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The Seasonal Influence of Invasive Shrubs on Light and Temperature in an Eastern Deciduous Forest Understory

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ABSTRACT

Invasive shrubs are flourishing in temperate, deciduous forest understories of eastern North America where resources, especially light, are limited. However, understory light is more available before the overstory canopy leaves emerge in the spring and after fall senescence. Extended leaf phenology of invasive shrubs in the spring and fall compared to native shrubs and the overstory canopy is conspicuous, as well as higher foliage abundance of invasive compared to native shrubs. Extended leaf phenology of invasive shrubs provides photosynthetic benefits, but also seasonally novel shade. Light and temperature regulate life history characteristics across taxa and influence ecosystem processes. Here, a long-term invasive shrub removal experiment is used to quantify the effect on light and air temperature over 3–4 y. There was a pattern of reduced maximum air temperature in the presence of invasive shrubs during the growing season of most years. We find less light energy infiltration (lumens m^{-2}) below invasive shrubs than native shrubs with mean differences largest in the spring (-1981 [-2604 , -1380], a 26.8% reduction relative to below natives). Differences diminish through summer (-1038 [-1221 , -845]), fall (-547 [-660 , -429]), and winter (-257 [-372 , -151]). Invasive shrubs also filter more photosynthetically active radiation than natives (58.4 [38.5 , 78.7] $\mu\text{mol m}^{-2} \text{s}^{-1}$, a 39.4% reduction), but seasonal differences were not detected indicating denser canopy structure for invasive shrubs throughout the year. When compared to the native understory community, the presence of invasive shrubs seasonally reduces temperature and light availability near the forest floor, which could affect resident plant and animal species.

Index terms: central Appalachian hardwood; extended leaf phenology; invasive shrubs; lumens; phenology; novel shade; photosynthetically active radiation

INTRODUCTION

Natural areas of North America host more invasive shrub species than any other geographical region of the world (Rejmánek 2014). Most invasive plants are early-successional—adapted to rapidly use readily available resources (Lockwood et al. 2013). Indeed, invasive shrubs in the eastern United States are successful in old fields, roadsides, and waste places (Rhoads and Block 2007). However, invasive shrubs are also highly successful and problematic in temperate forest understories of eastern North America (Webster et al. 2006; Rhoads and Block 2007; Schulz and Gray 2013; Rejmánek 2014; Miller et al. 2020) where resources, especially light, are more limited (Martin et al. 2009; Dreiss and Volin 2013). These increases in invasive shrubs occur at the expense of native species abundance and diversity (e.g., understory plants, Maynard-Bean and Kaye 2019; amphibians, Watling et al. 2011; bees, Hanula and Horn 2011a; butterflies Hanula and Horn 2011b).

Most eastern deciduous forests have experienced some combination of fire suppression, increased deer pressure, and dramatic shifts in community composition with tree clearing, harvesting, and the repeated loss of dominant tree species to nonnative pests and pathogens (Yahner 2000). Ecosystem instability and disturbance facilitate invasion, largely through changes to resource use and availability (Lockwood et al. 2013). These ecosystem-based mechanisms certainly set the scene for invasions, but species-based mechanisms—species traits allow-

ing a nonnative to become invasive—help to complete the picture. Identifying the novel traits of invasive species provides insight not only for their success, but also for understanding the impacts to native ecosystems, the development of control methods, and predicting what nonnative species might become invasive.

Ecological theory identifies traits commonly contributing to successful plant invasion including greater plasticity, novel allelopathy and herbivore defense, and release from coevolved enemies with reallocation of resources to growth and reproduction (Lockwood et al. 2013). Of those that have been tested, some of these traits appear in invasive shrubs and some do not. For example, invasive shrubs do not have more plastic leaf traits than native shrubs in forest understories (Martinez and Fridley 2018). Dorning and Cipollini (2006) found strong allelopathic effects of Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim.), but Pisula and Meiners (2010) found very weak allelopathy in four other invasive shrub species. While Amur honeysuckle experiences insect enemy release compared to native species in eastern deciduous forests (Lieurance and Cipollini 2012, 2013), little is known of the insect herbivory of other invasive shrub species. However, there is a general pattern of reduced use of introduced compared to native woody species by butterflies and moths (Lepidoptera; Tallamy and Shropshire 2009). Furthermore, white-tailed deer (*Odocoileus virginianus* Zimmermann) tend to preferentially browse native woody species over invasive shrubs providing an advantage to invasive shrubs (Ward et al.

2013, 2017), yet in some cases prefer invasive shrubs over native (Shelton et al. 2014). Outside of common traits broadly contributing to successful plant invasion, additional insight for invasive shrub success may come from reflecting on light as a limiting resource in forest understories (Martin et al. 2009; Dreiss and Volin 2013). Indeed, a seasonally conspicuous feature appears to span shrub species that invade forest understories in the eastern United States: an extended leaf phenology compared to native shrubs and overstory tree species (Harrington et al. 1989; Xu et al. 2007; McEwan et al. 2009; Fridley 2012; Maynard-Bean et al. 2020; O'Connell and Savage 2020).

The seasonality of the overstory canopy dramatically influences the light environment of the understory in temperate, eastern deciduous forests (e.g., Figure 1). Spring ephemerals demonstrate the importance of seasonal understory light. This taxonomically unrelated group of native herbaceous species have aligned aboveground phenology with high-light availability prior to canopy closure in the spring and senesce as the overstory canopy closes (Augsburger and Salk 2017). So, beyond the photosynthetic advantages that extended leaf phenology (ELP) provides to invasive shrubs (Harrington et al. 1989; Xu et al. 2007; Fridley 2012; O'Connell and Savage 2020), the associated shade near the forest floor at a novel time of the year has negative implications for native species adapted for more open conditions. Even during the native shrub species growing season, invasive shrubs appear to produce denser understory foliage than both recent (e.g., uninvaded, Woods 1993; Maynard-Bean 2019) and historical conditions (Braun 1916 in Collier et al. 2002).

Changes to light and temperature near the forest floor influence plant growth and root activity (Smakman 1982; Pregitzer et al. 2000). Spring shading decreases tree seedling success (Augsburger 2008) as well as insect pollination and seed-set of a native forest herb (McKinney and Goodell 2010). Light and temperature impact the germination of most seeds, and seedling emergence for many species occurs early or late in the growing season, which would overlap with the ELP of invasive shrubs (Baskin and Baskin 2001). These impacts to growth, reproduction, and germination are important parameters for demographic models reflecting the potential for ELP to negatively impact native plant populations (Rockwood 2015). Novel shade could also help to explain the negative impacts of invasive shrubs to ectothermic species that are sensitive to light and temperature near the forest floor (e.g., communities of amphibians [Watling et al. 2011], bees [Hanula and Horn 2011a], and butterflies [Hanula and Horn 2011b]). Furthermore, ecological processes such as litter decomposition and nutrient cycling are regulated to a large extent by temperature, moisture, and their interaction (Singh and Gupta 1977).

Previous work demonstrates a negative influence of a community of invasive shrubs to light availability near the forest floor in the fall of one year (Kaye and Hone 2016). Additionally, reduced light and maximum spring temperatures were observed over two years (Chen and Matter 2017) and cooler ground temperature in one growing season (Watling et al. 2011) below one dominant invasive shrub (*L. maackii*). Given the importance of light and temperature for regulating life history traits across taxa and more generally to ecosystem processes, an examination

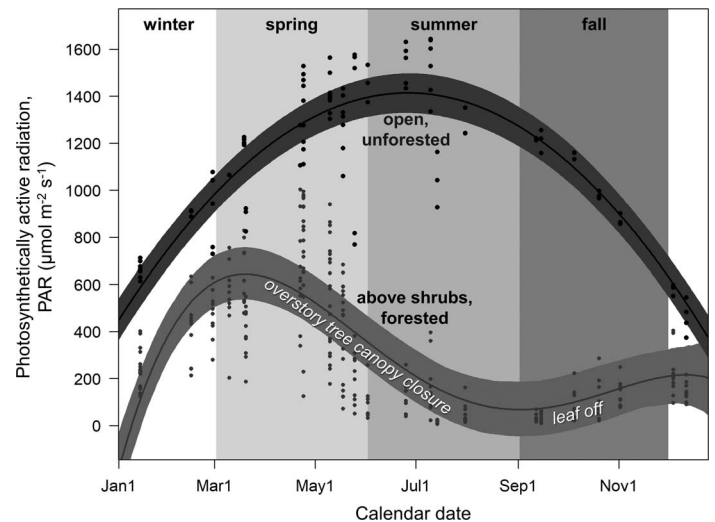


Figure 1.—Seasonal light availability in the open and below the overstory forest canopy. The vertical gray bands (background) are labeled by season. The points represent readings of PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) taken between March 2016 and January 2019 in the open (black) and above the shrub layer (gray). The black line and corresponding dark gray 95% confidence region correspond to the polynomial fit for light above the forest canopy across the calendar year ($P < 0.0001$, $R^2 = 0.83$). The gray line and corresponding 95% confidence region display the polynomial fit for understory light above the shrub layer across the calendar year ($P < 0.0001$, $R^2 = 0.67$).

of light and temperature across seasons and years for a community of invasive shrub species is warranted. An existing long-term invasive shrub removal experiment with paired treatment and control plots provides the opportunity to quantify these abiotic impacts of the novel leaf phenology and density of invasive shrubs relative to an abundant native understory community. After 7 y of maintained invasive shrub removal, the treatment plots had significantly increased in plant diversity and native shrub abundance (Maynard-Bean and Kaye 2019). Importantly, native plant regeneration in the removal treatments surpasses the abundance of native understory plants in uninvaded portions of the same forest, making comparison of invaded forest to the removal treatment more conservative than comparison to uninvaded forest. We hypothesize (H_1) decreased light infiltration due to an invasive shrub layer that is especially pronounced during the ELP of invasive shrubs, and (H_2) lower/colder daily maximum temperatures due to cooling from shade produced by a novel shrub canopy, as well as (H_3) higher/warmer daily minimum temperatures resulting from insulative effects of a novel shrub canopy increasing nightly lows. To test these hypotheses, we compared light and temperatures in treated plots with a robust native understory to paired control plots with an invasive shrub community still intact. We quantified light in two ways: (1) light available to plants as photosynthetically active radiation (PAR; 400–700 nm), which quantifies the number of photons per surface area and time; (2) light in terms of the energy in photons (lumens m^{-2}) across a wider range of the light spectrum (200–1200 nm) than PAR. The sensors used for light energy here extend into both the ultraviolet and infrared ranges, which is useful for understanding the transfer of heat by

light to surfaces, as well as providing information relevant to organisms that use ultraviolet light (e.g., pollinators, Koski and Ashman 2014) and infrared light (e.g., reptiles and amphibians, Enright et al. 2015). We find that invasive shrubs reduce PAR and cause a seasonal reduction to light energy and maximum temperatures.

METHODS

Study Site and Experimental Design

An invasive shrub removal experiment was initiated in 2009 at Hartley Woods, part of the Arboretum at the Pennsylvania State University. This woodlot is a remnant, mature, mixed-hardwood forest dominated by oak, hickory, and maple with 30–50 cm soil depth to a limestone bedrock substrate (USDA 2020). The experiment includes five sites each with a paired, 20 m diameter treatment (i.e., invasive shrub removal) and control (i.e., invaded) plot (10 plots in total, Kaye and Hone 2016). The invasive shrub removal treatment was first implemented in 2009 and treatments have been maintained since. The removal plots have seen a significant increase in the passive natural regeneration of native shrubs 1–4 m in height (847 individuals ha^{-1}), but there remains on average 8556 fewer individuals per hectare in this height class in the removal plots compared to plots with invasive shrubs (Maynard-Bean and Kaye 2019). This aligns with expectations for a mature eastern deciduous forest because invasive shrubs create a more closed understory than both recent (e.g., pre-invasion, Woods 1993) and historical conditions (Braun 1916 in Collier et al. 2002). In fact, the native plant abundance in the removal plots exceeds what was expected for native plant recovery based on uninvaded portions of the forest (Maynard-Bean and Kaye 2019). Because of the successful establishment of native understory plants, the removal treatment and control plots are referred to herein as invaded and native for simplicity. The four most abundant native and invasive shrub species and their abundances in unmanaged portions of the forest are listed in Table 1.

Light and Temperature Measurements

Photosynthesis is driven by the number of photons within the spectral range that plants use (400–700 nm), as opposed to the energy contained in each photon. Therefore, PAR is a measure of photons per surface area and time (e.g., $\mu\text{mol m}^{-2} \text{s}^{-1}$). Light was quantified with an LP-80 AccuPAR ceptometer (Decagon Devices, Pullman, Washington) above and below the shrub layer (3 m and 0.1 m from the forest floor, respectively) at the same 20 collection points (two points in each of the five treatment and five control plots) on 27 dates spanning three years (Mar 2016–Jan 2019). Measurements were taken with the ceptometer oriented in the four cardinal directions and averaged for each height at each collection point. Data were collected on sunny days during the 3 hr maximum daily zenith window. Frequently, the maximum zenith for a day was not sunny, resulting in uneven gaps between collection dates (i.e., 1–6 wk). Between measurements in each set of five paired native and invasive shrub plots, PAR measurements were taken at two collection points in the open, outside of the forest canopy, for comparison to the measurements taken in the understory.

Table 1.—The four most abundant native and invasive shrub species with abundances (unmanipulated) at the Arboretum at the Pennsylvania State University's Hartley Woods.

Common name	Scientific name	Stems/ha, mean (SE)
Invasive		
common privet	<i>Ligustrum obtusifolium</i> Siebold & Zucc.	40,680 (1367)
Linden viburnum	<i>Viburnum dilitatum</i> Thunb.	5793 (745)
Amur honeysuckle	<i>Lonicera maaackii</i> (Rupr.) Herder	2387 (270)
Morrow's honeysuckle	<i>Lonicera morrowii</i> A. Gray	2005 (187)
Native		
blackhaw	<i>Viburnum prunifolium</i> L.	3088 (122)
mapleleaf viburnum	<i>Viburnum acerifolium</i> L.	1082 (111)
bigfruit hawthorn	<i>Crataegus macrosperma</i> Ashe.	127 (12)
spicebush	<i>Lindera benzoin</i> L.	32 (6)

We measured light energy near the forest floor of native and invasive plots in lumens m^{-2} (also called lux). It is possible to convert lumens to PAR, but the relationship changes seasonally in an understory and is nonlinear (Long et al. 2012). Furthermore, we wanted to quantify a broader spectrum of light wavelengths that may affect the forest understory beyond PAR. HOBO Pendant Temperature/Light 8K UA-002-08 Data Loggers (Onset Computer Corporation, Bourne, Massachusetts) measure a range of the light spectrum extending into both ultraviolet and infrared light (200–1200 nm). The HOBO loggers were deployed in each of the ten 20 m diameter plots (i.e., five sites each with paired invasive and native plots). Each logger was mounted 0.5 m above the forest floor on a small wooden block attached to a metal stake driven 3 m in a random direction from plot center. To record hourly light (lumens m^{-2}), one sensor per plot was installed on 3 April 2015 (i.e., 10 loggers). A second sensor per plot was added on 14 October 2017 through 17 January 2019 in the opposite direction from plot center as the first logger (i.e., totaling 20 loggers). When two sensors recorded per plot, the data were averaged by plot prior to further analyses. Two gaps in the data collected within this time frame resulted from the memory filling up more quickly than anticipated omitting most of the summer of 2015 and the spring of 2016. Additionally, from 12 July 2016 through 17 January 2019 one sensor per plot recorded hourly air temperature data mounted on 0.5 m stands with wooden shade structures (to prevent direct sunlight and temperature inflation). The reported resolution of this instrument for temperature is 0.14 °C at 25 °C (0.25 °F at 77 °F), and accuracy is ± 0.53 °C from 0 to 50 °C (± 0.95 °F from 32 to 122 °F).

Phenology Measurements

Plant-level leaf phenology data were collected from January 2016 through February 2019 to understand the influence of the novel, extended phenological window of invasive compared to native shrub layers on the light and temperature data. Phenological data were collected for six individual shrubs of each of the four most common invasive shrub species and four most common native shrub species (Table 1) using standardized protocols from the USA National Phenology Network outlined below (Denny et al. 2014). The shrubs were located in

unmanaged areas among the five sites within the forest stand containing the invasive shrub removal experiment. The presence of leaves is defined as at least one base of a leaf, specifically the point of attachment with the petiole, emerged from a bud on a given plant. Dried or dead leaves are not considered as part of a “yes” for leaves present. The percentage of the potential canopy space is estimated categorically: less than 5%, 5–24%, 25–49%, 50–74%, 75–94%, 95% or more. Here, we consider the phenological window to begin and end when the canopy increases and decreases to 75–94% of full canopy, respectively. Each sampled shrub, 48 individuals, was visited at least twice per week during the beginning and end of the growing season and at least once per two weeks in the middle of the growing season.

Data Analyses

PAR data collected 3 m above the forest floor were used to model seasonal PAR available to the shrubs in the understory, generalizing point measurements to a continuous seasonal pattern. As expected, these data follow a sinusoidal curve across the collection years that aligns by day of year. Therefore, a fourth-order polynomial regression of the day of year (DOY) of data collection with year (year) and collection site (site) as random effects was fit as in Equation 1:

$$\begin{aligned} \text{PAR}_{ij} = & \beta_0 + \beta_1 * \text{DOY}_i + \beta_2 * \text{DOY}_i^2 + \beta_3 * \text{DOY}_i^3 \\ & + \beta_4 * \text{DOY}_i^4 + \text{site}_i + \text{year}_i + \varepsilon_{ij}, \quad \varepsilon_{ij} \sim N(0, \sigma^2), \\ & \text{site}_i \sim N(0, \sigma_s^2), \quad \text{year}_i \sim N(0, \sigma_y^2) \end{aligned}$$

Here, PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is light above either the invaded or native shrubs. All data analyses and figures herein were performed in the programming environment R 3.4.4 (R Core Team 2017). The above mixed-model was fit using the *lmer* function (*lme4* package, Bates et al. 2015) where β_0 , β_1 , β_2 , β_3 , and β_4 are the leading coefficients of the polynomial function, ε is residual error, and σ , σ_s , and σ_y represent the associated variance terms. The assumptions surrounding normality and homoscedastic variance were tested graphically using base plotting functions in R. The model estimates were tested using Satterthwaite’s method for approximating degrees of freedom for mixed models (*lmerTest* package, Kuznetsova et al. 2017). To quantify the variance in the data explained by the model including both fixed and random effects, the conditional coefficient of determination (hereafter, R^2) value was determined using the *r.squaredGLMM* function (*MuMIn* package, Barton 2018). To best represent the estimated fit line and to calculate the associated 95% bootstrapped confidence intervals (CIs), the *predict* function was used within the *bootMer* function to produce 1500 bootstrapped estimates of PAR available to the shrubs for each day of the year (*boot* package, Canty and Ripley 2017). To test whether the randomly assigned treatment and control differ in light infiltrating the overstory canopy, the same model was fit for the data split by native and invasive plots. There was no difference in the relationships, verifying no overstory canopy bias by treatment (results not shown).

Outside of the forest canopy there is a seasonal pattern to the light received from the sun at a given latitude. Seasonal light above the overstory tree canopy (i.e., in the open) was measured to contextualize light availability above the shrubs and near the

forest floor. This was modeled using a second order polynomial with year as a random effect as in Equation 2:

$$\begin{aligned} \text{PAR}_{ij} = & \beta_0 + \beta_1 * \text{DOY}_i + \beta_2 * \text{DOY}_i^2 \\ & + \text{year}_i + \varepsilon_{ij}, \quad \varepsilon_{ij} \sim N(0, \sigma^2), \\ & \text{year}_i \sim N(0, \sigma_y^2) \end{aligned}$$

Here, PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the light in the open. The above mixed model was fit using the *lmer* function (*lme4* package, Bates et al. 2015) where β_0 , β_1 , and β_2 are the leading coefficients of the polynomial function, ε is residual error, and σ and σ_y represent the associated variance terms. The assumptions and model effects were tested, R^2 calculated, and relationships and CIs estimated as described for Equation 1 models, above.

The photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at 3 m and 0.1 m was used to calculate the amount of PAR filtered by the shrub layer at a given sampling point (i.e., above minus below). The difference in PAR filtered between each of the five paired plots (i.e., invasive minus native) provides the light filtered out by invasive shrubs as compared to or relative to the native shrub layer. To provide a context for this metric, we also calculated percent reduction in PAR filtered by dividing the difference by the light below native shrubs. As no relationship adequately fit these relatively noisy time series data in terms of significant estimates that did not violate test assumptions related to normality, the data were bootstrapped using the *boot* package (Canty and Ripley 2017). Bootstrapping with replacement (1000 replicates) across sites for each of the 27 sampling dates ($n = 5$) was used to estimate means as well as the “percentile” 95% CIs appropriate for data that diverge from normality and data of small sample size (Davison and Hinkley 1997; Carpenter and Bithell 2000). These mean values of PAR filtered and percent reduction in PAR for each date were bootstrapped by the four meteorological seasons: spring (March through the end of May), summer (June through August), fall (September through November), and winter (December through January). The PAR filtered and percent reduction for the dates specifically falling during the ELP of invasive shrubs compared to native shrubs was also calculated (i.e., spring ELP, fall ELP). The mean effect of invasive shrubs on light filtered by the shrub layer can be tested for significance ($\alpha = 0.05$) by 95% confidence intervals (CIs) that do not overlap with zero.

The light intensity data (lumens m^{-2}) was recorded hourly at 0.5 m above the forest floor. The difference in daily average intensity between the paired invasive and native plots was calculated to provide the effect of invasive shrubs on light infiltration (i.e., invasive minus native). To provide a context for this metric, the percent reduction in light was calculated by dividing the difference in infiltration by the light intensity below native shrubs. These data contained too much variability to fit a reliable relationship with significant estimates that did not violate test assumptions, similar to differences and percent reduction in PAR. The difference in light energy available below invasive relative to native shrubs and the percent reduction in light energy for the five paired plots were bootstrapped with replacement (1000 replicates) by calendar week ($n = 35$). The weekly values were used to calculate seasonal means and confidence intervals following the methods described for the

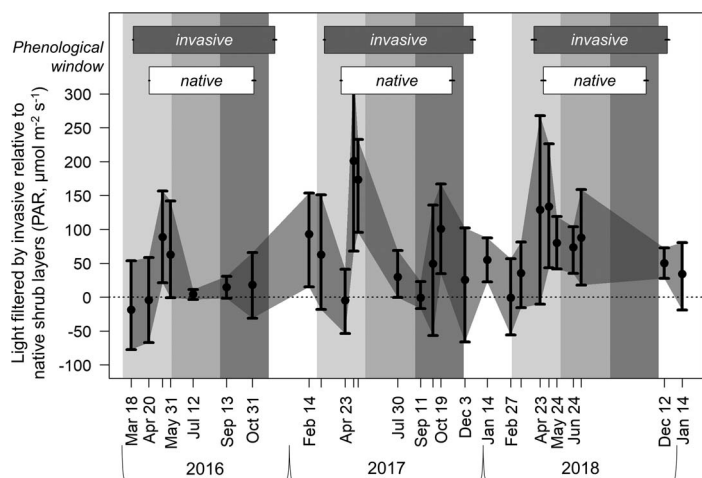


Figure 2.—Light filtered out by invasive relative to native shrub layers with phenological windows. The vertical background bands represent the seasons as indicated in Figure 1. The black points are the bootstrapped mean difference in light intercepted by the shrub layer for each sampling date with 95% confidence intervals ($n = 5$). The confidence intervals are connected by transparent gray bands for visualization purposes. Black confidence intervals that overlap the dotted line ($y = 0$) indicate that invasive and native shrubs do not differ in the amount of light filtered for a given sampling date. If the confidence interval is entirely above the dotted line, invasive shrubs filter more PAR than native shrubs. The gray and white rectangles represent the phenological windows for invasive and native shrubs, respectively, with the black bars indicating 95% CIs around dates of emergence and senescence. The model estimates and coefficients for phenology data are available in Supplementary Content at BioOne online.

effect of invasive shrubs on PAR filtered by the shrub layer, above.

Temperature data ($^{\circ}\text{C}$) was also recorded hourly, and daily minimum and maximum values were summarized. To understand the influence of invasive shrubs on the daily minimum and maximum temperatures, the difference between the paired invasive shrub plots and native plots was calculated (i.e., invasive shrubs minus native shrubs). The daily difference in minimum and maximum temperatures were each bootstrapped with replacement (1000 replicates) by calendar week following the methods described above for the effect of invasive shrubs on PAR filtered by the shrub layer.

Differences in leaf phenology by species and origin (native vs. invasive) were estimated using a nested ANOVA framework for day of year (DOY) of leaf emergence and DOY of leaf off for each year. The models were fit as in Equation 3:

$$\text{DOY}_{ijk} = \mu + \alpha_i + \beta_{ij} + \varepsilon_{ijk}, \quad \varepsilon_{ijk} \sim N(0, \sigma^2)$$

Here, one model was fit for each DOY leaf emergence and leaf off and for each year with μ as the overall mean (or common value of DOY), α as the effect of origin, β as the effect of species nested within origin, ε as residual error, and σ represents the associated variance term. The model was fit using the *lm* function, which provides tests of the model estimates and a model R^2 value. The assumptions were tested as described for the Equation 1 model above. Because of the nested effects, effects were tested and group means determined using estimated marginal means, also known as least-squares means (*emmeans* package, Lenth 2018).

RESULTS AND DISCUSSION

Light and Phenology

Light and phenology in the understory are constrained by the phenology of the deciduous forest overstory (Martin et al. 2009). In the open, away from the forest canopy, the annual maximum PAR peaked between June and July, while below the tree canopy and above the shrub layer the peak occurred between March and April at 45% of the peak in the open (Figure 1, model estimates and coefficients available in Supplementary Content at BioOne online). Invasive shrubs either filter more PAR than natives at each sampling date (40.7% of the 27 sampling dates), or there is no difference in the amount of PAR filtered by the shrub layers (59.3% of the 27 sampling dates, Figure 2). On average, invasive shrubs filter $58.36 [38.46, 78.74] \mu\text{mol m}^{-2} \text{s}^{-1}$ more PAR than native species corresponding to a 39.4% reduction in PAR relative to native shrubs. This supports the first part of the hypothesis (H_1) that less light will infiltrate the invasive shrub layer, but the ELP of invasive shrubs compared to native shrubs in the spring appears to filter greater PAR than in the fall (Figure 2, 95% CIs during ELP are above zero in all three springs, but only one of two falls). However, the average PAR filtered during the ELP windows does not significantly differ from other seasons (i.e., 95% CIs of ELP overlap with CIs of other dates, Table 2). Relatively wide confidence intervals reflect high heterogeneity in

Table 2.—The seasonal influence of invasive shrubs on light relative to native shrubs.

Season	PAR filtered out by invasive relative to native shrubs at max zenith (Figure 2)			Light energy available below invasive relative to native shrubs (Figure 3)		
	mean ($\mu\text{mol m}^{-2} \text{s}^{-1}$) [95% CI]	% reduction [95% CI]	<i>n</i>	mean (lumens m^{-2}) [95% CI]	% reduction [95% CI]	<i>n</i>
all	58.4 [38.5, 78.7]	39.4 [25.4, 54.5]	27	−891 [−1072, −735]	34.4 [29.0, 41.1]	175
spring	78.3 [40.5, 118.5]	27.1 [13.9, 41.4]	12	−1981 [−2604, −1380]	26.8 [15.8, 39.6]	37
spring ELP ^a	135.5 [94.3, 176.8]	44.4 [31.5, 58.5]	5	−2809 [−3500, −2109]	50.2 [27.2, 73.5]	13
summer	48.9 [17.1, 80.7]	77.4 [48.3, 100.4]	4	−1038 [−1221, −845]	41.2 [32.6, 50.2]	41
fall	36.5 [9.2, 70.0]	51.7 [0.5, 102.9]	5	−547 [−660, −429]	40.0 [32.2, 47.9]	52
fall ELP ^a	55.1 [14.8, 100.8]	91.0 [31.0, 131.2]	3	−722 [−841, −570]	52.8 [42.5, 65.2]	14
winter	42.9 [20.7, 66.3]	28.2 [15.4, 40.6]	6	−257 [−372, −151]	27.9 [14.3, 49.5]	45

^a The window where invasive shrubs have extended leaf phenology (ELP) compared to natives (Figure 2, see Supplementary Content for model estimates of phenological windows).

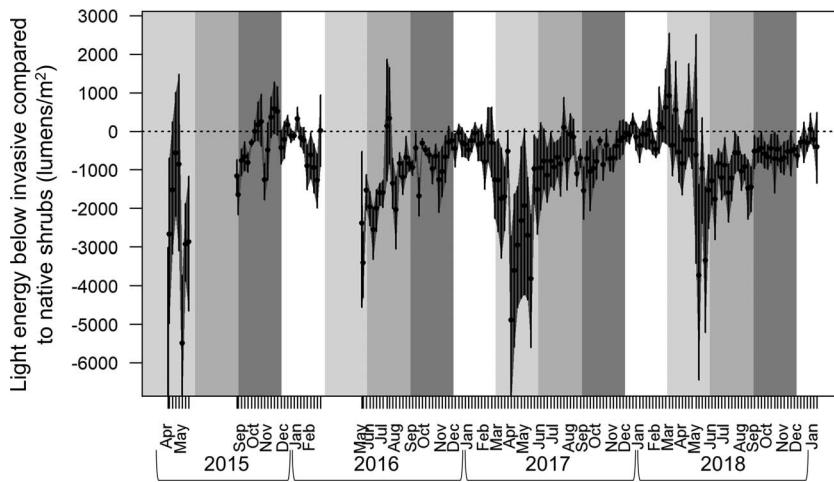


Figure 3.—Light energy available below invasive relative to native shrubs. The vertical background bands represent the seasons as indicated in Figure 1. The black points and corresponding error bars are the bootstrapped weekly mean difference of the daily average light intensity below invasive and native shrubs with associated 95% CIs ($n = 35$). The intervals are connected by the dark gray bands for visualization purposes. Intervals that overlap the dotted line ($y = 0$) indicate that the invasive and native shrubs do not differ. If the confidence interval is entirely below the dotted line, there is significantly less light available below invasive shrubs as compared to native shrubs. Table 2 shows the bootstrapped means and 95% CIs for seasonal differences.

understory light availability along with relatively small sample sizes. Still, we find that invasive shrubs filter more PAR than natives across seasons, indicating that native shrubs do not produce as much shade as invasives even when they both have leaves in the summer (Figure 2). Furthermore, differences that occur in the winter months indicate that even leafless branches of invasive shrubs filter more PAR than the native community. Together this verifies observations of greater foliage density or leaf area index for invasive compared to native shrubs in the understory of deciduous forests (e.g., Woods 1993, Maynard-Bean and Kaye 2019). The range of PAR available below invasive shrubs was great ($3\text{--}988\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$), and rarely approached the light compensation point for understory herbs (e.g., $5\text{--}16\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, Hull 2002) and woody seedlings (e.g., $5.3\text{--}9\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, Craine and Reich 2005) common to eastern North American deciduous forests. Even so, the negative effect of invasive shrubs on PAR that we found here has the potential to dramatically influence the carbon budget of shade-adapted understory species (Chazdon and Pearcy 1991).

In addition to PAR, we also measured light energy (lumens m^{-2}) spanning a larger range of the electromagnetic spectrum. The light energy of invaded plots is significantly reduced in 60.6% of weeks sampled from 2015 to 2019 (i.e., 106 of 175 weeks, Figure 3). Seasonally, invasive shrubs allow significantly less light infiltration compared to native shrubs. The largest difference in light infiltration occurs in the spring (-1981 [$-2604, -1380$] lumens m^{-2}), with the magnitude of difference decreasing each season through summer, fall, and winter (Table 2). This seasonal trend corresponds to light availability in the understory (Figure 1), and when taken relative to understory light availability as the percent reduction in light there are not differences by season (Table 2). So, despite a similar percent reduction in light energy, mean light energy is much lower during the spring ELP of invasive shrubs (-2809 [$-3500, -2109$]) than for fall ELP (-722 [$-841, -570$]). Spanning nearly four years, light infiltration was generally reduced by the presence of invasive shrubs. Similar to PAR, this lends further support to observations of greater foliage density for invasive

compared to native shrubs in the understory of deciduous forests. Decreased understory light energy negatively influences the movement and behavior of invertebrates (McKinney and Goodell 2010), birds (Bennett and Cuthill 1994), and amphibians (Enright et al. 2015) and has the potential to incur indirect impacts to species and ecosystem processes through reductions in the transfer of light energy to heat at the forest floor.

Temperature

Due to the novel shade produced by the invasive shrub canopy, we hypothesized (H_2) lower/colder daily maximum temperatures. Invasive shrubs decreased the maximum temperature in the summer and fall of 2016, and the spring and summer of 2017, but there was no effect on air temperature for 2018 (Figure 4b). This may be related to abnormally wet weather in 2018. Compared to the average of 2016 and 2017 (which aligned with 1981–2010 climate normals), the mean monthly maximum air temperature was $1.2\ ^\circ\text{C}$ lower and precipitation was 70% greater in 2018 (NOAA 2020). The high specific heat of water means that it requires a lot of energy to change temperature compared to the rest of the forest floor. A moist understory in 2018 likely influenced the transfer of light energy to heat. Nevertheless, this pattern of invasive shrubs reducing maximum air temperature during the growing season of two years strengthens existing knowledge of this effect observed for one invasive shrub species (*L. maackii*, Watling et al. 2011, Chen and Matter 2017). Because of the potential insulative effects of a novel shrub canopy, we hypothesized (H_3) higher/warmer daily minimum temperatures. Minimum air temperatures were not clearly influenced by the novel shade produced in the understory by invasive shrubs. The coarse resolution of temperature measurements ($\pm 0.5\ ^\circ\text{C}$) may not detect the fine resolution differences that invasive shrubs could cause. Additionally, a small difference in air temperature between invasive and native plots could be masked by air movement in the forest understory. Even with the large sampling plots used here (20 m in diameter) as well as the placement of sensors within 3 m of plot center, the air temperature of the regenerated native community is likely

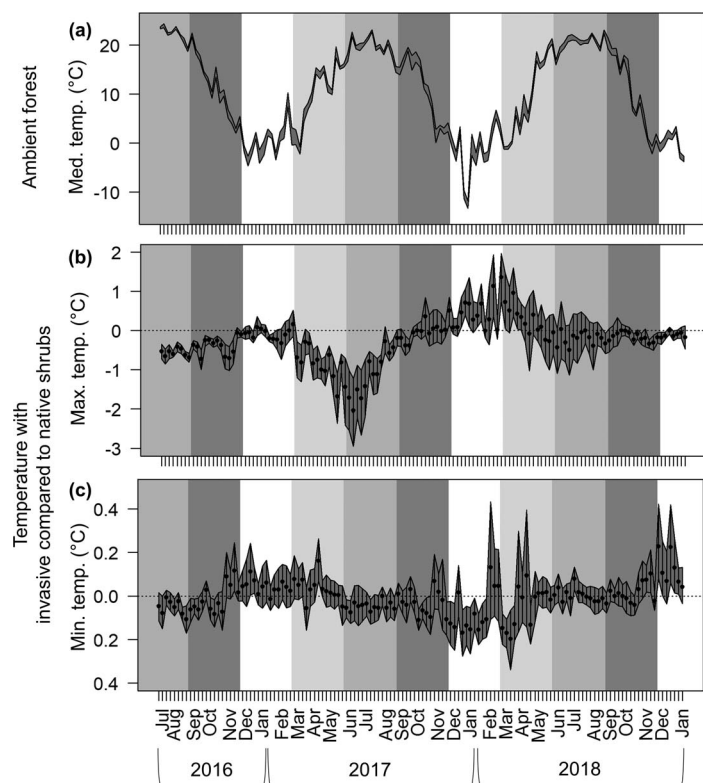


Figure 4.—The influence of invasive shrubs on daily minimum and maximum air temperature compared to native shrubs. The background gray bands represent the seasons as indicated in Figures 1–3. The darkened areas indicate the bootstrapped weekly 95% confidence regions of the (a) median understory forest temperature across date, and the difference between the (b) maximum and (c) minimum air temperature around invasive compared to native shrubs. The black points and corresponding error bars are the bootstrapped weekly mean difference in the daily (b) maximum or (c) minimum air temperature in the understory with associated 95% CIs ($n = 35$). Black CIs that overlap the dotted line ($y = 0$) indicate that the invasive and native shrubs do not differ for a given weekly value. If the confidence interval is entirely above the dotted line, invasive shrubs increase that temperature value compared to natives. If below, invasive shrubs decrease temperature compared to natives. However, results less than about 0.5°C in difference should be interpreted with caution (instrument accuracy $\pm 0.53^{\circ}\text{C}$ from 0 to 50°C).

still influenced by the surrounding matrix of invasive shrubs. Placing multiple sensors in the upper soil layers may ameliorate this effect because soil temperature changes more slowly than air temperature.

Significance

In the deciduous forest understory, there is less light energy (lumens m^{-2}) available below invasive shrubs than below native shrubs with mean differences largest in the spring and differences decreasing through summer, fall, and winter. Likely related to light energy reductions, maximum air temperature was reduced during the growing season of two years. Invasive shrubs filter more available PAR than natives, and seasonal differences were not detected. Light is an important resource in the understory of deciduous forests, and modest changes have

the potential for dramatic consequences to carbon budgets (Chazdon and Pearcy 1991). Also, the light environment alters nutrient allocation for shade-tolerant understory species, with more nitrogen allocated to leaves under lower light conditions (Niinemets 1997). This has potential implications for increased resource competition between native understory plants and invasive shrubs, and for litter quality and decomposition rates. The darker, cooler conditions with shrub invasion have the potential to exacerbate the mesophication of eastern deciduous U.S. forests—a phenomenon that has resulted from a positive feedback loop of fire suppression allowing mesophytic, shade-tolerant native species to shift the understory toward more cool, damp, and shaded conditions resistant to burning (Nowacki and Abrams 2008). Additionally, quantifying the changes to seasonal light could allow adjustments to models predicting native species populations or ecosystem processes. For example, the influence of light on germination rates are known for many plant species (Baskin and Baskin 2001) and could be used to modify demographic models to estimate changes to population growth rates. Furthermore, the changes to light quantified here can be used to experimentally manipulate understory light availability or growth chamber conditions to disentangle the influence of the novel shade of invasive shrubs on, as examples, seed production, plant growth, and invertebrate transit, development, or emergence. The presence of invasive shrubs reduces average PAR availability by 39.4% [25.4, 54.5] compared to an abundant native understory community with seasonal influences on light energy and temperature near the forest floor, which can negatively impact native species and ecosystem processes.

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