

THE IMPACT OF LAND-USES ON THE RECRUITMENT DYNAMICS OF TREE SPECIES

by

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Abstract

Patterns of human land use vary as distance from an urban center increases. These changes in land use alter nutrient loads, invasive species pressure and have been associated with altered patterns in plant communities. Additionally, habitat fragmentation increases in the proximity of urban centers ushering in further environmental changes (increasing edge effects, dispersal distance, isolation, etc.) that also affect plant communities. The combined impacts of habitat fragmentation and human land use patterns surrounding remnant forest patches may further alter plant communities. Few studies however, have empirically tested the impacts of these combined effects on plant species. Here, I study the impacts of the surrounding landscape on the growth and survival of eight native and two invasive tree species in remnant forest patches. For that I planted seedlings of these species at 4 forests along a 40 km urban-rural gradient in southeast Michigan. Seedlings were planted at three different forest habitats, forest edge, middle distance to the edge, and forest interior. Over the course of the summer I measured seedling growth and mortality, in addition to environmental characteristics of the sites, i.e., soil moisture and light availability. To analyze the data, I constructed hierarchical models using a Bayesian framework that reflected the spatial scale of my data.

My results shows differential growth and survival along this land use gradient for each of the studied species. In general, the invasive species had greater survival closer to urban areas, while several large seeded native species had lower survival rates closer to urban centers. Later successional and more shade tolerant species had higher survival in more rural forests. Other species had higher growth and survival at specific landscape-habitat combinations. For example, *Acer saccharum* tended to have higher growth and survival in the more shaded interior plots than edge plots across the land use gradient. On the other hand, *Prunus serotina* had higher survival in the edge plots, but only at the two more rural sites. These results suggest that human land use patterns have the potential to affect species composition in remnant forest patches.

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Introduction

During the next few decades, land use change will have a greater impact on terrestrial biodiversity than climate change (Sala et al. 2000). Beyond the fact that suitable habitat for populations of plants and animals is being lost, the widespread expansion of urban areas is also associated with numerous changes in the biotic and abiotic environments in remnant patches of vegetation (McDonnell et al. 1997, Pickett et al. 2001). Changes in microclimatic conditions caused by fragmentation and urbanization will have an effect, but so will the configuration of the surrounding land use matrix as different landscapes have the potential to alter species interactions differently, e.g., degree of herbivory, seed predation, competition, etc. In particular, the ability of forest patches to maintain healthy tree populations could be affected as the growth, fecundity and recruitment of new individuals may be altered by human development of the landscape. In this study, we assess the effects of varying landscapes along an urban-rural gradient on remnant forest patches; specifically we investigate the impact of the land use surrounding forest fragments on the establishment of tree seedlings along an urban-rural gradient.

The expansion of human settlements in North America and subsequent land use change has transformed the landscape from largely contiguous forests to a patchwork of vegetation fragments (Curtis 1956): by 1900 over 50% of the region's forested land had been cleared (Smith et al. 2000). This fragmentation drives a host of environmental changes, abiotic and biotic, that impact forest species (Chen et al. 1999, Porter et al. 2001, McDonald and Urban 2004).

A major effect of urbanization on the physical environment of remnant vegetation patches is an increase on the local temperature, the urban heat island effect (McDonnell et al. 1997, Fig. 1). If some species are more responsive to higher temperatures than others we might expect a shift in species composition between urban and rural areas. Human activities in urban areas also alter the characteristics of soils compared to less developed areas. Urban soils tend to have higher concentrations of heavy metals, organic matter, and salts (Pouyat et al. 1995, Pouyat et al. 2008). They also tend to have lower soil pH relative to rural areas. The changes in soil chemistry due to urbanization could reduce the habitat suitability for some species but not for others.

Specific human land uses can have impacts on nutrient cycling. Residential and agricultural fertilization can increase soil nitrogen (Kahan, et al. unpublished manuscript) and phosphorus as landscape development increases (Pouyat et al. 1995, Hansen et al. 2005). And, these increases in soil nutrients often reduce the diversity of plant communities (Vitousek et al. 1997). Litter decay tends to be slower in urban areas and organic carbon tends to accumulate in soils. Humans also generally suppress fires in developed areas (Hansen et al. 2005). Suppression of periodic fires can allow non-fire adapted native and exotic species to encroach into forest patches at the expense of fire adapted native species.

Increasing urbanization also leads to numerous changes in the biotic environment and interspecific relationships of remnant forest patches. Human land use changes invasive species pressure (Vila and Ibáñez 2011). The specific characteristics of the land use bordering forests can determine exposure to exotic species. The abundance of invasive species increases in urban areas (Porter et al. 2001), but the type of the development may also have an effect. Cutway and Ehrenfeld (2009) examined forest patches in New Jersey, found that forests adjacent to predominantly residential areas tend to have a higher number of invasive species compared to those surrounded by industrial land. Urbanization can also impact the abundance of certain seed predators and important herbivore browsers (Tighlman 1998, Augustine and Jordan 1998,

Rizkalla and Swihart 2009). Many vertebrates that are part of forest communities have particular patterns of population density along urbanization gradients. Herbivores can have a substantial impact on forest regeneration (Tilghman 1989, Augustine and Jordan 1998). Many species of herbivores have population density patterns associated with human land use types. For example, white-tailed deer (*Odocoileus virginianus*) have higher population densities in forest patches at intermediate distances from urban centers than where forest patches are found within a matrix of agriculture and low density development (Tilghman 1989). High levels of deer browsing can impede the ability of slow growing species to regenerate.

Land-use change can also affect the soil microbial communities by altering nutrient inputs (Peacock et al. 2001). Many urban soils have lower soil microfauna and fungal densities and higher bacterial densities. Groffman et al. (1995) found lower microbial biomass in urban versus rural soils. Other studies have shown higher rates of litter decomposition in urban versus rural forests (Pouyat et al. 1996). Goldman et al. (1995) found higher potential N mineralization rates in rural forests and higher nitrification rates in urban forests along a 140 km transect stretching northward from New York City. Also earthworms tend to increase in abundance in urban areas (McDonnell et al. 1997), and their presence and abundance can have profound impacts on soil nitrogen chemistry (Steinberg et al. 1997). These soil community differences combined with litter quality differences and increased temperatures in urban areas may explain altered biogeochemical cycling in urban soils.

Through their interactions with forest species, these changes in biotic communities can have substantial impacts on community composition in remnant vegetation patches. In the case of tree species, tree mortality is heavily weighted towards early life stages (Harcombe 1987). In particular, the biggest population bottlenecks for tree species are the seed and seedling stages. Seedlings are a particularly vulnerable life history stage for trees. As such, seedlings could be very sensitive to the abiotic and biotic gradients associated with the landscape matrix surrounding forest fragments. Therefore, comparing seedling growth and mortality among tree species at different sites along an urbanization gradient can provide an excellent indicator of how land use impacts forest regeneration. This information will be paramount in understanding how the combination of land use change and climate change will impact forest in coming decades.

Here we seek to address how human land use impacts population dynamics, i.e., recruitment of new individuals, within forest fragments along an urbanization gradient. Specifically we test how the composition of the land use matrix impacts growth and mortality of different tree seedlings and how this effect compares to other environmental factors. The specific questions we aim to address in our work are: 1) Does land use surrounding a site have the potential to impact regeneration of forest tree species? 2) What is the importance of the surrounding landscape with respect to other environmental variables in tree seedling recruitment? 3) Do species differ in their responses to the land use matrix surrounding forest fragments? Answers to these questions will allow a greater understanding of how the configuration of a landscape impacts tree species regeneration within remnant vegetation patches. Information derived from this work will also be critical in our efforts to predict future forests ability to adapt to global change in the context of a shifting landscape.

Methods

We carried out a tree seedling transplant experimental along a 40 km transect stretching from Ann Arbor, MI (urban center) to rural Livingston County (42°16'53"N 83°44'54"W; Fig. 1). This experimental set up was designed to ensure that the land-use matrix surrounding our study sites encompassed a variety of levels of urbanization and human use. For two summers, we transplanted seedlings of dominant tree species into edge, middle and interior plots to capture the effects of a variety of habitat types within each landscape. During the growing season, we recorded individual seedling survival and measured growth in height at the end of the summer. With these data, we modeled species-specific survival and growth based on individual seedling responses to the landscape surrounding each site, their habitats, and other environmental factors. This type of inference allowed us to make predictions, probability of survival and maximum growth rate, about each species performance under a gradient of environmental conditions and land-uses.

Study sites

We obtained 2005 land use data for the study area from the Southeast Michigan Chamber of Governments¹. We created a simplified land use classification system with six categories, developed, agricultural, open, forest, water and wetland, using ArcMAP 10 (ESRI 2010). To find the extent of each land use surrounding our study sites, we calculated a 1 km circular buffer around each sites centroid. We then estimated the area of each land use type surrounding each site.

Our four study sites were located along a 40 km urbanization gradient running from the city of Ann Arbor northwest to rural Livingston County (Fig. 1). The most urban site (UR) was located in Miller Woods, an Ann Arbor City Park. This 9.1 ha park is situated in a residential neighborhood, and within 1 km 97.8% of the land is developed and 2.2% forested. The forest is dominated by *Acer negundo*, *Juglans nigra*, *Ailanthus altissima*, *Lonicera maackii* and *Populus deltoids*.

The first suburban site (SU1) was located in Radrick Forest, a 18 ha mixed-oak research forest located on University of Michigan property approximately 8 km east-northeast of Ann Arbor, MI. Within 1 km of SU1, 57.9% of the land is developed and 13.2% is forested (Fig. 1).

The second suburban site (SU2) was located in a mixed-oak forest in Stinchfield Woods, a 314 ha University of Michigan research forest approximately 30 km northwest of Ann Arbor. The land within 1 km of SU2 is 12.9% developed and 78.8% forested (Fig. 1).

The rural site (RU) was located in an oak-hickory forest in the Edwin S. George Reserve, a 525 ha fenced research preserve that belongs to the University of Michigan. Within 1 km of RU 0% of the land is developed and 54.7% is forested (Fig. 1).

Within each site, plot locations were selected to account for the natural variability of microhabitats and edge effects. Studies of edge effects in temperate forests measure environmental factors along transects of varying distances: Matalack (1993) used 40 m transects; Chen et al. (1999) measured environmental change across 60 m transects; Moffatt et al. (2007) used transects up to 250 m in length; Hewitt and Kellman (2004) defined forest interior as greater than 50 m from forest edge in their transect experiment. Several studies that measure environmental change relative to edges (e.g., Chen et al. 1995, Chen et al., 1999) show relative stability in many environmental factors beyond 50 m – 60 m from the edge. In order to capture

¹ www.semco.org

the variation in microenvironmental factors due to edge effects, we planted seedlings into three types of plots at each site: edge, middle and interior. Pairs of edge plots were located at forest edges. Pairs of middle plots were located 30 m into from forest edges. Pairs of interior plots were located 60 m from forest edges.

Planting and censuses

In order to capture the community level impact of surrounding land use on forests regeneration, we selected a variety of representative forest species from several functional groups, i.e., pioneer, mid-successional and late successional species, in addition to two invasive species (*Celastrus orbiculatus* and *Elaeagnus umbellata*) (Table 1). Seeds collected from nearby wild populations were germinated in a greenhouse and transplanted into field sites after the last spring frost: early June in 2010, mid-May in 2011. We planted 15 individuals from each species into rows 25 cm apart. The seedlings were separated by 25 cm in each row. Before planting seedling height was recorded. After planting, seedling survival was monitored every 3-4 weeks during the growing season. At the end of the growing season, seedling height was recorded at field sites.

Soil moisture and light data

Volumetric soil water content was measured in the top 7.5 cm of soil during each census with a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Plainfield, IL, USA). Four soil moisture measurements (one at each corner) were taken for each seedling plot at each census. For our analysis, average summer soil moisture values for each plot were used. We estimated the proportion of full sunlight each seedling received from hemispherical canopy photographs (Rich et al. 1993). In August a photograph was taken above each seedling plot. Photographs were taken with single lens reflex camera with a Sigma 8 mm 1801 fish-eye lens a (Ronkonkoma, NY, USA). From these photographs, the proportion of full sunlight reaching the forest floor at each plot, the global site factor (GSF), was calculated using the software package HEMIVIEW (Delta-T Devices, Cambridge, UK).

Model of seedling survival

To be able to account for both the abiotic factors affecting seedling survival and the impacts derived from the effects of the surrounding landscape we used a counting process in a Cox survival model (Andersen et al. 1993). This type of survival model allows the inclusion of fixed and random effects in the frailty or risk portion (Clark 2007). Here the data for each seedling we studied and each time t , N_{it} , is coded as 0 if the seedling is alive or as 1 if the seedling was recorded as dead that period of time, which would be the last time period accounted for. The likelihood of the model accounts for the number of failures at each time:

$$N_{it} \sim \text{Poisson}(\lambda_{it})$$

where the mean λ is then estimated as a function of the intrinsic rate of mortality, or hazard h , and the extrinsic risk of mortality, or risk μ .

$$\lambda_{it} = h_t e^{\mu_i}$$

Parameters in the model were then estimated following a Bayesian approach that allowed us to consider the different sources of uncertainty associated with the data, the process, and the parameters (e.g., Clark 2007, Gelman and Hill 2007). The hazard was estimated at the species level for each time step, h_i , from a gamma distribution with non-informative parameter values, $h_i \sim \text{Gamma}(0.01, 0.01)$. This intrinsic mortality rate would then reflect the temporal variability in mortality that is not accounted for by the risk function.

The risk, μ_i , was estimated as a function of the covariates included in the analysis, $\mu_i = X_i B$. X_i is the matrix of covariates associated to each seedling i . B is the vector of fixed effect coefficients associated to each covariate. We tried several combinations of covariates and random effects (e.g., plot and year) and selected the model that best predicted the data. For the final survival model the covariates included in the analysis were: seedling height at the time of planting, soil moisture, light level, and habitat type (edge, middle, or interior), this last variable combined with landscape type (urban, suburban 1, suburban 2 and rural). Height, soil moisture, and light measurements were standardized to facilitate convergence of the model runs.

$$\mu_{it} = \alpha_{\text{landscape,habitat}} + \gamma_1(\text{soilm}_i) + \gamma_2(\text{light}_i) + \gamma_3(\text{height}_i)$$

To account for the varying impact of habitat type depending on the surrounding landscape, habitat was nested within landscape in a hierarchical framework (Fig. XX), $\alpha_{\text{landscape,habitat}} \sim \text{Normal}(\alpha_{\text{landscape}}, \sigma_{\text{landscape}}^2)$ where $\alpha_{\text{landscape}} \sim \text{Normal}(0, 10000)$ and $\sigma_{\text{landscape}} \sim \text{Uniform}(0, 1000)$. Parameters γ were estimated from normal distributions with non-informative parameter values, $\gamma_k \sim \text{Normal}(0, 10000)$. To test the difference between the landscape and habitat combinations (parameters $\alpha_{\text{landscape,habitat}}$), we estimated the difference between the associated parameters; a significant difference would then have a 95% credible interval around the posterior mean that does not include zero. We report parameters α and γ multiply by -1 to reflect their effect on survival (the Cox model estimates mortality).

Models were run in OpenBUGS 1.4 (Thomas et al. 2006); simulations were run until convergence of the parameters was ensured (~25,000 iterations). Models were then run for another 100,000 iterations from which posterior parameter values and predicted survival rates were estimated. Final model selection was based on DIC (Deviance Information criterion), the model with the lowest values of DIC was selected (Spiegelhalter et al. 2000). Predicted survival for each species in each site habitat combination, $\hat{S}_{\text{landscape,habitat}}$, was estimated for average height seedlings under habitat-specific average soil moisture and light conditions for the summer.

Model of seedling growth

As with seedling survival, we modeled seedling growth at the individual level. Only seedlings that exhibited positive growth over the study period were included in the analysis (as negative growth might have indicated herbivory or a substantial measuring error). Also, when fewer than five individuals of a species at a given site-habitat combination survived the summer those individuals were removed from the analysis, as the data would not have been sufficient to estimate growth under those conditions. Total growth, the difference between height at planting and final census, was modeled as a saturation function of light (Pacala et al., 1994, 1999 et al. 2003, Kobe 2006, Mohan et al. 2007). The growth of individual i was modeled as follows:

$$\text{Growth}_i \sim \text{Normal}(G_i, \sigma^2)$$

Where σ^2 is the species specific variance, $1/\sigma^2 \sim \text{Gamma}(0.01, 0.01)$, and G_i comes from the light saturation equation:

$$G_i = G_{max_i} \frac{\text{Light}_i - l_{0_i}}{\text{Light}_i + \theta_i}$$

here G_{max_i} is the maximum growth for an individual modeled as function of landscape and habitat (\ln transformations were used to ensure positive growth values):

$$\ln(G_{max_i}) \sim \text{Normal}(G_{max_M}, \sigma_g^2)$$

The mean of the log normal distribution is estimated for each landscape and habitat combination such that $G_{max_M} = \beta_{landscape, habitat}$, and $1/\sigma_g^2 \sim \text{Gamma}(0.01, 0.01)$. The amount of light needed for growth to begin, l_{0_i} , was estimated as $l_{0_i} = \delta_1 + \delta_2 \times \text{height}_i$. Here we estimated δ_k as $\delta_1 \sim \text{logNormal}(0, 10000)$ and $\delta_2 \sim \text{Normal}(0, 10000)$. The half saturation point, θ_i , was calculated as $\theta_i = \rho_1 + \rho_2 \times \text{soil moisture}_i$, $\rho_1 \sim \text{logNormal}(0, 10000)$ and $\rho_2 \sim \text{Normal}(0, 10000)$. To ensure l_{0_i} and θ_i were positive, their values were constrained between 0 and 1.

The model was run with two chains of parameters until convergence (~50,000 iterations) The model was then run for an additional 100,000 iterations from which posterior parameter values were estimated. To test the difference between the different landscape and habitat combinations, we estimated the difference between the associated parameters ($\beta_{landscape, habitat}$); a significant difference would then have a 95% credible interval around the posterior mean that does not include zero. Significance was determined for the other covariates (δ_2 , and ρ_2) if the 95% credible interval did not contain zero.

Integrated assessment of seedlings performance

For those landscape-habitat combinations we have sufficient data, we calculated an integrated assessment of species performance by multiplying predicted survival ($\hat{S}_{landscape, habitat}$) and maximum growth rate parameters ($\beta_{landscape, habitat}$).

Results

Survival Model

Hazard

Hazard, a species intrinsic probability of mortality at each census, varied over the course of the growing season (Supplemental Information). Hazard curves were diverse among species. Several species, *Acer saccharum*, *Elaeagnus umbellata*, *Prunus serotina*, *Quercus rubra*, and *Q. velutina*, experienced increasing mortality probability until the second or third census, after which mortality decreased, this is a common trend in transplant experiments reflecting a delayed transplant shock. Three species, *Celastrus orbiculatus*, *Nyssa sylvatica*, and *Robinia pseudoacacia*, had hazard curves that increased throughout the growing season.

Landscape effects

The impact of landscape type on survival ($\alpha_{landscape}$ comparisons) was only different among landscape types for *E. umbellata*, where urban and rural plots had higher survival than the suburban sites (Table 2). For the other species significant differences took place between particular landscape type and habitat combinations (Fig. 2). For *A. rubrum* survival in rural middle and interior, but not edge, plots was higher than in urban and suburban sites. For *A. saccharum* we observed the same pattern except that urban middle plots had survival rates as high as those in the rural plots. *Quercus rubra* had higher survival in some urban sites in comparison with suburban sites. *Robinia pseudoacacia* was the only species with higher survival in suburban sites than in urban and rural ones.

Habitat effects

While looking at each landscape site we were able to assess the effect of habitat on seedling survival ($\alpha_{landscape, habitat}$ comparisons). Results again varied among the studied species and landscape sites, with no overall patterns of particular habitats always benefiting or reducing survival (Table 2). *A. rubrum* survival was higher in interior and middle habitats than at the forest edge in all landscape types. *A. saccharum* had significantly higher survival in middle than in edge plots in the urban landscape. In one of the suburban settings *C. orbiculatus* showed higher survival in the interior plot than at the edge of the forest. And *N. sylvatica*'s survival only significantly varied in the rural plots, with higher survival in the middle and interior with respect to the edge.

Effects of the covariates (soil moisture, light, planted height) on survival

The effect of soil moisture on seedling survival was significant, and positive, for *A. saccharum*, *C. orbiculatus*, and *N. sylvatica* (Table 2). High light levels had also a positive effect on *A. saccharum* and *E. umbellata* (Table 2). The variability on initial seedling height at the time of planting it does not seem to have influenced survival during the summer (Table 2). And although no significant, there is a trend for most species to have higher survival under high soil moisture and light levels.

Growth Model

Landscape effects and light requirements

We used the values of the parameters $\beta_{landscape,habitat}$, lo (δ_l) and θ (ρ_l) to compare species according to their light requirements and growth responses (Table 3). The effects of landscape habitat combination on seedling growth ($\beta_{landscape,habitat}$) do not show strong patterns for any of the studied species (Table 3). For several species, *A. saccharum*, *C. glabra*, *E. umbellata*, *N. sylvatica*, and *Q. velutina*, most combinations seem to have similar maximum growth rates. At the urban site *R. pseudoacacia* experienced a higher growth rates, but only on at the edge and middle sites (Fig. 3). And suburban habitats were best for *C. orbiculatus* and *P. serotina*. Across sites, *A. saccharum* had the lowest maximum growth rate in edge sites. The light levels required to start growth for average height seedlings varied among the species, with *P. serotina* and *Q. velutina* having the highest and the two invasive species, *C. orbiculatus* and *E. umbellata*, the lowest. The half saturation constant (parameter θ at average soil moisture) ranked *P. serotina* and *R. pseudoacacia* at the top and *A. saccharum* and *E. umbellata* at the bottom (Table 3).

Effects of the covariates (soil moisture and planted height) on growth

All species had a significant response to soil moisture, the higher the level or soil moisture the less light needed to reach the half maximum growth rate. However, the effect of soil moisture varied among species (Table 3). Generally, the more shade tolerant species, *N. sylvatica* and *A. saccharum* needed less soil moisture to reach their half maximum growth rate, while more light demanding species, *C. orbiculatus*, *E. umbellata*, *Q. velutina* and *R. pseudoacacia* needed more soil moisture to reach maximum growth under high light conditions. With respect to planted height, only *A. saccharum* and *C. orbiculatus* showed a significant response. For these three species, larger seedlings needed less light to begin growing. *C. orbiculatus* showed the strongest response to planted height.

Integrated assessment of seedling recruitment.

Integrated performance, the product of predicted survival and maximum growth, showed how each species performed at each landscape-habitat combination (Fig. 4). At the urban site, *E. umbellata* performed well at all site habitat combinations, though *A. saccharum* surpassed it in the middle plots. At the suburban1 site, *R. pseudoacacia* performed the best at the edge plots, *E. umbellata* performed the best at the middle plots and *C. orbiculatus* performed the best at the interior plots. At the suburban2 site, *C. orbiculatus* and *P. serotina* performed the best at the edge plots while *E. umbellata* performed the best at the middle and interior plots. At the rural site, *A. saccharum* and *C. orbiculatus* performed the best, while *A. saccharum* performed the best at the middle and interior plots.

Discussion

In this study our goal was to quantify the ability of dominant tree species to recruit new individuals in remnant forest patches along an urban-rural gradient. Besides changes in the microclimate conditions of these forest patches, forest fragments have the potential to also be affected by the surrounding landscape. Distinct types of landscapes, e.g., agricultural land vs urban development, may exert a different influence in forest patches by shaping some species interactions that are critical for recruitment, e.g., seed predation, herbivory, plant-soil feedbacks. Though there is substantial literature on the impacts of individual abiotic gradients on tree seedlings, few studies have explored the impacts of the unique environments created by the combinations of biotic and abiotic factors found along urbanization gradients.

By comparing survival and growth rates among species growing within different land use matrices our results show that species vary in their responses to the unique environments imposed by the combination of landscape and habitat. In addition, results also indicate that these trends in seedling survival and growth also differed among species. This has potential implications for forest regeneration as some species may have higher recruitment rates than others at different landscapes.

Effects of the surrounding landscape on tree seedling survival

In our results, the overall effect of landscape type on seedling survival had a significant impact on only one species, *E. umbellata* (Table 2). The invasive *E. umbellata* had higher survival in the urban and rural sites than the suburban sites. It is possible *E. umbellata* experienced greater mortality at the suburban sites due to factors not taken into account in our study including herbivory and/or fungal pathogens. But this general lack of significance among landscape types reflected the large variability of performances observed at each of those landscape types (Table 2). Results indicate species-specific responses to each landscape-habitat combination. Such range of variation suggests that the overall impact of landscape type is complex and it interacts with the differential effects of the habitats nested within each landscape.

Once soil moisture and light were accounted for, results still point out at differences in survival among habitats and sites (Table 2), and suggest there are factors beyond just the environmental variables included in the analysis that are impacting the survival of the species at these site-habitat combinations. Although soil moisture values did not correlate with habitat, there was a strong relationship between habitat type and light: edge plots had the highest light levels within each site while middle and interior plots had lower light levels (Fig. 5). The survival model showed light had a significant effect on the survival of two species, *A. saccharum* and *E. umbellata*. Interestingly, *E. umbellata* tended to have a stronger site-habitat effect (Fig. 9) in sites with lower light levels. Similarly, the impacts of site-habitat on *A. saccharum* survival were the most positive in the lower light interior plots (Fig. 9) indicating that the regeneration niche is defined by more variables than those we measured.

The unique environments created by the combination of landscape and habitat could explain the differences between site-habitat survival rates for some species. The importance of the different habitats to seedlings survival depended on site for some species. For example, the effects of site-habitat on *Nyssa sylvatica* do not differ greatly for all the sites except at the rural site. There, *N. sylvatica* had significantly higher survival in the middle and interior plots than at the edge (Fig. 11). Additionally, *A. rubrum* had the highest parameter values at the rural site, but

only at the middle and interior habitats (Fig. 9). Indeed, the predicted survival results (Fig. xx) show for most species and at most site-habitat combinations, interior plots tended to have higher survival. This relationship was true even for *A. saccharum* and *E. umbellata*, the two species whose survival was positively impacted by light despite light levels being lower in the interior plots (Fig. 9).

Effects of landscape type and habitat on seedling growth

The results of the growth model add greater depth to the predictions of forest regeneration across the landscape. Despite limited results, some species tended to have a higher maximum growth rate in specific landscapes (Fig. 3). *A. saccharum* showed a higher maximum growth in the urban and rural site, while *C. orbiculatus* had the highest maximum growth rate in the rural site and in one of the suburban sites. *R. pseudoacacia* had its highest growth rate at the urban site.

Generally there were few significant differences in maximum growth between the various site-habitat combinations. This could be due to the fact that we measured growth in first year seedlings that are still highly dependent on the seed resources. This would also explain the very low values estimated for minimum amount of light required to start growth and the level of light needed to reach half of the maximum growth rate. Still we were able to observe some patterns.

The habitat type within different landscapes altered maximum growth rates for some species. *A. saccharum* and *E. umbellata* tended to have the highest maximum growth rates in interior plots at all landscapes even if these two species highly depended on light to survive. Other species had their highest maximum growth rate at a particular site-habitat combination. For example, *R. pseudoacacia* had significantly higher maximum growth in the edge and middle habitats at the urban site (Figure 3). Thus we might expect it to have a competitive advantage in this location relative to the other site-habitat combinations.

Implications for future forests (integrated assessment)

Human land uses alter the environment in forest patches by decreasing interior habitat, increasing temperature, changing nutrient cycling and patterns of animal abundance. Other than affecting the local environment (e.g., light, soil moisture), very little attention has been given to the potential effect of the surrounding landscape on these forest patches (but see McDonnell et al. 1997, Pickett et al. 2001). And in particular, there is practically no work looking at how the combination of landscape structure and microsite, i.e., habitat, may play a role on tree species recruitment of new individuals. For example, recruitment sites at the edge of a forest may be highly favorable for light demanding species as light levels are usually higher (Whitmore & Brown 1996, Coates 2001), but the degree at which this is a favorable site may also be influenced by the herbivory pressure associated with that particular location. As deer densities tend to be higher in suburban landscapes than in more rural areas or urban centers, seedlings recruitment in edge sites may be jeopardize in suburban forest patches but highly favored in rural and urban areas.

Our results show forest species respond differently to the environments created by anthropogenic land uses. Some species in the study had higher survival at particular locations along the urbanization gradient: *Robinia pseudoacacia* had higher survival in the two suburban sites; *Celastrus orbiculatus* and *E. umbellata* had the highest survival at the urban site; *A.*

rubrum had higher survival in the middle and interior plots of the rural site. These findings suggest that in a scenario where the landscape experiences an expansion of urban areas, species such as *A. rubrum* may lose out to species with higher survival in the more suburban and urban forests. Conversely, with regeneration of forests from agriculture abandonment, species favored by more rural landscapes may increase in abundance. Other species, e.g., *Q. rubra*, whose survival is not significantly impacted by landscape may not experience changes in abundance with increased urbanization (Fig. 2).

These differences in recruitment will shape future forests' structure and function, and consequentially affect the forests' potential to respond to other drivers or change, e.g., global warming, pollution, and/or invasive species. Therefore, forests capacity for carbon sequestration, replenishment of the water table, and soil retention may also be altered not only by the extent and location of future forests but also by the specific composition of their surrounding landscapes.

The results of our integrated performance metric suggest which of our study species may be “winners” at specific points along our urbanization gradient (Fig. 4). The results from the integrated performance show that in the more urban landscapes the invasives, *C. orbiculatus* and *E. umbellata* outperform the majority of native species. However, at the rural site many of the native species had performance that was on par with the invasives.

There are many other environmental variables that affect seedling growth and survival that our study does not take into account: soil type, nutrients, heavy metal pollution, herbivory (large and small mammal, insects), mycorrhizal associations, incidence of soil pathogens, etc. Still we were able to observe and quantify recruitment patterns along a landscape gradient. Our results indicate the need for further studies that focus on the actual mechanisms giving rise to those patterns.

Conclusions

Most forests in eastern North America are being influenced by the human uses of the landscape surrounding them (Riitters et al. 2012). Pristine forests are rapidly disappearing and more and more the only remnant patches of forested vegetation are those embedded in a matrix of highly altered landscapes. However, most of our knowledge about tree species recruitment dynamics comes mainly from studies in intact forests (Canham et al. 1990, LePage et al. 2000, Siemann & Rogers 2003) and from old-field succession dynamics (De Steven 1991ab, Bakker et al. 2004). And, even in this last setting, old-field succession, recruitment studies have mainly focused on the particular conditions taken place at the microsite level, and a landscape perspective is commonly missing.

Human alterations of the landscape affect forest species differently. Expansion of urban areas, abandonment of agricultural land, and restoration of forested land can all have impacts on the environment of adjacent forest patches and the species living in them. The effects of different land uses on the survival and growth of tree species could have a tremendous impact on how forests respond to future stresses such as climate change and species invasions. The ability of forests to provision essential ecosystem services (i.e., water, pollution control, soil retention) and their stability and resilience to disturbances depends on the species composition of these forests (Tillman 1996). Therefore understanding the complex effects of human land use on forests is essential to ensure forests continue to provide these services humans depend upon.

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Table 1. Species list, years planted, growth, and habitat requirements.

Species	Common Name	Code	2010	2011	Growth	Light	Soil
<i>Acer rubrum</i>	Red maple	acru	x	x	Moderately fast	Mid tolerant	Moist
<i>Acer saccharum</i>	Sugar maple	acsa		x	Slow	Very shade tolerant	Moist well drained
<i>Carya glabra</i>	Pignut hickory	cagl	x		Slow	Mid tolerant	Dry tolerant
<i>Celastrus orbiculatus</i>	Oriental bittersweet	ceor	x	x	Rapid	Sun to partial shade	Dry tolerant
<i>Elaeagnus umbellata</i>	Autumn-olive	elum	x	x	Rapid	Sun to partial shade	Dry tolerant
<i>Nyssa sylvatica</i>	Black tupelo	nysy	x	x	Slow	Shade-tolerant	Wet-mesic
<i>Prunus serotina</i>	Black cherry	prse	x		Fast	Mid tolerant	Not wet tolerant
<i>Quercus rubra</i>	Northern red oak	quru	x	x	Moderately fast	Sun to partial shade	Mesic
<i>Quercus velutina</i>	Black oak	quve	x	x	Moderately fast	Shade-intolerant	Dry tolerant
<i>Robinia pseudoacacia</i>	Black locust	rops		x	Fast	Shade-intolerant	Not wet tolerant

Barnes & Wagner 2004, www.na.fs.fed.us/spfo/pubs/silvics-manual

Table 2. Parameter estimates from the Survival analysis, means and standard deviations. Statistically significant differences among the alpha parameters for each landscape type and habitat combination are shown in Fig. 6. Values in bold for the covariates (soil moisture [Y_1], light [Y_2], and planted seedling height [Y_3]) indicate the 95% credible interval around the posterior mean did not include zero. E: edge habitat, M: middle habitat, and I: interior habitat.

		Urban			Sub1			Sub2			Rural			Urban	Sub1	Sub2	Rural	SoilM	Light	Height
		E	M	I	E	M	I	E	M	I	E	M	I							
Parameter		$\alpha_{\text{site.habitat}}$			$\alpha_{\text{site.habitat}}$			$\alpha_{\text{site.habitat}}$			$\alpha_{\text{site.habitat}}$			α_{site}				γ_1	γ_2	γ_3
acru	mean	2.11	3.17	3.84	1.97	2.81	2.98	0.47	3.53	3.07	1.58	5.57	5.77	3.00	2.55	2.31	4.24	-0.04	1.01	1.97
	sd	0.74	0.76	0.86	0.65	0.68	0.68	2.68	0.71	0.71	1.77	1.05	1.22	7.52	6.17	10.80	12.52	0.17	0.66	2.14
acsa	mean	1.18	5.74		1.98	2.41	2.19	2.75	3.91	3.01	3.87	5.42	7.18	15.12	2.19	3.20	5.42	0.54	2.07	0.21
	sd	0.82	1.39		0.61	0.82	0.68	1.99	0.66	0.60	1.32	0.88	1.53	45.16	5.35	8.78	11.03	0.27	0.77	1.47
ceor	mean	5.81	5.36	5.24	2.78	4.19	5.43	4.85	5.20	4.56	4.40	6.21		5.44	4.12	4.85	14.49	1.35	0.93	-1.16
	sd	1.28	0.99	1.04	1.10	1.35	1.43	2.20	0.95	0.87	1.71	1.47		6.29	9.47	8.37	41.07	0.38	1.05	1.93
elum	mean		6.69	8.09	2.92	3.96	4.53		5.45	4.95		7.94	7.60	13.06	3.80	1.35	4.00	-0.10	2.56	8.06
	sd		1.52	1.77	1.04	1.10	1.10		1.11	1.15		1.62	1.96	34.03	7.92	20.39	19.70	0.29	1.07	4.54
nysy	mean	2.59	2.43	2.17	2.15	2.22	2.44	2.42	2.80	2.72	1.70	3.52	3.88	2.39	2.27	2.63	3.01	0.34	0.46	0.48
	sd	0.58	0.53	0.54	0.50	0.54	0.53	1.06	0.49	0.48	0.84	0.54	0.63	4.57	4.18	5.51	8.93	0.15	0.35	0.82
prse	mean				4.02	3.25	3.52	10.73	2.44	3.00	7.31	2.38	0.24		3.59	5.20	3.04	0.20	-1.86	-6.35
	sd				0.93	1.50	1.32	7.30	1.70	1.68	5.24	2.09	2.78		6.06	17.30	16.19	0.27	1.44	6.37
quru	mean	2.93	3.12	2.96	2.59	2.72	2.57	2.72	2.69	2.44	2.18	3.00	2.83	3.01	2.61	2.62	2.68	0.06	-0.12	0.37
	sd	0.57	0.56	0.57	0.56	0.62	0.58	0.93	0.50	0.49	0.84	0.53	0.56	3.58	3.26	5.31	5.84	0.13	0.39	0.76
quve	mean	2.05	2.73	2.18	2.95	2.75	3.13	3.43	2.98	2.85	2.53	3.29	3.77	2.30	2.95	3.06	3.21	0.10	0.21	-0.03
	sd	0.57	0.54	0.52	0.52	0.56	0.57	1.01	0.49	0.48	0.79	0.54	0.64	5.30	4.24	5.26	6.94	0.14	0.40	0.74
rops	mean	2.46	2.27	2.44	4.18	3.91	3.69	3.97	3.88	3.48	2.76	2.87	2.98	2.37	3.90	3.76	2.87	0.10	-0.71	0.70
	sd	0.75	0.59	0.63	0.67	0.70	0.67	0.92	0.58	0.56	0.74	0.56	0.61	4.12	4.43	5.46	4.05	0.22	0.53	0.64

Table 3. Parameter estimates from the growth model, posterior means and standard deviations. Statistically significant differences among the α parameters for each landscape type and habitat combination are shown in Fig. 9. Values in bold for the covariates (β_2 , and Y_2) indicate the 95% credible interval around the posterior mean did not include zero.

		Urban			Sub1			Sub2			Rural						
		E	M	I	E	M	I	E	M	I	E	M	I	$\beta_1: I_o$	$\beta_2: \text{Height}$	$Y_1: \theta$	$Y_2: \text{SoilM}$
Parameter		α															
acsa	mean	3.27	5.69	4.82	3.58	5.04	5.26		3.91	4.01	3.91	5.55	5.65	0.0004	0.0182	0.8310	-0.9860
	sd	0.40	0.27	0.27	0.38	0.27	0.21		0.45	0.39	0.25	0.23	0.17	0.0011	0.0068	0.0855	0.1138
cagl	mean							3.03	4.45	3.73	3.50	4.40	4.68	0.0007	0.0171	0.5226	-0.7381
	sd							0.27	0.65	0.69	0.37	0.70	0.82	0.0037	0.0147	0.2512	0.2243
ceor	mean	3.22	3.32		3.71		4.85	3.93			2.90	2.93	4.84	0.0000	0.0335	0.4594	-0.2006
	sd	0.31	0.51		0.40		0.50	0.41			0.46	0.52	0.44	0.0001	0.0108	0.0448	0.0017
elum	mean	4.10	4.91	4.96	3.78	4.27	3.94	4.19	4.80	4.69	3.76	4.84	5.28	0.0002	0.0113	0.8475	-0.2849
	sd	0.19	0.22	0.20	0.15	0.37	0.43	0.19	0.21	0.22	0.15	0.16	0.19	0.0005	0.0078	0.0670	0.0529
nysy	mean				3.13		5.05	2.63			4.51		4.90	0.0010	0.0872	0.8140	-2.3960
	sd				0.38		0.61	0.58			0.86		0.40	0.0017	0.1223	0.0843	0.0752
prse	mean							2.96	1.95			2.22		0.0094	-0.0248	0.0207	-0.4486
	sd							0.46	0.30			0.36		0.0172	0.0385	0.0277	0.2591
quve	mean	2.57	3.64				3.89	3.35		3.22		4.74	4.40	0.0011	0.0133	0.2483	-0.1638
	sd	0.63	0.52				0.44	0.31		0.30		0.40	0.29	0.0031	0.0145	0.0645	0.1028
rops	mean	4.19	4.45	2.81	2.81		3.07	2.66	2.53	3.35	2.52	3.74	3.60	0.0003	-0.0063	0.0536	-0.1137
	sd	0.21	0.27	0.30	0.24		0.35	0.40	0.37	0.31	0.42	0.40	0.25	0.0007	0.0157	0.0083	0.0090

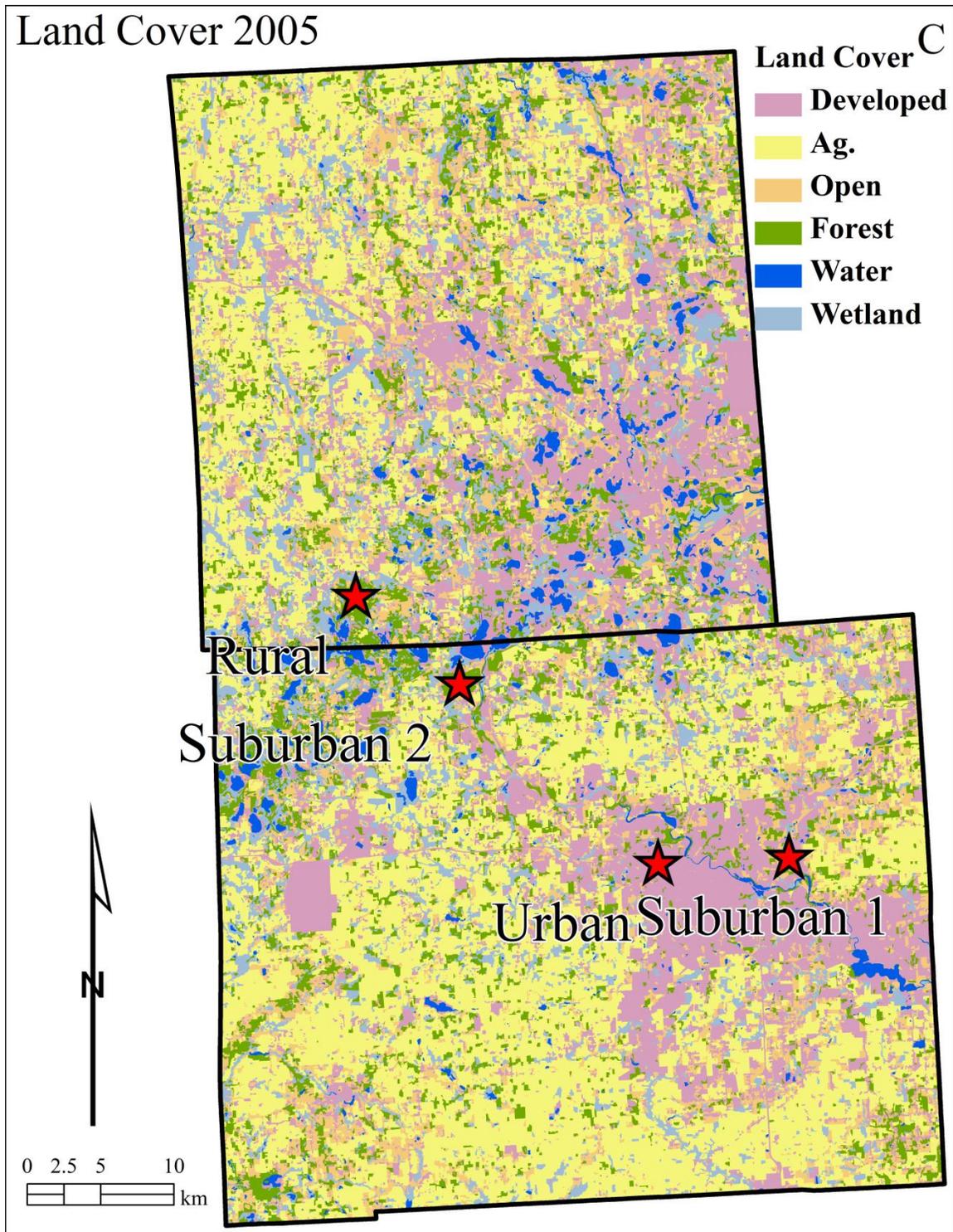


Figure 1. Forest fragmentation and land use in Washtenaw and Livingston Counties, South East Michigan. The extent of pre-settlement forest (A) has been greatly reduced to produce today's fragmented network of forest patches (B). Presently forests exist within a matrix of other land uses (C) adding to the environmental from pre-settlement conditions. Study sites along of the urban-rural gradient are indicated with a star (C).

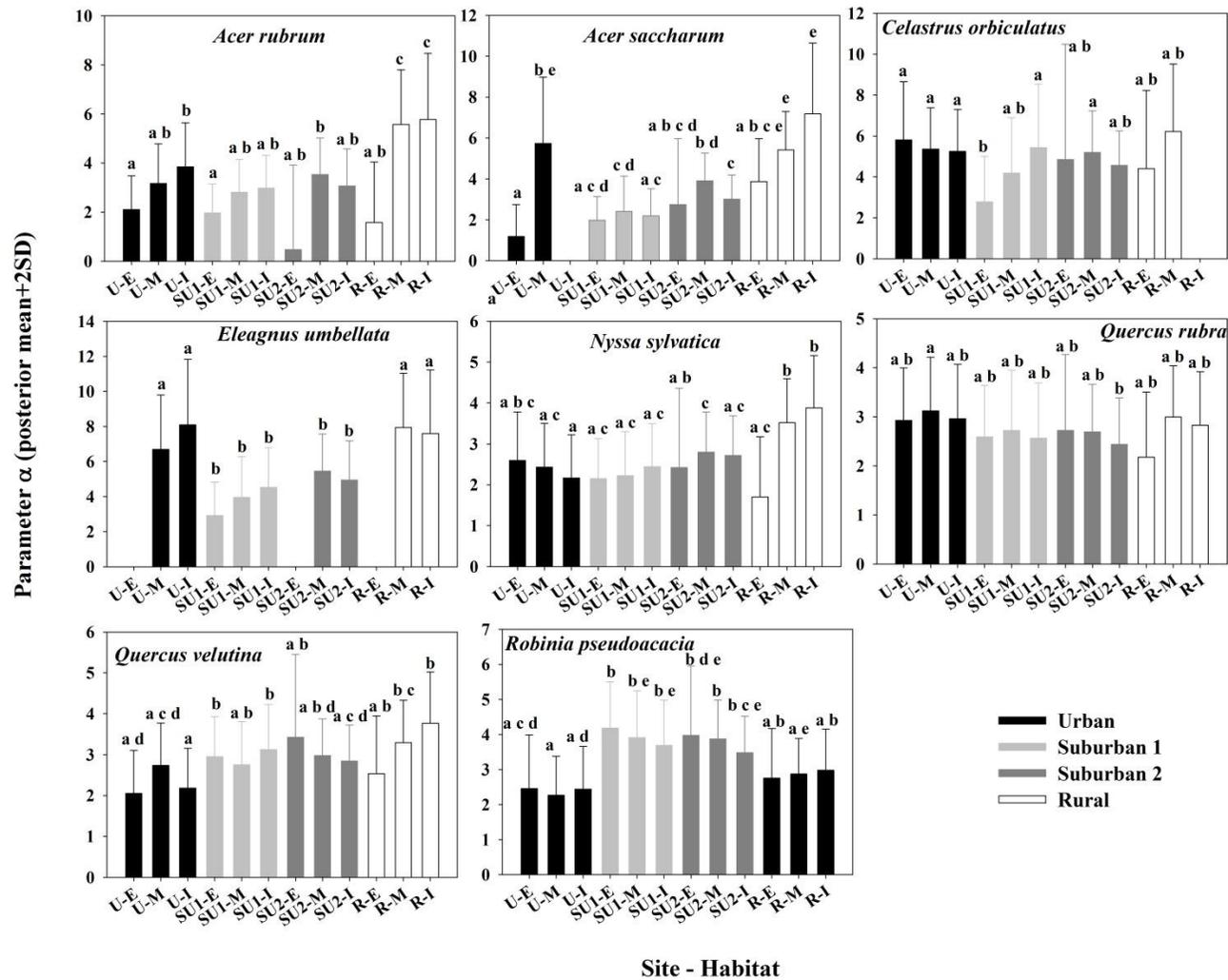


Figure 2. Posterior means (+2sd) for the parameters $\alpha_{\text{site,habitat}}$, indicating the effect that each landscape type and habitat combination had in seedling survival. Letters indicate statistically significant differences among the different landscape habitat combinations. Landscapes U: urban, SU1: suburban 1, SU2: suburban 2, R: rural. Habitats E: edge, M: middle, I: interior.

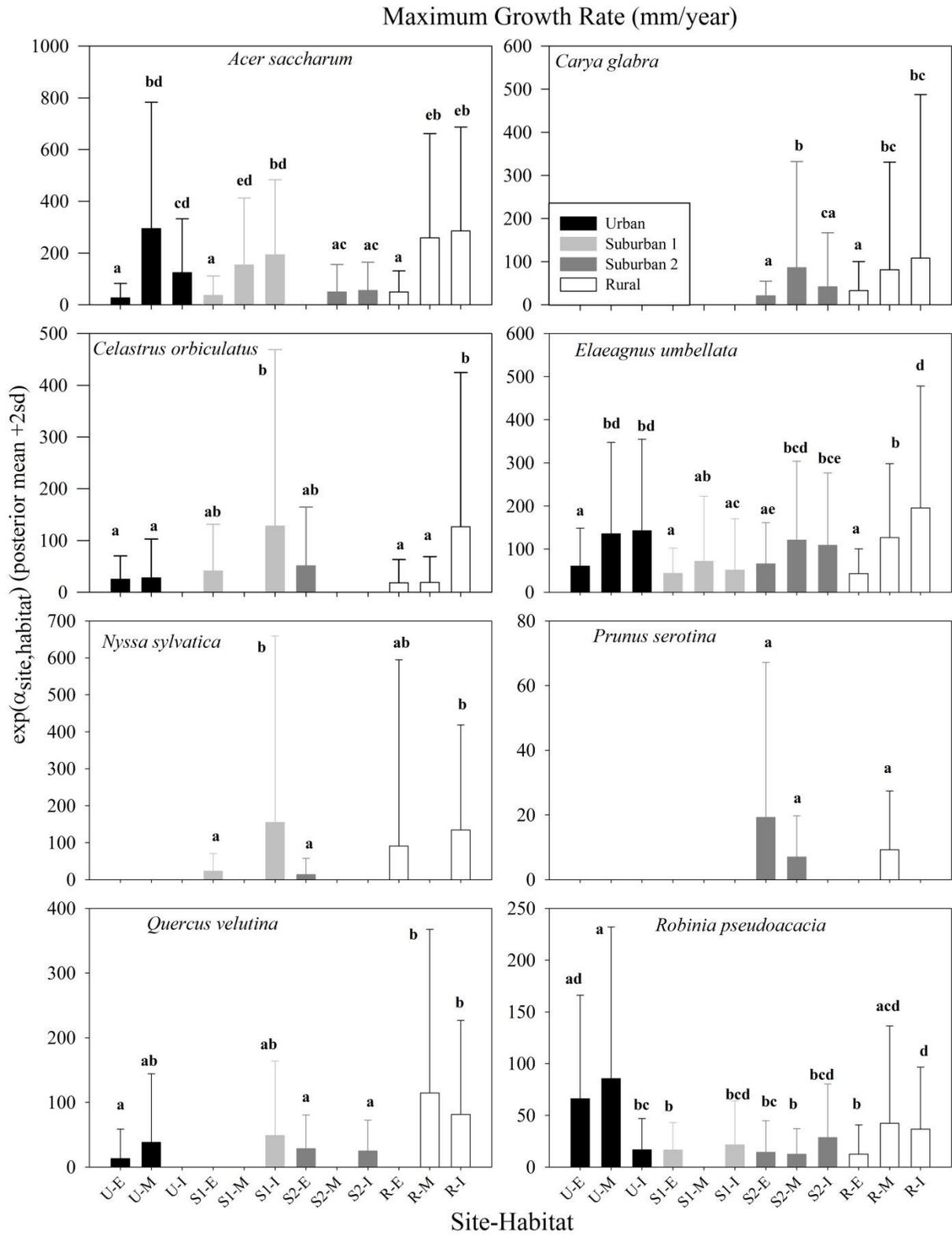


Figure 3. Impact of site-habitat combination on maximum growth rate (mm/summer). Posterior means and +2sd). Landscape type U: urban, Sub1: suburban 1, Sub2: suburban 2, R: rural.

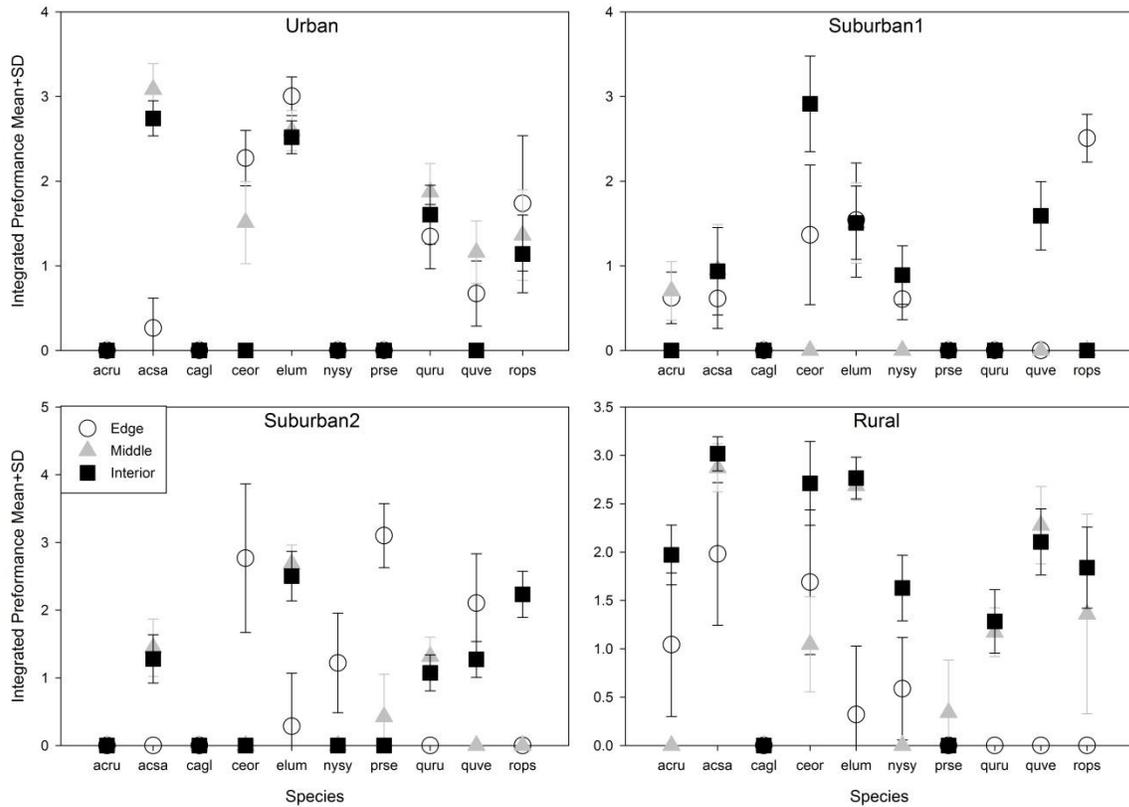


Figure 4. Integrated performance (mean+sd) for the studied species at each landscape type and habitat combination. Integrated performance was estimated as the product of predicted survival under average light and soil moisture conditions and predicted maximum annual growth.