata similarities. Similarities were expressed as correlation values (Legendre and Legendre 1998), and Monte Carlo procedures with 999 permutations were employed for significance testing (McCune and Medford 1999).

PC-ORD (version 4.01) was used to perform cluster analysis, MRPP, indicator species analysis, Mantel tests, and calculate Bray-Curtis similarities (McCune and Mefford 1999). NCSS was used for regression and ANOVA calculations (Hintze 2000). All tests were considered significant if $P < 0.05$.

Results. Forest Stand Characteristics. Sampled canopy trees were generally even-aged, and trees had a median age of 55.2 ± 5.2 SE yrs. Sites ranged in canopy age, density, and basal area, but pooled invaded sites were not significantly different than non-invaded sites with respect to these variables ($P \geq 0.14$). Forest patches were 112.9 ± 20.3 ha in size. Overstory tree density was 370.0 ± 30.1 stems ha^{-1}, and basal area was 27.2 ± 2.3 m^2 ha^{-1}. Canopies were composed mainly of *Fraxinus americana* (34.4%) but consisted of a mixture of moderately common species (5–10% each species): *Acer saccharum*, *A. negundo*, *Juglans nigra*, *Liriodendron tulipifera*, *Quercus alba*, *Celtis occidentalis*, and several more rare species (< 5% each species, e.g., *Carya cordiformis*, *Carya ovata*, *Q. rubra*, *Q. prinus*, *Q. muehlenbergii*, *Fraxinus quadrangulata*, *Acer saccharinum*). Cluster and MRPP analyses revealed that canopy composition was not significantly different among invasion chronosequence levels or between non-invaded versus invaded groups ($P \geq 0.61$, Fig. 1). Canopies contained the least number of species of any layer (31) with increasing richness represented in the sapling (33),

seedling (39), germinable seed bank (52), and herb (68) layers. For greater detail on site parameters, consult Hartman and McCarthy (2007).

Lonicera maackii Characteristics. Sites were initially invaded by *Lonicera maackii* 12 to 26 yrs before sampling in 2000. Mean *L. maackii* density was 2951 ± 453 plants ha^{-1} (range 1887 to 6208). Mean *L. maackii* basal area was 3.0 ± 0.7 m^2 ha^{-1}, and mean *L. maackii* biomass was estimated at 2098.7 ± 536.4 kg ha^{-1}. Basal area of *L. maackii* was found to be the best predictor of individual shrub biomass (*L. maackii* biomass per individual (kg) = basal area (in cm^2 units) $\times$ $0.907 + 0.147$, $R^2 = 0.91$). These data compared quite similarly to measurements collected by Luken (1988) in terms of range and prediction equations for aboveground biomass for *L. maackii*.

Changes of Within-layer Structure and Species Richness. Comparing along the invasion chronosequence, regression analyses and ANOVAs provided strong evidence of reductions in within sub-canopy layer densities (i.e., structural differences, $P \leq 0.01$). For long-invaded versus non-invaded sites, the herbaceous layer demonstrated a 57% reduction in cover, and seedlings exhibited a 58% stem density reduction (i.e., 14300 ± 2595 fewer stems ha^{-1}). Saplings demonstrated the greatest structural difference with 90% fewer stems in long-invaded versus non-invaded sites (i.e., $6645 \pm$ fewer 472 stems ha^{-1}, Fig. 2). Conversely, the seed bank density of non-invaded sites exhibited 78% more germinable seeds than long-invaded sites. We found that comparisons using all sites (with controls included), versus using invaded sites only, did not affect the significance of the results.

Significant declines in species richness along the invasion chronosequence were also detected in the sapling (58.2%) and seedling layers (34.9%) along the *Lonicera maackii* chronosequence using ANOVA and Bonferroni post hoc tests (Table 1). Interestingly, despite findings of reductions in herb density with increasing *L. maackii* age, no significant declines in herb species richness were detected. The germinable seed bank, however, did exhibit significant species richness reductions (41.4%, Table 1). Also interesting was that few germinable *L. maackii* seeds were found in soil
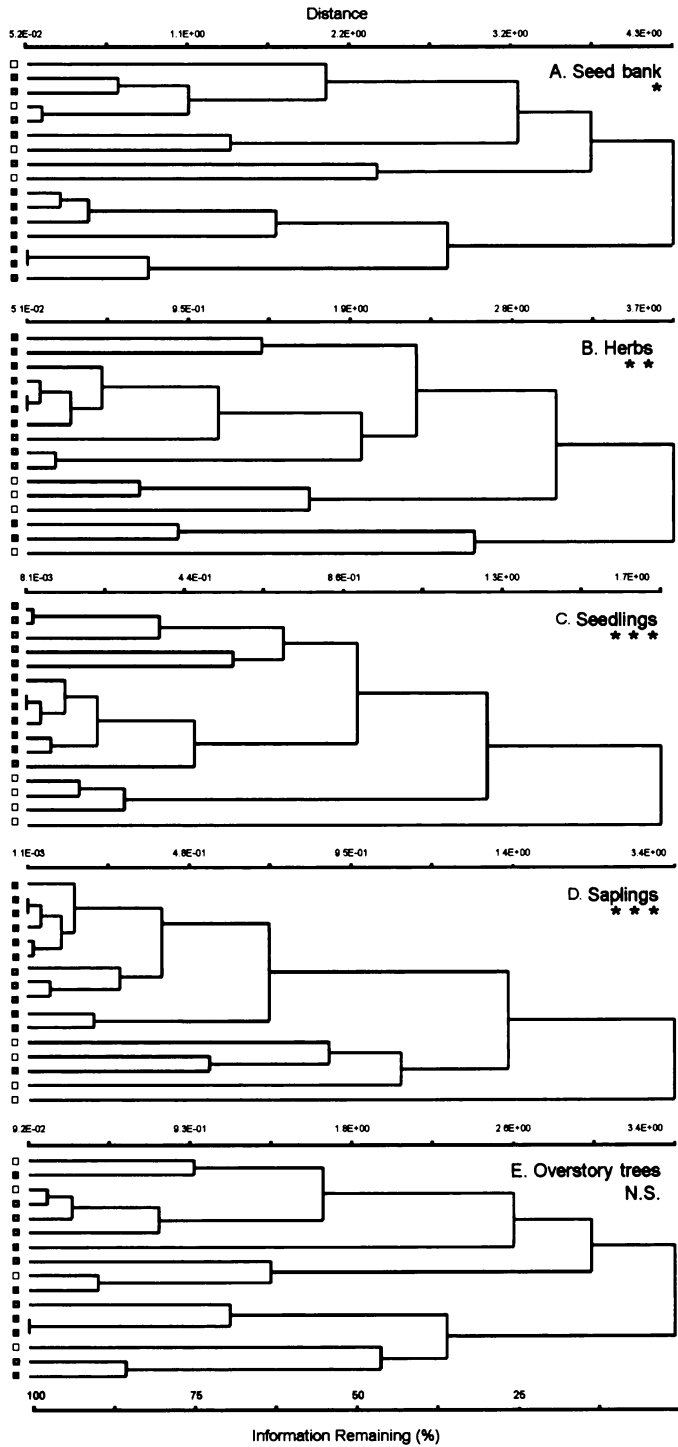
Fig. 1. Comparison of within-stratum species composition for sites among three levels of *Lonicera maackii* invasion. Beta-flexible cluster analysis ($\beta = -0.2$) was used to create dendrograms for each forest layer using Bray-Curtis similarity values. Levels of invasion are indicated by open squares for non-invaded sites, half-open squares for recently-invaded sites, and solid squares for long-invaded sites. Significant ($P <$ 0.05) differences in species composition among invasion levels were tested using multivariate response permutation procedures (MRPP). Differences are indicated when all levels of invasion are significantly

samples for both recently-invaded and long-invaded sites, 6.2% of samples.

CHANGES IN WITHIN-LAYER SPECIES COMPOSITION. Multivariate species composition was examined using beta-flexible clustering and MRPP analyses and revealed that there were significant differences in non-invaded versus invaded sites for all sub-canopy forest layers (MRPP, $P < 0.03$, Fig. 1). Cluster analysis of the seedling and sapling strata showed significant differences in species composition among the non-invaded, recently-invaded, and long-invaded sites (MRPP, $P < 0.01$). The herbaceous stratum did not show significant differences between the recent- and long-invaded sites, but sites were different in composition for pooled invaded versus non-invaded sites (MRPP, $P \leq 0.03$). The seed bank stratum did not show significant separation of the non-invaded sites versus recently-invaded sites; however, long-invaded sites clearly clustered separately from the other sites (MRPP, $P \leq 0.002$, Fig. 1).

SPECIES AFFINITY WITHIN INVASION CHRONOSEQUENCE LEVELS. Indicator species analysis found that certain species showed affinities for sites at specific stages in the invasion chronosequence (Table 2). Few species were significantly associated with long-invaded sites within the seedling, sapling, and seed bank strata as relatively low species frequencies and abundances were observed in these layers at long-invaded sites. Exceptions were *Pilea pumila* and *Leucospora multifida* which were common in the seed bank in long-invaded sites but were not found aboveground in large numbers at any site. In the herb layer, *Eupatorium rugosum*, *Glechoma hederacea* and others were associated with non-invaded sites but less so with recently-invaded and long-invaded sites. Conversely, *Alliaria petiolata*, *Geum vernum*, and *Parthenocissus quinquefolia* were common in the long-invaded sites but not in non-invaded sites. Several woody species were found in both the seedling and sapling layers including *Acer saccharum* and *Prunus serotina* were found in the sapling layer but not significantly in the seedling layer. In the

seedling and sapling layers, all woody species exhibited reduced IVs at invaded sites except *Cercis Canadensis*, *Rosa multiflora*, and *Cornus racemosa*, which were most strongly associated with recently-invaded sites (Table 2).

CHANGES IN BETWEEN-LAYER SPECIES COMPOSITION. Cross-strata congruence analysis found a strong pattern of reduced between-strata species similarity in sites with greater length of *Lonicera maackii* occupancy regardless of the layers being analyzed. The greatest between-strata compositional linkages were found for the non-invaded sites (mean $r = 0.51$, $P = 0.03$), followed by recently-invaded sites (mean $r = 0.37$, $P = 0.07$), and long-invaded sites (mean $r = 0.16$, $P = 0.11$, Fig. 3). Also, greater patterns of similarity were found between certain layers, despite invasion status. For example, the layers with the greatest compositional similarities were tree vs. seedling, followed by tree vs. sapling, and sapling vs. seedling. All strata comparisons in the long-invaded sites except tree vs. seedling were not significant ($P \geq 0.16$); therefore, compositional similarity of strata was most reduced with greater time of *L. maackii* occupancy (Fig. 3).

Discussion. Our study of forest infestation by *Lonicera maackii* is an effective demonstration of how an aggressive, ecologically filtering, invasive species can potentially influence patterns of community structure and dynamics. We found compelling evidence of reduced density and species richness in herbaceous and woody recruitment layers and differences of within-stratum species composition along the invasion chronosequence. The potential strength of this type of investigative approach, particularly in forested ecosystems, is that it combines chronosequence techniques with invasive species studies to lend insight into the temporal and spatial regeneration dynamics and possibly the competitive mechanisms of invaded forest communities.

Typically, following disturbances in mixed deciduous forests in the eastern United States, a successional sequence is initiated which most often progresses through stages of stem initia-

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different (***), when non-invaded and pooled invaded levels are different (**), when non-invaded and long-invaded levels are different (*), or when no levels are significantly different (NS).

tion, reorganization, aggregation, re-initiation, and old growth (Nyland 2002), and with the exception of a brief period following canopy closure, an increase in understory recruitment and sub-canopy stratification occurs (Frelich 2002). In maturing forests in our sampled area, one typically expects to find a taxonomically diverse, vertically stratified system of overstory trees and sub-canopy regeneration layers (Braun 1916). We, however, found sites which were long-invaded by *Lonicera maackii* and consisting only of overstory trees and *L. maackii* shrubs. In sites that were long-invaded by *L. maackii*, we and others found that forests are virtually two-tiered systems consisting only of overstory trees and *L. maackii* shrubs with few plants in the understory and midstory recruitment strata (see Collier *et al.* 2002).

These forest patterns indicate that changes in structure and reduction in diversity likely occurred followed *Lonicera maackii* invasion. Also, the reduced compositional similarity between forest strata in long-invaded forests compared to *L. maackii*-free stands indicates that sites invaded by *L. maackii* may have experienced a shift in successional trajectory relative to non-invaded sites. Furthermore, we found a reduction in cross-strata similarity with increasing time of *L. maackii* occupancy (Fig. 3). These are the general patterns that we observed, but identifying the processes that created those patterns may be more difficult.

Forests are composed of a mixture of occupants that maintain themselves in existing understory layers (i.e., layer-persistent) or are potentially able to outgrow their current stratum (i.e., layer-transient) as described by Gilliam and Roberts (2003). For example, further complexity is added in predicting outcomes by plants that inhibit the germination, survival, and growth of neighbors through production of dense leaf layers (George and Bazzaz 1999). Thus, is does seem possible that *Lonicera maackii* has the potential to limit the success of lower strata such as seed bank and herb layers and also potential shrubs and trees within the regeneration layer. The extended outcome of *L. maackii* invasion is unclear, but infested transient and persistent understory layers in forest stands seem to be experiencing a pronounced reduction in aboveground stem density and species richness for both woody and herbaceous species. These reduced regeneration patterns, in extreme

scenarios, could eventually result in a time delayed pattern of extirpation for certain species similar to that described by Tilman et al. (1994).

While a significant change, it is interesting that the potential elimination of native individuals in *Lonicera maackii*-invaded sites may result in novel interactions and new competitive outcomes during various stages of understory growth and development. Species abundance and composition are often correlated with forest overstories (Gagnon and Bradfield 1986); therefore, with modifications in understory composition below canopies, reciprocal linkages of recruiting layers and the overstory may be altered. Reductions in linkage may be well visualized in non-invaded versus long-invaded sites in our cross-strata congruence analysis (Fig. 3). Eastern forests are also affected by feedback loops (i.e., complex combinations of biotic and abiotic processes; DeMars and Boerner 1997), and while we did not specifically test processes affecting species interactions and outcomes, these are important to consider if *L. maackii* is indeed causing wholesale changes in forest structure, diversity, composition, and successional trajectory.

Native shrubs, ironically, are a rarely encountered life form throughout the region where we conducted our study (Braun 1916), and despite its relatively recent introduction, *Lonicera maackii* has been able to effectively spread and dominate forest interiors (Hutchinson and Vankat 1997). Several studies have reported that forest interiors frequently have fewer successful exotics (McCarthy et al. 2001, Robertson et al. 1994, Webb and Kaunzinger 1993), and new life forms, especially exotics, can be particularly successful at establishing and dominating ecosystems (Richardson 1998). When forests in our sampled area are invaded by non-indigenous shrubs, communities may be "competitively naïve" in experiencing shrub competition, thus as *L. maackii* invades, it may be occupying a previously unfilled midstory niche.

While certain non-native shrubs including *Lonicera maackii* may alter forest vegetation patterns and recruitment, the possible mechanism of low forest layers, such as *L. maackii*, acting as an ecological filter may require further investigation. Native ferns have been shown to have negative impacts, especially on the survival, spatial distribution, and composition of tree seedlings (Cox 1999, de la Cretaz
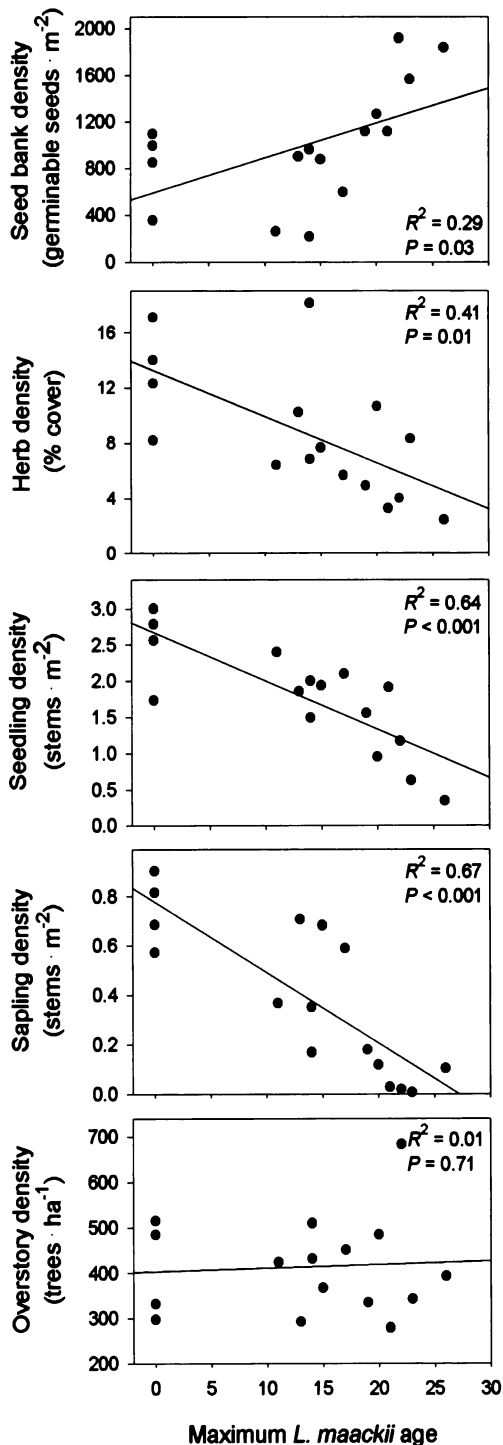
Fig. 2. Regressions of within-stratum changes in density with increasing *Lonicera maackii* age. Sites with *L. maackii* age of zero have not been invaded, and other sites are of various *L. maackii* ages (maximum age 12–26 yrs). R^2-values indicate data's goodness of fit to regression lines, and P-values

and Kelty 1999). This pattern of poor performance for certain tree species below ferns may be due to a number of factors including light reduction, a difficult-to-penetrate frond layer, and possible alterations in the behavior of seed predators below ferns (Cox 1999). Similarly, *Lonicera maackii*, also has a dense canopy and an extended period of leafout which may also result in both quantitative and temporal light attenuation as well as create a physical barrier retarding the growth of native seedlings (Trisel 1997).

Other studies have suggested that dense shrubs and understories can alter microhabitat conditions and reduce understory regeneration. Beckage et al. (2000) found that seedling recruitment and understory light levels did not increase beneath *Rhododendron maximum* shrubs during a four-year period following large gap creation via overstory tree removal. The authors suggested that the dense *Rhododendron* shrub layer may neutralize recruitment opportunities and proposed that a large-scale disturbance of both the understory and overstory may be needed in order to enable tree seedling establishment. In *Lonicera maackii* thickets, tree recruitment may be difficult to initiate as well. Luken et al. (1997) found that tree seedling recruitment was not augmented during a three-year period after gap creation via *L. maackii* removal. Other studies involving native shrubs (Niering et al. 1986), bamboo (Griscom and Ashton 2003), and understory grasses (Bowersox and McCormick 1987) have similarly found that sub-canopy vegetation can act as an ecological filter, which can cause delays and/or inhibition of forest succession.

Despite observations that native shrubs are historically rare in forests of our study region, invasive, non-indigenous shrubs may become more common members of the flora. Increases in geographic range have been documented for invasive shrub species, and these increases are frequently accompanied by reductions in native seedling and sapling recruitment. The occurrence of the shrub *Ligustrum sinense* in North Carolina mixed hardwood forests was associated with an almost complete reduction in tree regeneration and a 42% reduction in herb species richness (Merriam and Feil

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indicate significant changes in strata densities with changing *L. maackii* ages.

Table 1. Comparison of mean species richness (± SE) for each site along invasion chronosequence. Means are compared within each stratum via Bonferroni post hoc tests, and significant differences ($P < 0.05$) are indicated by lowercase letters. Percent difference reflects non-invaded vs. long-invaded sites.

Stratum	Non-invaded	Recently-invaded	Long-invaded	% difference
Seed bank	14.50 ± 1.25 a	10.66 ± 1.05 a	8.50 ± 1.38 b	− 41.4%
Herb	19.00 ± 1.87 a	23.50 ± 1.23 a	18.16 ± 0.99 a	− 4.4%
Seedling	11.00 ± 1.57 a	9.83 ± 1.31 b	7.16 ± 1.01 b	− 34.9%
Sapling	8.75 ± 1.18 a	7.16 ± 1.30 a	3.66 ± 1.03 b	− 58.2%
Overstory tree	28.50 ± 3.05 a	30.75 ± 3.50 a	32.50 ± 2.75 a	+ 1.4%

(2002). In two studies in New Hampshire, Frappier et al. (2003) found that *Rhamnus frangula* presence was more important than abiotic factors in explaining herb abundance and native tree seedling density and species richness, and Fagan and Peart (2004) found that *R. frangula* was associated with reduced native sapling survival and growth as well as a

Table 2. Indicator species results for invasion chronosequence levels within forest strata. Indicator value (IV) is given for each invasion level as well as overall IV. Only statistically significant species with IVs ≥ 5.0 are listed. Non-native species are indicated with an asterisk. IVs denote the relative level of species occurrence per group ranging from 0 (no indication) to 100 (perfect indication).

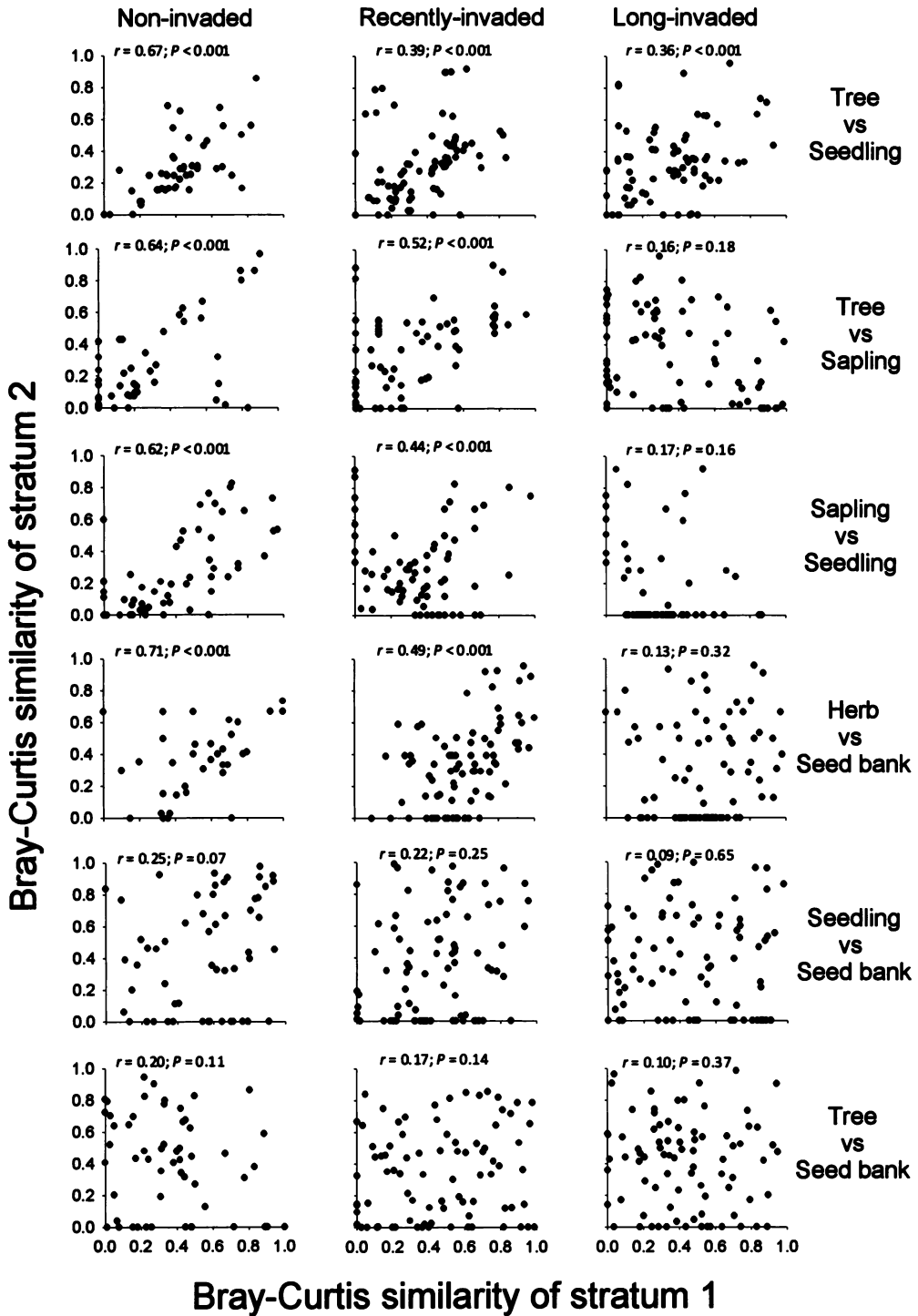| Stratum	Non-invaded	Recently-invaded	Long-invaded	Indicator value
Seedlings				
Acer saccharum	19	6	2	19.1
Prunus serotina	15	1	0	14.8
Cercis canadensis	0	6	0	6.0
Rosa multiflora*	0	5	2	5.1
Saplings and shrubs				
Acer saccharum	18	6	2	17.8
Fraxinus americana	6	17	0	16.7
Prunus serotina	14	0	0	14.1
Ulmus americana	14	0	0	13.5
Lindera benzoin	6	0	0	6.2
Cornus racemosa	0	5	0	5.1
Herbs and vines				
Geum vernum	7	6	31	31.2
Parthenocissis quinquefolia	5	8	19	19.5
Cryptotaenia canadensis	0	17	1	17.3
Eupatorium rugosum	17	3	5	16.8
Vitis spp.	14	1	6	14.4
Toxicodendron radicans	3	14	2	13.8
Sanicula canadensis	0	0	13	13.4
Carex vulpinoidea	0	11	0	11.3
Alliaria petiolata*	2	8	11	10.6
Impatiens pallida	0	10	2	10.4
Glechoma hederacea	10	1	0	10.1
Osmorhiza claytonii	0	8	3	7.6
Smilacina racemosa	6	0	0	6.2
Polygonum pennsylvanicum	3	6	1	6.0
Erigeron philadelphicus	0	5	0	5.5
Poa sylvestris	1	5	0	5.1
Seed bank				
Juncus tenuis var. tenuis	4	15	1	14.6
Oxalis stricta	14	3	2	14.1
Pilea pumila	0	1	13	12.6
Molluga verticillata*	0	8	0	8.1
Leucospora multifida	0	0	7	7.4
Carex blanda	5	0	0	5.3
Muhlenbergia schreberi	5	0	0	5.3
Stellaria media*	5	0	0	5.0
Mean	5.7	5.2	3.6	11.4

FIG. 3.   Cross strata congruence analysis using pair-wise comparisons of forest layers for non-invaded, recently-invaded, and long-invaded *Lonicera maackii* sites. Standardized vegetation abundance values were used to calculate Bray-Curtis similarity values at each PCQ sampling point. Mantel tests were used to compare matrices to examine between-strata similarities. Perfect congruence of species composition between strata appear as points on graph panels from lower left to upper right, and reduced correlation in species composition appear as clouds of points. Points on axes indicate that species were found in only one forest layer.

shift in composition toward more shade tolerant species. In a forest restoration experiment in Ohio, Hartman and McCarthy (2004) reported that several species of tree seedlings experienced reduced survival and growth below *Lonicera maackii* thickets.

Impacts on lower forest recruitment layers can be ecologically significant because seedlings and saplings are the investment capital for future overstory development (Kozlowski 2002). One model of community dynamics suggests that species that do survive have specific traits that allow them to successfully pass through various hierarchically arranged biotic and abiotic filters, such as site suitability, species availability, competitive ability, and individual performance (Lawton 1987, Pickett et al. 1987). Other models that may explain our results include individuals in the most heavily invaded habitats may be more stress tolerant or competitive (Grime 1977). Our indicator species analysis suggests that certain species may be less able to compete successfully or tolerate abiotic conditions in *Lonicera maackii* dominated plots. Researchers have found that most species of annual and perennial herbs (Gould and Gorchov 2000, Miller and Gorchov 2004), vines (Collier et al. 2002), and tree seedlings (Hutchinson and Vankat 1997, Gorchov and Trisel 2003, Hartman and McCarthy 2004) are frequently less successful in sites occupied by *L. maackii*, thus the data suggest that *L. maackii* likely has the potential to determine, or at least influence, the composition and structure of forests and their regeneration. Clearly more work needs to be performed to elucidate mechanisms of action for *L. maackii* and other co-invading species as well as species-specific responses to invaders.

While these studies report changes in native species abundance, diversity, and/or composition following non-native shrub invasion, many investigations are limited in spatial, temporal, and biological scope, which may sacrifice the validity and interpretive power of the investigation (Booth et al. 2003). One problem with invasive species ecology is that many studies frequently report impacts at only a few locations, using only a few biological variables, and over a relatively short period of time (Parker et al. 1999), thus there is a need for the investigation of long-term changes in patterns and alteration of higher order processes (such as succession) which are associated with invasion.

Admittedly certain caveats must be added with regards to our study. First, chronosequence studies assume that sites are comparable across space with the exception of the variable of interest (in our case, time of invasion), and naturally, the composition and structure of forests in our study area differ with topography, soil type, species availability, stochastic forces, and stages of succession (Forsyth 1970). Second, chronosequence studies also assume that space is a valid substitution for time (Pickett 1989). Another related non-testable assumption is whether observed disparities were due to pre-invasion differences among sites. Our cluster analysis, MRPP, and *t*-tests demonstrated that individual sites were different in terms of species composition, stand age, and basal area, but there were no significant groupings based on *Lonicera maackii* invasion status. Thus, the observed differences were not likely attributable to these biotic forest stand factors as well as pre-invasion abiotic differences. Also, it has been long debated if certain sites have attributes which make them more invasible (Lonsdale 1999), and it may be these same attributes which predispose invaded sites to inhibited regeneration, reduced species richness, and less compositional similarity versus non-invaded sites. While we are unable to test the invasibility of these sites, we believe that the appropriate use of the chronosequence method does give validity to this investigation in that spatial, temporal, and stochastic variability has been incorporated. Another caveat is that relatively speaking, this plant is a recent addition to the regional flora of this area (Luken 1990); therefore, given the long lifespan of forest species relative to our chronosequence study, longer-term consequences of *Lonicera maackii* invasion are unknown.

Conclusions. Overall, we have found that sites invaded by *Lonicera maackii* were different from non-invaded sites in a number of attributes including reduced species richness, density, within-stratum species composition, and between-strata compositional similarity. These results suggest that invaded sites are experiencing different successional pathways than non-invaded sites. Our sampled communities may fit an indeterminate pattern such that these forests may exhibit multiple successional pathways (see Drake 1990). For example, *L. maackii*-invaded versus non-invaded

sites may be experiencing divergent successional trajectories, or alternatively, sites with similar levels of invasion may be experiencing convergent successional trajectories. Invasive species are proving to lend valuable insight in testing complex ecological theories, and we recommend that additional studies be employed using chronosequence methods to investigate potential invasive species' effects on ecological patterns and processes in long-term settings.

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