

Community control on growth and survival of an exotic shrub

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Abstract A top priority in the field of invasion ecology is to investigate the mechanisms that lead to the successful establishment and spread of harmful exotic species. Studying plant invasions in the context of the invaded community can help us to understand those mechanisms. In this study, we follow a community approach where we describe establishment and growth patterns of an exotic shrub, *Elaeagnus umbellata*, with respect to the local woody plant community. Primarily focusing on a forest ecosystem, we expect light availability to be a driving factor in the recruitment of *E. umbellata* individuals; however, this is not supported for seedling recruitment as light becomes detrimental to survival in conditions exceeding 30 % full sun. Instead, growth of first year seedlings is primarily affected by soil

moisture. Forest census data of adult individuals show that growth of *E. umbellata* is affected by light and small-scale neighborhood density (i.e., limited in the understory by space or resources), suggesting a shift in resource requirement. Overall, our study indicates that although *E. umbellata* individuals are likely to recruit and persist in the understory, successful growth to adulthood is controlled by competitive interactions.

Keywords Temperate forest community · Empirical modeling · Transplant experiment · Light competition · Biotic resistance · Bayesian analysis

Introduction

The threat of invasive species to native ecosystems has been well documented along continental scales (e.g., Vitousek et al. 1996; Pimentel et al. 2000; Sakai et al. 2001); however, regional and local impacts are nearly impossible to predict from generalizations of current broad-scale invasions (Pyšek and Richardson 2007). Previous studies have attempted to link invasion mechanisms to generalizations of community susceptibility or have identified particularly invasive traits associated with the successful introduction, establishment (e.g., Rejmánek and Richardson 1996; Shea and Chesson 2002), and spread of the exotic species (e.g., Theoharides and Dukes 2007).

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The vast majority of these studies use multispecies datasets to compare invasive species with other invasive species or to compare invasive species with closely related non-invasive exotics or native species (Pyšek and Richardson 2007; Diez et al. 2009). Other studies have considered the richness and functional diversity of the target community in relation to the potential invasion (e.g., Pokorný et al. 2005; Fargione and Tilman 2005; Mwangi et al. 2007). But, few studies of invasive species have taken a community-level approach to explore species interactions and related impacts, especially considering plant traits (e.g., Callaway et al. 2012; Preston et al. 2012). To this end, we posit that a community-level analysis will better characterize invasion events, as they assess the competitive ability of the exotic species in relation to the invaded communities, and may be useful when predicting potential establishment and spread. In this study, we investigate the circumstances that lead to the invasion of a woody plant community by an exotic shrub with the purpose of identifying habitat requirements and biotic interactions that led to the invasion.

As recruitment and growth of exotic species are dependent on favorable abiotic and biotic conditions, the observed distribution of an invasive species reflects both dispersal and establishment processes. Once a species becomes widely introduced into an area, availability of propagules may not limit establishment. At that point, the invasion pattern of a prolific disperser will be a reflection of resource requirements (e.g., light, water, nutrients) and of biotic resistance of the invaded community (e.g., competitive interactions, herbivory pressure, seed predation; Bazzaz 1979; Johnstone 1986; Keddy 1992; Shea and Chesson 2002). Thus, to better assess an invasion event, we should pursue our study within a community context that accounts for both the abiotic and biotic barriers (e.g., Richardson and Bond 1991; Naeem et al. 2000; Martin and Marks 2006).

This research seeks to characterize the local distribution of an exotic species as it relates to environmental factors and the interactions with the native woody plant community being invaded. The specific questions we aim to answer are: (1) What are the abiotic factors determining recruitment patterns of *Elaeagnus umbellata*? (2) How does the spatial structure of the local woody plant community affect the establishment of this species? and (3) How does

the relative performance of this species compare with respect to the native plant community along environmental gradients? *E. umbellata* is widely introduced to the areas surrounding our study site in central Michigan (e.g., EddMaps 2014). With establishment not limited by propagule dispersal, looking at patterns of seedling survival and growth will inform us of the abiotic filters affecting the spread of the invasive, while looking at its adult performance with respect to the local community will point at the biotic constraints controlling its spread. With information regarding establishment and growth within the context of the invaded community and as a function of environmental conditions, our work provides valuable insight into the mechanisms promoting the establishment and growth of this exotic species.

Methods

A seedling transplant experiment was carried out to assess what environmental factors influence the establishment of *E. umbellata*. To complement the work on recruitment, data from a forest census were used to estimate growth rates of the exotic species and compare them to the most common species of the woody plant community.

Target species description

Elaeagnus umbellata Thunb. (autumn-olive) is a shrub native to the sub-Himalayan regions of northern Pakistan, as well as China, India, Japan, and Korea (Ahmad et al. 2006). It was first introduced to the US as a horticultural species from Japan in 1830 (Black et al. 2005) and was widely used as wildlife cover and forage in the 1960s as part of the restoration of disturbed habitats for its ability to colonize marginal land (Ebinger 1983). *E. umbellata* was later considered for use as a potential agricultural crop species for its edible and lycopene-rich fruit (Black et al. 2005). In its native range it is considered shade-intolerant, occurring primarily in open habitat (Ahmad et al. 2006); however, within its invaded range, *E. umbellata* has been observed in both edge and interior conditions (Yates et al. 2004; Orr et al. 2005), and sometimes in monotypic stands (Catling et al. 1997). *E. umbellata* is widely established along roads, open spaces and forests edges in the eastern

United States. It tolerates a large variation of pH (4–8) and soil moisture availability ranging from drought to swampy conditions (Ahmad et al. 2006). It may synthesize allelopathic chemicals (Orr et al. 2005) and exhibits a symbiotic relationship with nitrogen fixing bacteria (Pashke et al. 1989). Seeds are contained in nutrient rich fruits, which are dispersed by birds (LaFleur et al. 2007). All these characteristics make it a successful invader in open to semi-open habitats, but suggest it might be poorly adapted to forest interiors with low light conditions (Catling et al. 1997; Edgin and Ebinger 2001).

Study site

This research was conducted at the University of Michigan's E.S. George Reserve in Livingston County, MI (42°27'24.36"N, 84°00'40.03"W). The 525-ha reserve allows researchers to establish sites among environmental gradients given by varying slopes (7.33–52.51 %) and aspects (22.9°–179°, 180°–346°). The forest community explored in this study is a mid- to late-successional forest dominated by oak (*Quercus velutina*) and hickories (*Carya glabra* and *C. ovata*) following a grazing land-use history. Maples (*Acer rubrum*) and cherry (*Prunus serotina*) are moving into the canopy due to current fire suppression. *E. umbellata* was first observed at the study site in the early 1980s (Francis Evans, pers. comm.; Earl Werner, pers. comm.). Although most problematic in semi-open habitats, it is now prolific not only in the open grasslands, but also along the roads, forest edge, and understory habitats at the study site.

Transplant experiment

Experimental set up

In order to study the recruitment of *E. umbellata* seedlings under a variety of environmental conditions, we conducted a transplant experiment at two sites (elevations: 275, 300 m) that mainly differ in their soil water content given their topographic characteristics and soil structure. Percent soil moisture ranged from 8 to 73 %, where lower sites were significantly drier than upper sites (26.21 ± 9.56 vs. 32.46 ± 13.34 %; *t* test, $p < 0.001$). The low elevation sites were located on a local prominence (high point) and also had coarser soils (i.e., more sand) than

the high elevation site, which was located at mid-slope of a small hill. Lower sites were characterized by having sand to sandy loam texture while upper sites were characterized by sandy loam and sandy loam textures over clay (Greiling 2000). At each site we established two 100 m long transects that covered the transition from canopy openings to forest understory including edge habitat. Within each transect six $1 \text{ m} \times 15 \text{ m}$ plots were set up perpendicular to the transect at 20 m intervals (0, 20, 40, 60, 80, 100 m; Fig. 1). At each plot six points, separated by 3 m, were flagged for the seedling transplants (a total of 144 experimental points were established, 2 sites \times 2 transects \times 6 plots \times 6 points).

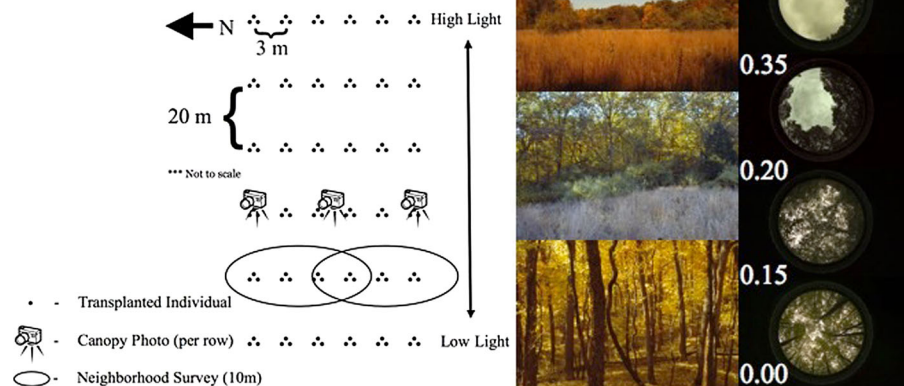
Seedling transplants

Seeds of *E. umbellata* were collected from natural populations in the previous fruiting season, fall 2009, from nearby areas. To break dormancy, seeds were scarified and stratified for 71 days, and then planted in a medium sized plastic container filled to about 25 cm depth of potting soil and perlite. Seedlings were watered daily. After being allowed to grow for 7 weeks, seedlings were removed from the potting soil and individually placed in a plastic bag for transport to the study site. A mark was placed on the stem at the former soil level and measured from this point to the base of the terminal bud. Three individuals were planted at each point along the plots removing any groundcover for ~ 10 cm surrounding planting site (April 2009). In the event of large neighbors, the point was shifted as needed to allow for 10 cm clearance. A total of 432 seedlings were planted (144 experimental points \times 3 seedlings). Seedlings were monitored approximately every 3 weeks throughout the summer and recorded for time of death. At the completion of the experiment (130 days; August 2009), all remaining seedlings (216) were extracted from the ground, separated into leaves, roots, and stems and weighed for dry biomass after at least a 72-h air dry at 60 °C.

Environmental data

Light availability was quantified along the established transects using canopy photos (Anderson 1964). Photographs were taken using a digital camera (Sigma SD 14) with a 4.5-mm fisheye lens (Sigma EX DC HSM) placed on a tripod 1 m above ground

Fig. 1 Site map describing the layout of transects in the transplant experiment with site photographs and canopy photos arranged according to light availability (*I* full sun, *O* no sun)



level. Three photographs were taken for each plot at three points (the two ends and the middle). The photographs were analyzed with a computer program (HemiView v2.1, Delta-T Devices) outputting percent visible sky, a measure of direct and indirect radiation reaching the forest floor as a fraction of total available light with values between 0 (no sun) and 1 (full sun; Fig. 1). Individuals at points where the photos were taken (ends and middle of the plot) were given the direct value of the canopy measurement, while the individuals from in between two overlapping photos (taken 6 m apart) were given the average of those canopy measurements. Moisture data (volumetric%) were gathered twice throughout the summer, after a major rain event and after an extended drought, using a soil moisture probe (Aquaterr M-300). At each of the 144 experimental points, the probe was placed approximately 10 cm into the ground in the middle of the three planted seedlings. The value was recorded after equilibrium was reached. Time between measurements was limited to the early afternoon on a single day in order to reduce differences in soil moisture from sampling. Analysis uses the average of the two moisture readings at each point.

Analysis of transplant data

Environmental data were combined with seedling census and harvest data to analyze establishment performance (i.e., survival and growth during the first growing season) as a function of the environmental conditions under which the seedlings grew. The final best-fit models are discussed below, but multiple submodels were tested (see Supplemental Information,

Tables S1–S3). A Bayesian approach (i.e., parameters were estimated from distributions) was used in order to account for the uncertainty in the different components of the models, data, process and variables (Gelman et al. 1995; Clark 2005).

To analyze survival data we followed the Cox proportional hazards model (Cox 1972), which permitted us to deal with censored data (some seedlings were still alive at the end of the experiment). To avoid including seedlings that died due to transplant shock we only used survival data for those seedlings that survived at least to the first week after transplant. We then estimated the associated parameters within a Bayesian framework to allow for higher flexibility in the risk function (Congdon 2003). The time of death (census at which the seedling was found dead, D) for each individual i , was estimated from a Weibull distribution, with shape parameter r and scale μ .

Likelihood: $D_i \sim \text{Weibull}(r, \mu_i)$

Process model: $\mu_i = \alpha_0 + \alpha_1 W_i + \alpha_2 L_i + \varepsilon$

The risk, μ , was estimated as a combination of fixed effects (α_*) of environmental variables that may have contributed to survival (W : point average soil moisture, L : light level), and of individual random effects, ε . Estimates of the effect from light, α_2 , were binned along the range of light values at approximately 0.025 intervals to determine if the effect of light is consistent among all habitat conditions (i.e., increasing light may have a beneficial effect at low light levels, but a detrimental effect at high light levels). Environmental data were standardized to optimize convergence of the parameters and allow for comparison of parameter values. In addition, all parameter values were multiplied

by -1 following analysis in order to report effect on survival from a model that estimates the effect on mortality. Fixed effect coefficients (α_*) were estimated from distributions with uninformative prior values: $\alpha_* \sim \text{Normal}(0, 10,000)$, the random effects from $\varepsilon \sim \text{Normal}(0, \sigma^2)$ and $\sigma^2 \sim \text{Gamma}(0.01, 0.01)$, and the intrinsic rate of mortality, or hazard, $r \sim \exp(0.001)$. Uninformative priors were chosen to ensure posterior distributions would reflect only the data.

Harvested dry mass (M) for each individual i was estimated from a lognormal distribution (to ensure positive values), with mean η and variance σ^2 :

$$\begin{aligned} \text{Likelihood: } & M_i \sim \log\text{Normal}(\eta_i, \sigma^2) \\ \text{Process model: } & \eta_i = \beta_0 + \beta_1 H_i + \beta_2 W_i + \beta_3 L_i \end{aligned}$$

The parameter η was then estimated as a combination of fixed effects (β_*) associated to measured variables that may have contributed to the final biomass (H : initial seedling height, W : point average soil moisture, L : light level). Covariates and environmental data were standardized to optimize convergence of the parameters and allow for comparison of parameter values. Fixed effect coefficients (β_*) were estimated from a normal distribution with uninformative prior parameter values: $\beta_* \sim \text{Normal}(0, 10,000)$, and the variance, σ^2 , was estimated as $\sigma^2 \sim \text{Gamma}(0.01, 0.01)$.

Models were run for at least 50,000 iterations in OpenBUGS to ensure convergence and then run for an additional 30,000 iterations to estimate parameter (α , β ,

r , and σ^2) posterior mean values and variances (Lunn et al. 2009). Above-ground biomass and biomass of roots were analyzed independently with similar models (see Supplemental Information, Table S3).

Forest census

Census data

The forest census data were collected for ~15,000 individuals, in an area that covers 12 ha of transition forest currently dominated by oak, maple, and hickory (Allen et al. 2009). All woody plants with circumference >10 cm at breast height were mapped, identified, tagged, circumference measured, and tracked. The baseline survey in 2003 and the first follow-up in 2008 were included in this analysis.

Species analyzed

The forest census includes 32 species of which 15 species were included in the final analysis. Only species with a sample size (N) of >30 individuals were used to ensure sufficient data to discriminate environmental and biotic effects. The analyzed species were categorized into two functional groups, understory shrubs and canopy trees (Table 1). Within the understory group we focused on three focal species, the exotic shrub and two native species

Table 1 Species included in the final forest census analysis. Sample size, functional group and description of light requirements are listed (Barnes and Wagner 2004)

Species	N	Group	Description
<i>Elaeagnus umbellata</i>	50	Understory	Shade-intolerant invasive shrub
<i>Sassafras albidum</i>	128	Understory	Shade-intolerant native tree × shade-tolerant as seedling
<i>Hamamelis virginiana</i>	77	Understory	Shade-tolerant native shrub
<i>Amelanchier arborea</i>	914	Understory	Shade-tolerant native tree
<i>Cornus florida</i>	62	Understory	Shade-tolerant native tree
<i>Ostrya virginiana</i>	3,403	Understory	Shade-tolerant native tree
<i>Acer rubrum</i>	86	Canopy	Shade-moderate native tree
<i>Carya glabra</i>	622	Canopy	Shade-moderate native tree
<i>Carya ovata</i>	533	Canopy	Shade-moderate native tree
<i>Fagus grandifolia</i>	300	Canopy	Shade-tolerant native tree
<i>Prunus serotina</i>	3,649	Canopy	Shade-intolerant native tree × shade-tolerant as juvenile
<i>Quercus alba</i>	1,677	Canopy	Shade-moderate native tree
<i>Quercus velutina</i>	431	Canopy	Shade-moderate native tree
<i>Tilia americana</i>	379	Canopy	Shade-tolerant native tree
<i>Ulmus americana</i>	209	Canopy	Shade-moderate native tree

closest to *E. umbellata* in their functional role in the community, *Sassafras albidum* and *Hamamelis virginiana*. Although the native species are not nitrogen fixers, they are the most common understory woody plant species in the community and co-occur at similar sizes to *E. umbellata*. *S. albidum* is a native shade-intolerant tree with similar leaf functional traits to *E. umbellata* (Brym et al. 2011). *H. virginiana* is a native shade-tolerant shrub that is perhaps the most direct competitor with *E. umbellata* in the understory as it is the only understory woody species at a canopy height similar to our target species.

The relative growth rate (G) for each individual i of a given species was established as growth in circumference at breast height (g = trunk girth 2008 – trunk girth 2003) standardized by the initial size (I = trunk girth 2003; $G = g/I$). Due to potential error within circumference measurements and the power-law relationship with biomass (Hunt 1982), we did not convert circumference to biomass as we expected this calculation would introduce undue error into the evaluation of the model. As circumference can be directly related to biomass (Enquist et al. 1998), we assert this growth in circumference can be used as an indicator of individual success (when compared among all species) and therefore reflects the response to the surrounding environment, abiotic and biotic. Individuals whose relative growth rate was ≤ 0 were excluded from the final analysis as these estimated rates are likely due to measurement error.

Neighborhood density (B_{Ri}) was calculated from the spatially explicit data as total basal area of neighboring stems >1 cm dbh within a maximum distance. Large-scale neighborhood densities were calculated with a radius of 10 m (B_{10}) and small-scale neighborhood densities were calculated with a radius of 1 m (B_1).

Environmental data

Slope (S), aspect (A), and elevation (E) layers developed by Severtson (2005) and the Livingston County Soils data (SEMCOG 2010) were evaluated with the Spatial Analyst Tool in ArcMap to characterize the study area (ESRI 2010). We matched the location of each individual with the environmental variables using layering of GIS data. Soil type (Boyer series) across the site did not vary greatly with relation to the biologically significant O and A horizons (Engberg and Austin 1974). Aspect, in

degrees, was transformed to values of -1 (north) to 1 (south) to reflect the effect aspect has on light availability and therefore growth of tree species. Light availability (ψ_{Li}) was modeled as a function of the large-scale neighborhood density (B_{10}) using the relationship between the light data collected in the transplant experiment and corresponding neighborhood density in a 10 m radius surrounding each point photos were taken [$\psi_{Li} = -0.1631 \times \ln(B_{10i}) + 1.7032$; $r^2 = 0.73$; see Supplemental Information, Fig. S1]. Light values were additionally estimated using a normal distribution: $Z_i \sim \text{Normal}(\psi_{Li}, 0.1)$.

Analysis of forest census growth data

We combined environmental variables established from GIS databases and neighborhood densities calculated from the forest census data into an empirical model that estimated relative growth rate, G , of selected woody plant species. The final best-fit model is discussed below, but multiple submodels were tested (see Supplemental Information, Table S4, S5). A Bayesian approach was used again in order to specify uncertainty in components of the model and its predictions (Gelman et al. 1995; Clark 2005).

Relative growth rate (G) was estimated as a function of a number of environmental (γ) and biotic (λ) variables, as well as initial size (ϕ). We used a lognormal distribution for the likelihood as growth is a continuous positive variable, for each individual i of a given species. Species were analyzed independently as:

$$\text{Likelihood: } G_i \sim \log\text{Normal}(\chi_i, \sigma^2)$$

$$\text{Process model: } \chi_i = \gamma_1 + \gamma_2 S_i + \gamma_3 A_i + \gamma_4 Z_i + \lambda B_{1i} + \phi I_i$$

γ_1 is the species specific intercept value within the model; S accounts for the slope of the terrain and we used it as proxy for water available in the soil (higher in flat areas, lower at steep slopes); A is the transformed aspect, a proxy for solar radiation throughout the day, this would affect both soil moisture and light levels; Z represents light availability as a function of neighborhood density (B_{10}); B_1 represents additional effects of neighborhood density on individual i at a 1 m radius, a metric for the crowding or competition from the closest surrounding individuals (e.g., moisture, nutrients, space); and I represents the initial size of the individual. Although growth rate is standardized for

size, accounting for initial size is still important as it may determine the plants position in the canopy and therefore the light available to the individual. Data were standardized to optimize convergence of the parameters and allow for comparison of parameter values.

The parameters were estimated from distributions with uninformative parameter values: γ_* , λ , and $\varphi \sim \text{Normal}(0, 10,000)$, $\sigma^2 \sim \text{Gamma}(0.01, 0.01)$. Models were run for at least 30,000 iterations in OpenBUGS to ensure convergence and then run for an additional 20,000 iterations to estimate posterior mean parameter values (Lunn et al. 2009). Following the estimation of mean coefficients, growth predictions were generated for each species along a gradient of light availability maintaining all the other variables constant at their mean value.

Results

Transplant experiment

Survival

Results from our best-fitted model indicate that survival decreases over the growing season (r 's

95 %CI 1.35–1.62). For all transplant individuals surviving after the first week, effect of moisture on survival was non-significant (Table 2). Total light fraction, which varied from 0.06 to 0.78 across sites, had a statistically significant negative effect on survival only after 0.30 fraction of full sun and had no effect at low light levels.

Growth

For the growth model, results were similar for total biomass, aboveground biomass, and root biomass. Soil moisture and initial seedling height had a significantly positive effect on total seedling biomass at harvest. Light did not have a strong effect on seedling growth (Table 3).

Additional findings

In our study light was not correlated with moisture ($R^2 = 0.006$). No relationship was found between presence of naturally occurring *E. umbellata* seedlings and light availability ($R^2 = 0.023$). The highest density of naturally recruited *E. umbellata* seedlings was observed in a closed canopy (0.13 total light fraction), and *E. umbellata* seedlings were still observed with as little light as 0.06 full sun.

Table 2 Results of the best-fit survival data model for individuals in the transplant experiment

Parameter	Range	N	Mean estimate (SD)	95 % CI
α_0 : Intercept		408	7.029 (0.428)	6.197, 7.787
α_1 : Moisture		408	−0.228 (0.115)	−0.456, 0.002
α_2 : Light	0.000–0.075	12	−0.362 (0.889)	−2.125, 1.377
	0.076–0.100	35	0.364 (0.856)	−1.309, 2.121
	0.101–0.125	67	0.419 (0.954)	−1.375, 2.400
	0.126–0.150	54	0.656 (1.271)	−1.735, 3.267
	0.151–0.175	101	1.937 (2.038)	−1.862, 6.235
	0.176–0.200	57	4.281 (3.304)	−2.164, 11.090
	0.201–0.300	16	1.753 (2.478)	−2.864, 6.928
	0.301–0.500	17	−1.271 (0.550)	−2.374, −0.186
	0.501–1.000	41	−0.620 (0.202)	−1.031, −0.231
r : Shape parameter		408	1.489 (0.709)	1.351, 1.620
σ^2 : Variance		408	379.9 (409.3)	33.23, 1,410.0

Parameter values indicate effects on survival. Bold values indicate that the 95 % credible interval did not include zero and are considered statistically significant

Table 3 Results of the best-fit model explaining growth of total dry biomass for the transplant experiment

Parameter	Mean estimate (SD)	95 % CI
β_0 : Intercept	1.4100 (0.407)	0.628–2.164
β_1 : Initial size	0.0118 (0.004)	0.004–0.019
β_2 : Moisture	0.0424 (0.009)	0.027–0.063
β_3 : Light	0.0953 (0.505)	–0.895 to 1.089
σ^2 : Variance	3.326 (0.323)	2.724–3.985

Bold values indicate that the 95 % credible interval did not include zero and are considered statistically significant

Relative growth analyses from the forest census

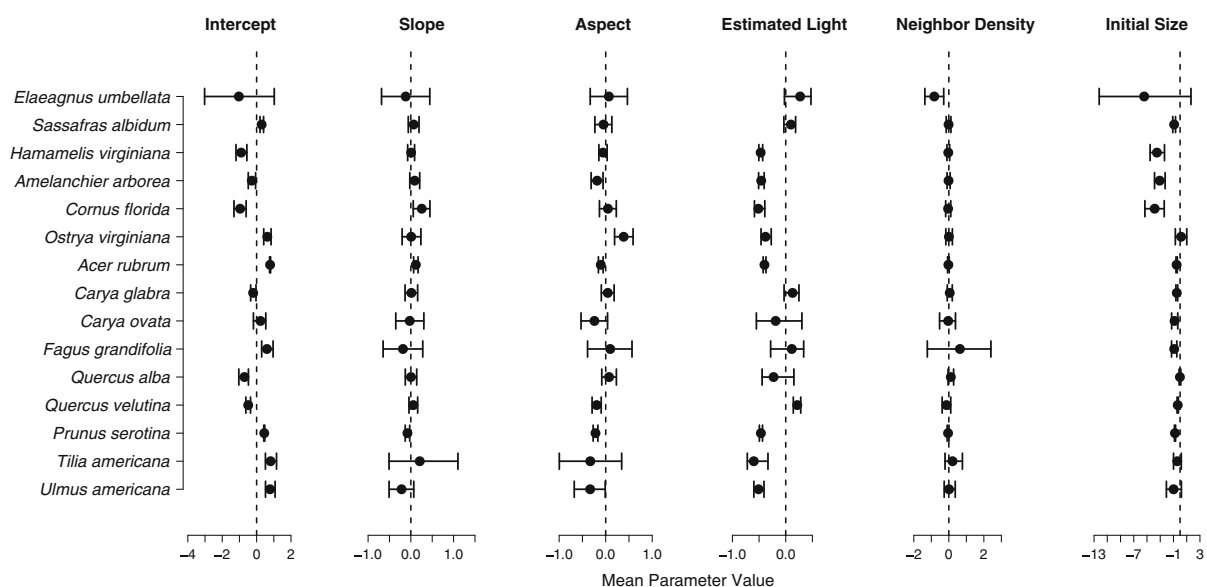
Model results varied among species, but showed patterns among functional groups. The model fit between predicted and observed growth rates (R^2) ranged from 0.303 to 0.986 with an average of 0.737 (see Supplemental Information, Fig. S2). For all species, the environmental parameters slope and aspect, did not have a significant effect on relative growth (Fig. 2). The effects of light, estimated from large-scale neighborhood density, on growth were positive but not significant (higher growth in open spaces) for *E. umbellata* and *S. albidum*, but was significantly negative for *H. virginiana* and all remaining understory species (lower growth in open

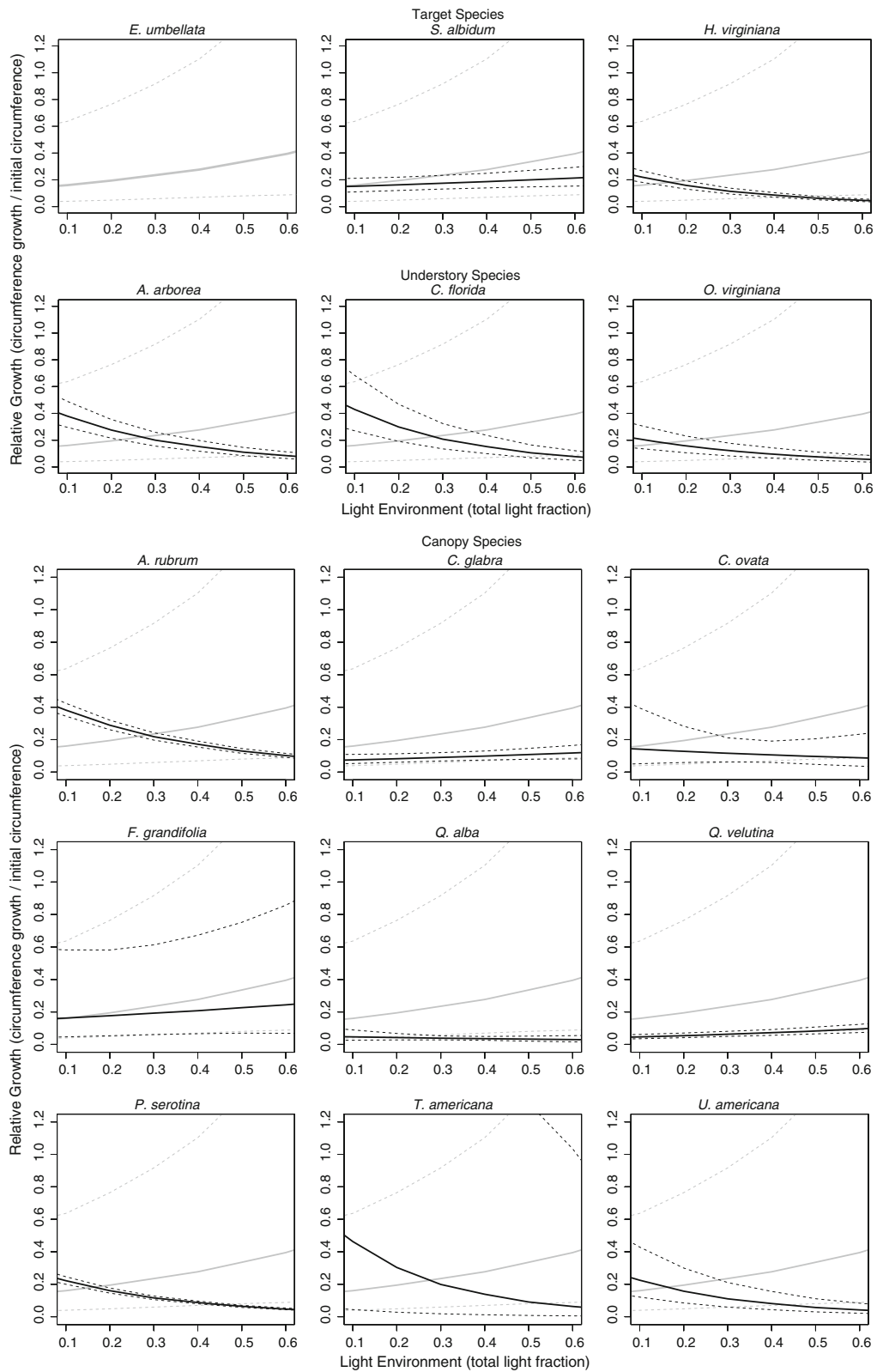
Fig. 3 Predictions [means (solid lines) and 95 % predicted intervals (dashed lines)] of relative growth rate over a gradient of light availability for all species. Native species (black lines) are organized by functional group. *E. umbellata* is shown in grey for reference

spaces, Fig. 2). The target exotic species, *E. umbellata*, experienced the only significant negative effect from small-scale neighborhood density on growth (lower growth at higher densities; Fig. 2). The focal native understory species, *S. albidum* and *H. virginiana*, show a significant negative effect from initial size (bigger individuals had lower growth; Fig. 2); however, *E. umbellata* has a mean coefficient value that is much lower than the native species but shows a larger credible interval, which suggests a more variable response on relative growth along individual sizes. In general a high variation in fixed-effect parameter values was observed for *E. umbellata*, while native species showed much less intra-species variability.

Predicted growth along the light gradient

Predicted growth rate for *E. umbellata* was higher than those of the native species at high light levels (although 95 % CIs did overlap, Fig. 3). This occurred for all of the understory species and for

**Fig. 2** Posterior mean fixed effect coefficient values and 95 % credible intervals of all analyzed species for the effect of slope (γ_2), aspect (γ_3), light (γ_4), small-scale neighborhood density (β), and initial size (λ) on growth



four of nine canopy species (Fig. 3). This model predicts that *E. umbellata* has a higher competitive ability than all native species as described by comparing standardized growth at roughly 0.30 total light fraction (Fig. 3). When considering the focal species, *E. umbellata* showed a higher variation in predicted growth rates than both *S. albidum* and *H. virginiana* (Fig. 3). Still, the invasive species had a larger increase (steeper slope) in growth rate with increased light than *S. albidum*, while *H. virginiana* had a negative slope (Fig. 3).

Summary of species associations

As part of the neighborhood density (B_R) calculation, species associations with *E. umbellata* were summarized as the percent of individuals in a species that contained at least one *E. umbellata* individual within the target radius (Table 4). We observe a lack of *E. umbellata* in close proximity to the native species included in this study. Data suggests that *E. umbellata* is often much closer to conspecific individuals than it is to any other species. The species that most commonly appear in the neighborhood of *E. umbellata* are *E. umbellata*, *Amelanchier arborea*, and *Q. velutina*. Of all *E. umbellata* individuals 77.9 % occur within 10 m of another *E. umbellata* individual, 17.0 % of *A. arborea*, and 16.1 % of *Q. velutina*.

Table 4 Percent of individuals in a species with presence of *E. umbellata* within a given radius

Species	5 m	10 m	20 m
<i>Elaeagnus umbellata</i>	68.8	77.9	93.5
<i>Sassafras albidum</i>	0.2	0.7	4.6
<i>Hamamelis virginiana</i>	0.1	1.1	6.7
<i>Amelanchier arborea</i>	4.7	17.0	35.2
<i>Cornus florida</i>	3.3	5.7	15.0
<i>Ostrya virginiana</i>	0.0	0.0	0.5
<i>Acer rubrum</i>	1.2	5.2	15.3
<i>Carya glabra</i>	0.8	4.0	14.2
<i>Carya ovata</i>	1.2	5.8	20.9
<i>Fagus grandifolia</i>	2.0	2.0	14.0
<i>Prunus serotina</i>	2.2	7.4	20.7
<i>Quercus alba</i>	2.8	9.9	23.6
<i>Quercus velutina</i>	7.2	16.1	30.4
<i>Tilia americana</i>	0.0	0.0	6.5
<i>Ulmus americana</i>	3.1	10.9	23.4

Discussion

Knowing how the combination of abiotic and biotic factors affects the invasion process in the context of a particular community is important for understanding the mechanisms behind the establishment of exotic species and for developing reliable predictions of spread. For our study system, we expected that light availability would determine the seedling growth and survival patterns of *E. umbellata* and that the adult individuals would show more vigorous growth in high light environments, consistent with the characterization of a shade-intolerant shrub. However, this study suggests that establishment of *E. umbellata* is limited by moisture and not light following use of initial seed reserves. Though as an adult, this species' growth rate depends on the neighborhood density, both as it pertains to light availability (large-scale density) and space (small-scale density). Here, we observe a shift in environmental filters acting on the establishment and later performance of the invasive shrub. Because of this potential shift in growing conditions from water requirements to light and space, we believe best management practices would target edge and gap individuals, or likely monotypic stands, where optimal conditions are experienced during both juvenile and adult stages.

Results from the seedling survival and adult growth models suggest that establishment of *E. umbellata* is greatest in intermediate canopy cover, likely due to optimal levels of moisture and light. As an adult, *E. umbellata* has a greater growth rate than native species at approximately 0.30 total light fraction or higher available light, a similar threshold to that suggested by the survival analysis (Fig. 3; Table 2). Interestingly, this light value corresponds with the intermediate canopy cover and edge habitat in the studied forest. Thus, *E. umbellata*'s spread into the understory would be controlled by competition for light and space from the native community, relegating adult growth to disturbed patches like canopy gaps and edge habitats. This supports previous studies that suggest biotic resistance limits but does not repel invasion (Levine et al. 2004; Martin and Marks 2006).

In order to develop predictions for the spread of *E. umbellata* as a result of biotic interactions with the forest community, we estimated growth of all analyzed species from our data along a gradient of

light (“Light Environment”), mimicking the transition of habitat type from shaded forest understory (0.00–0.30 total light fraction; Fig. 3), to open grassland (0.30–1.00), with edge and gap habitat in between (0.20 and 0.40). Within the variation of predicted growth, we observe a divergence in ecological strategy in relation to light availability with respect to the two target native species (Fig. 3). *S. albidum* exhibits characteristics of a shade-intolerant tree, experiencing a steady increase in relative growth rate with increasing light, whereas *H. virginiana* shows a decreased predicted growth rate as light increases (probably due to soil moisture levels that induce water stress in the higher summer temperatures associated with open habitats; e.g., Maroco et al. 2002). *E. umbellata* has higher growth rates than *S. albidum* at all light levels, suggesting it is more competitive with respect to this native shade-intolerant species. With respect to the shade tolerant native species, *H. virginiana*, *E. umbellata* would be outcompeted at low light levels. However, it shows the ability to rapidly respond to higher light availability outcompeting most native species (Fig. 3). The short-term success of *E. umbellata* in the understory may be possible due to the large intra-specific variability in growth. The large variation on relative growth rates show that the invasive shrub can experience a higher relative growth rate than any of the native species at all light levels, providing a mechanism for at least some individuals to temporarily succeed recruiting in the understory (Fig. 2).

In describing the conditions that determine the distribution of *E. umbellata* in our study site, some factors deviated from our initial hypothesis. As might be expected, moisture contributed positively to seedling growth during the first growing season, though light beyond the 0.30 full sun threshold negatively impacted seedling survival contrary to our assertion of *E. umbellata* being a drought tolerant, light demanding species. Contrary to our finding for adult distribution, no relationship was found between presence of naturally occurring *E. umbellata* seedlings and light availability. In fact, the highest density of naturally recruited *E. umbellata* seedlings was observed in a closed canopy and individuals were found with as little light as 0.06. Desiccation in high light conditions may have been the cause of this pattern, but light was not correlated with moisture as might be expected from general landscape scale

environmental gradients. This disconnect may suggest that additional factors were affecting the planted individuals (i.e., surface temperature, soil organic matter, moisture flux). Indeed, soil moisture content may be associated with additional characteristics of the soil, such as nutrient availability; however, previous research suggests that soil nutrient content had limited effect on woody species seedling recruitment during the first growing season among a variety of sites (nearby and similar to our sites) within the reserve (McCarthy-Neumann and Ibáñez 2012). We maintain that soil moisture is a primary driver of seedling recruitment as individuals achieve sufficient growth through seed reserves and nitrogen fixing capabilities in low light conditions congruent with our model findings and the prevalence of desiccation in high light environments (Jonsen and Bongarten 1992; Kennedy et al. 2004).

Nonetheless, the relationship between seedling growth and light changed in adult life stages. Light had a positive effect on growth of adult individuals of *E. umbellata*, showing a shift in requirements with life stage (e.g., Gabler and Siemann 2012). This result highlights the context dependent nature of invasion research and a requirement of a community context to adequately describe the biotic interactions in the system. Indeed, *E. umbellata* was the only species to be affected negatively by small-scale neighborhood density, perhaps due to high density monotypic stands or shading by taller native species (i.e., Adams et al. 2007; Fig. 2; see Supplemental Information Table S5). This finding suggests that *E. umbellata* adults are largely interacting with the native community primarily through competition, while it requires some facilitation for recruitment by means of soil moisture retention. In addition, the general absence of *E. umbellata* individuals in the dense neighborhoods of native individuals suggests that *E. umbellata* has not colonized or persisted in areas with limited light or space. In fact, the exotic species is most associated with *Q. velutina* and *A. arborea*, canopy and understory species respectively, that are noted for their persistence in savannah-like systems with xeric soils and high light penetration to understory canopies (Barnes and Wagner 2004; Table 4). These native understory species in particular may be negatively impacted (i.e., localized competitive exclusion) by the introduction of the invasive shrub, but we expect that the advantage that *E. umbellata* has growing at

relatively high understory light levels will not be sufficient to drive native species out of the forest community (Levine et al. 2004). From this perspective, management programs would be most successful by targeting areas not protected by biotic resistance.

In summary, at early life stages, *E. umbellata* is limited by moisture, promoting recruitment in the shade, while as an adult it is most affected by light, having more competitive growth rates in open sites. Thus, forest edges and canopy gaps are likely the habitats where *E. umbellata* is able to avoid the disconnect in environmental filters between juvenile and adult stages (Ibáñez and Schupp 2001). It is in these edge and gap habitats, with intermediate light levels, where we would expect *E. umbellata* to be able to outcompete native species given the high photosynthetic capacity of its leaves and nitrogen fixing capabilities and where managers might target individuals for control.

Conclusions

Some attention has been given to incorporate *E. umbellata* into American agriculture for its fruit's increased lycopene content over tomato, and for the possibility to be intercropped and harvested mechanically (Pashke et al. 1989; Black et al. 2005). With the potential of the introduction of *E. umbellata* as a cash crop, much work remains to be done in order to sufficiently understand the ecology of this invasive species before the availability of its propagules significantly increases through cultivation. This study highlights the importance of considering the relative growth rate of an invasive species in relation to the entire native community. By using demographic and environmental data we were able to describe the habitat requirements of an established exotic species and suggest potential mechanisms of invasion along environmental gradients. Such findings support the requirement of a community perspective to studying invasion ecology and predicting the establishment and spread of exotic species. Although, *E. umbellata* is defined as an invasive species in grassland habitat, it is likely to be outcompeted in the forest understory. Ultimately, the overall forest community dynamics are not strongly affected by the inclusion of the invasive shrub as seedlings establishing under the

forest canopy may not become vigorous sources of propagules; however, some functionally similar native species may be threatened by the invasion in edge and gap habitats. We recommend managers loosely monitor and eradicate late juvenile individuals in understory habitat to ensure persistence of functionally similar native species. Our findings also support the continued targeted eradication of individuals in high light and edge environments.

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