POPULATION ECOLOGY

Comparative performance of invasive and native *Celastrus* species across environmental gradients

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Abstract The ability to understand and predict the success of invasive plant species in their new ranges is increased when there is a sympatric native congener available for comparison. *Celastrus orbiculatus* (oriental bittersweet) is a liana introduced into the United States in the mid-1800s from East Asia as an ornamental plant. Its native congener, *Celastrus scandens* (American bittersweet), ranges from the east coast of the United States as far west as Wyoming. In the Northeastern United States, *C. orbiculatus* is continuing to expand its range while *C. scandens* appears to be in serious decline. One hypothesis for this decline is that *C. scandens* does not have such a wide range of ecological tolerances in the current landscape as *C. orbiculatus*, which seems to tolerate a greater range of resource conditions. To investigate this hypothesis, we transplanted these two species into ten sites that spanned a full range of light and soil moisture conditions to compare their establishment and performance in terms of aboveground growth (biomass and height) and mortality. After two years, *C. orbiculatus* showed significantly lower mortality and greater biomass across all resource conditions compared to *C. scandens*. In addition, *C. orbiculatus* preferred more mesic soil moisture conditions, while *C. scandens* performed better in drier soil moisture conditions. Since much of the Northeastern United States is now forested, this preference for mesic soil conditions could make it more successful than *C. scandens* in the region. This study shows the utility of manipulative experiments, particularly those using congeneric native species as benchmarks, for assessing the causes and predicting the course of invasions.

Keywords *Celastrus orbiculatus* · *Celastrus scandens* · Congeners · Invasive species · Lianas · Phytometer · Plasticity · Transplant study

Introduction

Researchers take a variety of approaches to determine what traits make a given invasive species successful. Some of these approaches are broad in scale, looking across life forms and taxonomic levels (Reichard and Hamilton 1997; Goodwin et al. 1999; Herron et al. 2007) in the hopes of predicting future invaders (Mack 1996; Mack et al. 2000), and are not experimental in nature. These approaches have had varying degrees of success, often examining general traits such as seed size (Rejmánek and Richardson 1996) and whether it is invasive elsewhere (Reichard and Hamilton 1997). However, traits that are more related to fitness, such as survival, growth rate and accumulated biomass (Grotkopp et al. 2002; Burns 2006), need to be examined experimentally.

Many of the empirical studies that focus on the traits of invasive species use native species for comparison (Baruch and Goldstein 1999; Durand and Goldstein 2001; Daehler 2003; Sanford et al. 2003). The problem with many of these comparisons is that they do not take phylogeny into account when making comparisons between plants that are

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inherently different. In contrast, congeneric species would be expected to show similar characteristics because of shared evolutionary history (Antúnez et al. 2001). This is especially true of congeners that share the same range, where an invasive congener that has been able to establish has presumably overcome barriers that restrict the performance of a native in the same range (Mack 1996).

It is important when studying these species to take into account the particular habitat into which the invader is introduced (Radford and Cousens 2000; Gerlach and Rice 2003; Burns 2006). An invasive species can have varying degrees of success in establishing and proliferating depending on the environmental conditions (Radford and Cousens 2000; Daehler 2003; Burns 2006; Richards et al. 2006). In fact, it has been argued that some native environments, especially if they are "extreme," can resist invaders (Daehler 2003), and thus an invader can often fail to establish (Mack 1996). Therefore, an experimental approach which examines the impact a full range of environmental conditions has on the recruitment of the invasive species is important when attempting to understand the conditions under which they can successfully establish. The habitats that allow these species to successfully establish are often directly related to the invader's plasticity (Richards et al. 2006).

One effective way to examine which traits make certain invasive species successful in a given environment is to experimentally transplant the species across a full range of environmental resources and conditions and then assess performance (e.g., Castillo et al. 2000; Radford and Cousens 2000; Silveri et al. 2001; Sanford et al. 2003; Sans et al. 2004). This experimental "phytometer" method (cf. Maurer and Zedler 2002; Huber et al. 2004) provides a more complete, realistic view of species-specific environmental tolerances across the landscape. Since the full range of ecological tolerances is likely unknown for an invasive species, transplants allow a direct ecological assay of the tolerances of a species using a regression design. This phytometer or ecological assay method has been widely used in previous studies (e.g., Sipe and Bazzaz 1995; Kobe 1999; Griffiths and Orians 2004; Schreeg et al. 2005) to determine the effects of various environmental factors on the growth and performance of a range of plant species under natural conditions.

We set out to use a congeneric approach in conjunction with a transplant ecological assay, using as a case study the exotic *Celastrus orbiculatus* Thunb. (oriental bittersweet) in comparison with its native congener, *C. scandens* L. (American bittersweet). *Celastrus orbiculatus* is an invasive liana that was introduced into the United States some time around 1860 (Patterson 1974). In the Northeastern United States, it is an aggressive species that can grow more than 30 m in height and 18 cm in diameter (McNab

and Meeker 1987; S. Leicht-Young, personal observation). It can cause damage to trees by girdling them (Lutz 1943), increasing tree susceptibility to ice damage (Siccama et al. 1976) or by interfering with forest regeneration by shading out young saplings (McNab and Meeker 1987). *Celastrus scandens* has an extensive native range in North America (USDA NRCS 2006); however, recent observations in the Northeast have indicated that this species is in serious decline (Fike and Niering 1999; New York State Department of Environmental Conservation 2000; Steward et al. 2003). Although the cause of the decline of *C. scandens* is not known, and its ecological tolerances have not previously been tested, loss of open habitats may be a factor.

To determine the success of *C. orbiculatus* and *C. scandens* across the New England landscape, we transplanted both species across a natural gradient of resource and environmental conditions using a regression design (e.g., Kobe 1999; Caspersen et al. 1999). In particular, light and soil moisture availability varied across transplant sites to span a full range landscape conditions. By studying the success of these two species, we sought to gain insight into not only the establishment and performances of native and invasive species, but also into how lianas, a poorly studied plant growth form, respond in differing conditions. In this way, we would be able to identify which factors specifically make *C. orbiculatus* such a successful invasive species. We predicted that *C. orbiculatus* would be more successful (as measured in terms of greater biomass and lower mortality) than *C. scandens* across many or most resource conditions. Previous studies using this type of congeneric comparison have shown that the invasive species is more successful than the native in a variety of conditions (Schierenbeck et al. 1994; Rejmánek and Richardson 1996; Schweitzer and Larson 1999; Radford and Cousens 2000; McDowell 2002; McDowell and Turner 2002; Gerlach and Rice 2003; Burns 2004, 2006).

Materials and methods

The species

Currently, *C. orbiculatus* ranges in North America from the east coast of the United States, north to Quebec and Ontario, south to Georgia, and west to Wisconsin (Ma and Moore 2004a; USDA 2006). The native range of *C. orbiculatus* is large, including the countries of Japan, North and South Korea and China north of the Yangtze River, ranging from approximately 150 to 100°E and from approximately 30 to 45°N (Hou 1955; Zheng et al. 2004; Leicht 2005). It occurs in lowland slopes, thickets, mixed forests and forest edges at elevations from 450 to 2,200 m (Zhixiang 2005). In its introduced range in the United

States, *C. orbiculatus* can be found in a wide variety of habitats, including forests, open fields and along the coast (Gleason and Cronquist 1991).

The native range of *C. scandens* is also large, north to the Canadian provinces of New Brunswick, Quebec, Ontario and Manitoba, south to Georgia, and west as far as Wyoming in the United States (Ma and Moore 2004b; USDA 2006). The habitat range of the North American native *C. scandens* appears to be more restricted than that of *C. orbiculatus* in that it also occurs in open fields, along edges and in sand dunes. Unlike its invasive congener, however, it is not commonly seen in the forest understory (Gleason and Cronquist 1991; S. Leicht-Young, personal observation).

Experimental design

Fruit of *C. orbiculatus* were collected from multiple individuals in both open and edge habitats in Connecticut in October 2002. Seeds of commercially grown *C. scandens* were purchased from Sheffield's Seed Company in Locke, NY. We did not use seeds from local sources because this species is in decline and a rare or listed "species of concern" in the Northeast (New York State Department of Environmental Conservation 2000). In a previous study, we determined in germination trials and in early seedling performance that there were no differences between plants grown from local and purchased seed (Leicht 2005; S. Leicht-Young, unpublished data). Seeds of both species were allowed to germinate in March 2003. Seedlings were transplanted into 12.7-cm pots and were grown in a greenhouse in full sun until May 2003, when they were brought out into a garden under light shade to be hardened off. They were transplanted in late May and early June 2003 after the last frost when they were approximately 15 cm in height.

We transplanted a total of 1,460 seedlings of *C. orbiculatus* and *C. scandens* directly into ten sites in eastern and western Connecticut creating a regression-ecological assay experimental design or phytometer study. Seven of the sites were located in eastern Connecticut on University of Connecticut forest and farm lands (in the vicinity of 41°49′N, 72°15′W) and the remaining three sites were located in northwestern Connecticut (in the vicinity of 41°58′N, 72°20′W). We selected our sites to span a full range of light (low, medium and high) and soil moisture (low, medium and high) conditions. In this way, we could focus on small-scale variation in soil (van Breemen et al. 1997; Finzi et al. 1998; Caspersen et al. 1999) and light (i.e., sunflecks and light gaps; Chazdon 1988), such that there would be variation even between neighboring plants. Thus, neighboring plants may have as much variation

between them as there is overall variation within or even among plots (Leicht 2005, Figs. 2.1, 2.2). We particularly focused on obtaining a diversity of lower light conditions (i.e., 0–18%) because much of the variation in functional response in woody plants inhabiting northeastern North American mixed conifer/hardwood forests is found in variation across lower light transmittances (Pacala et al. 1996; Caspersen et al. 1999). In addition, our soil moisture values explored the full range of conditions found in the upland New England landscape. When setting up our plots, natural site constraints (i.e., trees, boulders, etc.) prevented us from setting up a single large plot. Therefore, within each site, three replicate plots were placed so as to keep them within a similar range of light and soil moisture conditions while allowing an assessment of plot-level effects. Two of the three plots contained 49 seedlings and the third had 48. The native and invasive seedlings were planted in an alternating pattern 1 m apart to avoid direct competition between individuals, forming an area 7×7 m^2.

We collected data on the light and moisture environment that the seedlings were experiencing in each site over the course of the study. For each seedling, the amount of photosynthetically active radiation (PAR) that it received was measured using a pair of LI-COR 1400 data loggers and LI-COR 170SA quantum sensors (LI-COR, Lincoln, NE, USA) between the hours of 1000 and 1400. PAR was recorded on overcast days (Nicotra et al. 1999) over each seedling at a standard height (1.5 m). Simultaneously, the second quantum sensor and data logger recorded the PAR in an open area located close by. Using these data the percent of PAR transmitted to the understory (%T) was calculated. Light measurements were taken in June of 2003 and June of 2004 when the canopy had fully leafed out. In the three fully open sites, the %T was set to 100%.

Moisture was measured in 14 different locations in each of the three plots within a habitat using a Delta-Probe in August 2003, as well as once a month in May to August 2004. We took moisture readings at a coarser level than light within the plots, because in this system moisture variations occur at a larger scale than variations in light (Caspersen and Kobe 2001; Leicht 2005, Figs. 2.1, 2.2; S. Leicht-Young, personal observation). Therefore, the 14 readings per plot were adequate to assess within-plot variation in soil moisture. In our analysis, we assigned to each plant the moisture value of the nearest reading, which was a maximum distance of 20 cm. These moisture readings were corrected using soil-specific calibrations for the soil in each habitat type (Delta-T Devices 1998). Additionally, we did a functional assay of soil moisture at field capacity and at the permanent wilting point for *Celastrus* for the three main soil types that we encountered in the habitats: mucks, loams and sand. The soil moisture at both field

capacity and permanent wilting points was similar for all of the soil types except for the mucks (data not shown). Since muck soils in these habitats were permanently saturated throughout the growing season, there would be little variation with time in the soil moisture that would affect the performance of the plants. Thus, measuring plant performance in terms of percent soil moisture across all of the soils is appropriate in this study (Kramer and Boyer 1995).

The mortality of each of the seedlings was recorded during the growing seasons of 2003 and 2004. To obtain the final aboveground biomass of the plants in September 2004, plants were cut at ground level, dried, and weighed in grams. Herbicide was painted immediately onto the cut stems to prevent resprouting and the spread of the aggressively invasive species in the field.

Data analysis

We analyzed the effects of the range of environmental resource conditions (light and soil moisture) on the biomass and the mortality of each individual plant in a regression design. For the biomass data, we transformed the values by adding one to the biomass and then taking the natural log (ln) of that sum to normalize the data, and to avoid negative transformed values. In order to determine how the biomass of each species was affected by both light and moisture, a general additive model (GAM) was used to visualize the shape of the effect of the mean light and moisture values collected (Oksanen and Minchin 2002; Quinn and Keough 2002). The GAM model (results not shown) revealed that the influence of light and moisture on biomass was not linear. We then analyzed the data using a nonlinear mixed-effects model (cf. Pinheiro and Bates 2000; Beckage and Clark 2003):

$$E(\text{biomass}) = \alpha(\text{moisture}) + \gamma(\text{moisture})^2 + \frac{p_1 \times \text{light}}{\frac{p_1}{p_2} + \text{light}} + r$$

(1)

Light and soil moisture were defined as fixed effects within the model. Both the experimental data and the observed distributions of the species on the landscape strongly suggest that the soil moisture responses of the species are unimodal with poorer performance and maximum and minimum soil moisture levels, so we used a quadratic function as the simplest representation of this response pattern. α and γ are shaping coefficients for the moisture function, which determine the location and breadth of the function's peak. To describe the effect of light on the plants a saturating function was used, because this best represents the photosynthetic response of plants to increasing light. In the function describing the plants'

response to light, p_1 describes asymptotic growth and p_2 describes the change in biomass as a function of light at very low light (Pacala et al. 1994; Kobe 1999).

In order to take potential differences among sites that were not encompassed by light and moisture levels into account, and thereby to model the potential autocorrelation of performance within sites, we included site-level random effects in the models (represented by r in Eq. 1). In addition, we tested whether the models would be improved by adding plot-level random effects nested within site (the three triplicate plots within a site) to reflect possible microscale variations in conditions within sites (Beckage and Clark 2003). By capturing the individual variation related to sites and plots, the random effects allowed the models to identify these location-specific performance differences, while accurately describing how the remaining variation in plant responses related to light and moisture. We used Akaike's Information Criterion (AIC) to compare among models with and without subplot random effects. Finally, since there was greater variance in the model residuals at higher light levels, we modeled variance as a power function of light to account for this heteroscedasticity (Pinheiro and Bates 2000). For the biomass response, regression surfaces were generated in S-Plus in order to visualize the results.

To analyze mortality, we initially examined the effects of soil moisture and light on mortality using GAM models in order to visualize the shape of the light and moisture responses, as we did with biomass. As in the case of biomass, mortality was bell-shaped when related to soil moisture, and curvilinear when related to light. Thus, we used logistic regression in a generalized linear mixed model using the glmmPQL() function in S-Plus (Venables and Ripley 2002) to model mortality as a quadratic function of soil moisture and a square root function for light. As in the biomass models, we included site random effects in all models, and tested models with and without random effects for plot nested within site. We also tested whether including weights to represent potential scaling of variance with light would improve the mortality models, and compared these using AIC. All of the above analyses were conducted using S-Plus 6.2 (Insightful Corporation 2003).

Results

Celastrus orbiculatus was observed to have significantly higher biomass than *C. scandens* across the majority of resource conditions (Fig. 1). The values of the biomass response variable coefficients for *C. orbiculatus* and *C. scandens* differed (Table 1), with *C. orbiculatus* having larger values than *C. scandens*. Thus, the overall magnitude of the response of the biomass of *C. orbiculatus* to light and

moisture was greater than that of *C. scandens*. Both *C. orbiculatus* and *C. scandens* responded in a similar manner with increasing biomass with increasing light, eventually reaching a saturation point. Maximum biomass was achieved at higher soil moisture for *C. orbiculatus* than *C. scandens* (Fig. 2a).

The inclusion of site random effects improved the biomass models for both species (Table 2). For *C. orbiculatus*, there were two site effects that had substantial impacts on the model beyond the light and moisture effects (for sites F and RMR, see Fig. 3a). For *C. scandens*, however, site effects were small in magnitude and all within slightly more than one standard deviation of 0 (Fig. 3b). The addition of random effects for subplots nested within sites made the AIC score higher (worse) for both species (see Table 2). The magnitude of the actual subplot effect on growth was small, indicating little within-site variability in growth. Finally, allowing variance to scale with light level significantly improved the models for both species (Table 2).

Celastrus scandens showed greater mortality across all resource conditions than *C. orbiculatus* (Fig. 4a,b). Of the two species, 14% of the *C. orbiculatus* were dead across all sites at the end of the experiment, while *C. scandens* had more than twice the mortality (33%). In each site, the mortality of *C. scandens* was greater than that of *C. orbiculatus*. For both species, moisture had a significant effect on mortality, while light was not significant (Table 3). The response surfaces for the probability of survival and the effect of moisture on mortality showed that at the extreme ends of moisture (very wet and very dry), mortality in both species was higher than the more mesic conditions (Fig. 2b). Both species had higher mortality in the very wet sites, with *C. scandens* showing a
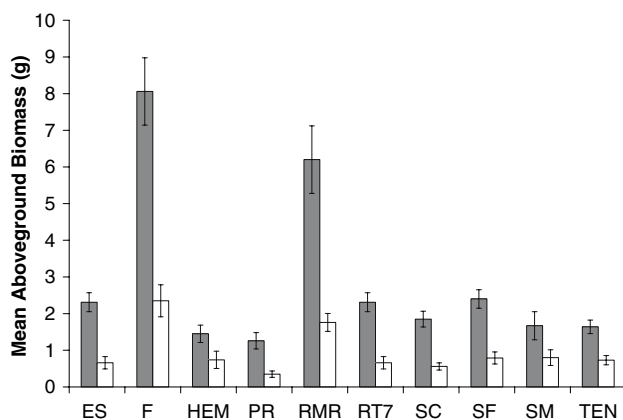
greater relative increase in mortality under the wettest conditions.

The random effects introduced to capture potential differences among sites and/or plots also revealed a difference between the spatial scales of heterogeneity in growth and mortality responses. As with biomass, the inclusion of site-level random effects improved the model AIC (Table 2). However, the mortality of the native as well as the invasive species was influenced by site effects (Fig. 3c,d). In addition, the subplot-level random effects were larger in magnitude and substantially improved the model AIC (Table 2), indicating that survival was spatially variable at the smallest scales, a result that is consistent with results in other transplant trials (e.g., Beckage and Clark 2003). Also in contrast to the models for biomass, including weights in the model to allow variance to scale with light increased the AIC of the models, and thus we excluded these weights from the models and only used those with the site/plot effects (Table 2).

Discussion

Celastrus orbiculatus performed better during establishment and early growth phases (e.g., higher biomass, lower mortality) across a broader range of light and moisture conditions than *C. scandens*. In other transplant experiments using native and invasive congeners, the invasive often outperformed the native as well (Radford and Cousens 2000; Sans et al. 2004). By using congeners in our study, we have shown the utility of making direct comparisons between closely related species. In this way, we were able to point to specific traits that make the invasive species more successful than the native in similar habitats.
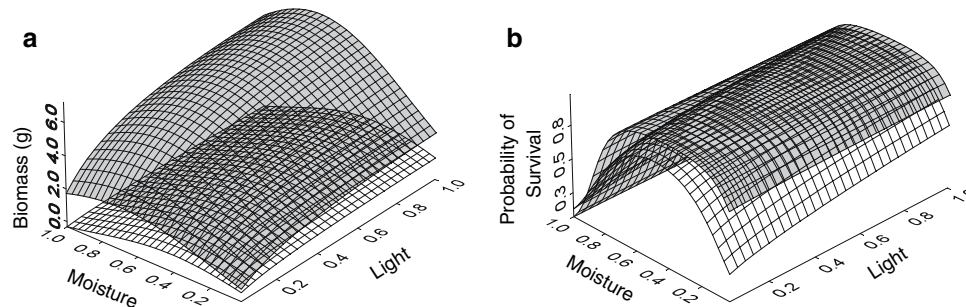
In the case of *Celastrus*, one such trait was the ability to tolerate low light, ranging on average from 0.8 to 6.4% transmittance (i.e., some individuals did survive); however, *C. orbiculatus* had much higher survival (90 vs. 68%) and almost three times the aboveground production (mean biomass of 1.93 vs. 0.67 g) in low-light habitats than *C. scandens*. The greater success of *C. orbiculatus* can be interpreted as this species having a better overall capacity for plastic growth (Schweitzer and Larson 1999; Daehler 2003; Burns and Winn 2006; Leicht and Silander 2006; Richards et al. 2006). Therefore, given sunflecks or areas of increased resources in an otherwise resource limited environment, *C. orbiculatus* would be more likely to show a functional response to increased resources than *C. scandens* (Leicht 2005).

The ability of *C. orbiculatus* and other invasive species to maintain themselves in unfavorable environments (i.e., low light) coupled with the capacity to outperform native species like *C. scandens*, even in favorable environments

Fig. 1 Bar plots of mean aboveground biomasses of *Celastrus*. *Light gray boxes* are *C. orbiculatus*, and *white boxes* are *C. scandens*. The *error bars* represent the 95% confidence intervals. The *letter codes listed* along the *x*-axis simply reference the ten different transplant sites. These are arranged arbitrarily

Table 1 Estimated parameters from a nonlinear mixed effects model of the effect of moisture and light on the biomass of *C. orbiculatus* (*df* = 595) and *C. scandens* (*df* = 455)

		Celastrus orbiculatus			*Celastrus scandens*		
		Value	Standard error	*t*-value	Value	Standard error	*t*-value
Moisture	α	2.642	0.673	**3.929**	2.073	0.366	**1.863**
Parameters	γ	–1.906	0.845	**–2.253**	–2.589	0.515	**–2.484**
Light	p_1	1.351	0.271	**4.992**	0.732	0.105	**3.257**
Parameters	p_2	9.855	5.604	1.758	4.701	2.835	1.234

Bold values indicate significance at the $P \leq 0.05$ level

Fig. 2a–b Nonlinear mixed-effects model surfaces for the response of **a** aboveground biomass to light and moisture in *C. orbiculatus* and *C. scandens*; aboveground biomass is untransformed for ease of interpretation. **b** Logistic regression surfaces for the probability of survival in response to light and moisture. The *gray surface* represents *C. orbiculatus* and the *white surface* is *C. scandens*

Table 2 Akaike's Information Criterion (AIC) values for the nonlinear mixed-effects models for biomass and the generalized linear mixed models for mortality of both *Celastrus* species

	Biomass model		Mortality model	
	C. *orbiculatus*	C. *scandens*	C. *orbiculatus*	C. *scandens*
Base model (site effects only)	668	273	4,140	3,516
+ Site effects + weighted variance	**627**	**245**	4,140	3,522
+ Site/subplots	668	273	**4,096**	**3,470**
+ Site/subplots + weighted variance	630	247	4,101	3,490

"Site effect" is the random site effect, "site/subplot" is subplot nested within site, and "weighted variance" means that we modeled the variance to scale with power-transformed light. The best model obtained by the AIC criterion for each species–response combination is marked in bold

that the native species prefers (i.e., high light), points to the superior plasticity of invasive species (Richards et al. 2006). The success of *C. orbiculatus* in low-light environments, and its prominence on the landscape is mirrored by several other successful invasive species in the Northeastern North American landscape, which is naturally covered by heterogeneous forests (Foster et al. 1998). These species, such as *Berberis thunbergii* (Japanese barberry, Silander and Klepeis 1999) and *Acer platanoides* (Norway maple, Webb et al. 2000; Martin and Marks 2006), are able to survive and reproduce in shaded environments more successfully than their native counterparts and can therefore dominate forest understories.

Lianas, as a result of being able to use neighboring vegetation as a support, have a highly plastic growth form (Schnitzer and Bongers 2002). They are often thought of as being "edge" or "gap" species, as they tend to grow in areas with high light and small diameter supports (e.g., shrubs and tree saplings) for climbing (Putz 1984). Besides *C. orbiculatus*, other invasive liana species, such as *Lonicera japonica* (Japanese honeysuckle), are also able to withstand the low light environment of the forest understory by photosynthesizing effectively, even in deep shade (Carter and Teramura 1988). By overrunning edges and gaps, as well as infiltrating low-light environments, exotic temperate liana species have the capability to fill a largely open niche in the Northeastern United States (Mack 2003) posing a significant threat to natural environments.

The specific environment in which a given invasive species is introduced has a great effect on its ability to

Fig. 3a–d Site random effects for mixed models for *Celastrus orbiculatus* and *C. scandens*: **a** *C. orbiculatus* biomass; **b** *C. scandens* biomass; **c** *C. orbiculatus* mortality; **d** *C. scandens* mortality. The points are the maximum likelihood estimates for the random effects, and the *lines* extend one standard deviation above and below the point estimate. The scale has been preserved for direct comparison of the magnitude of the random effects across species
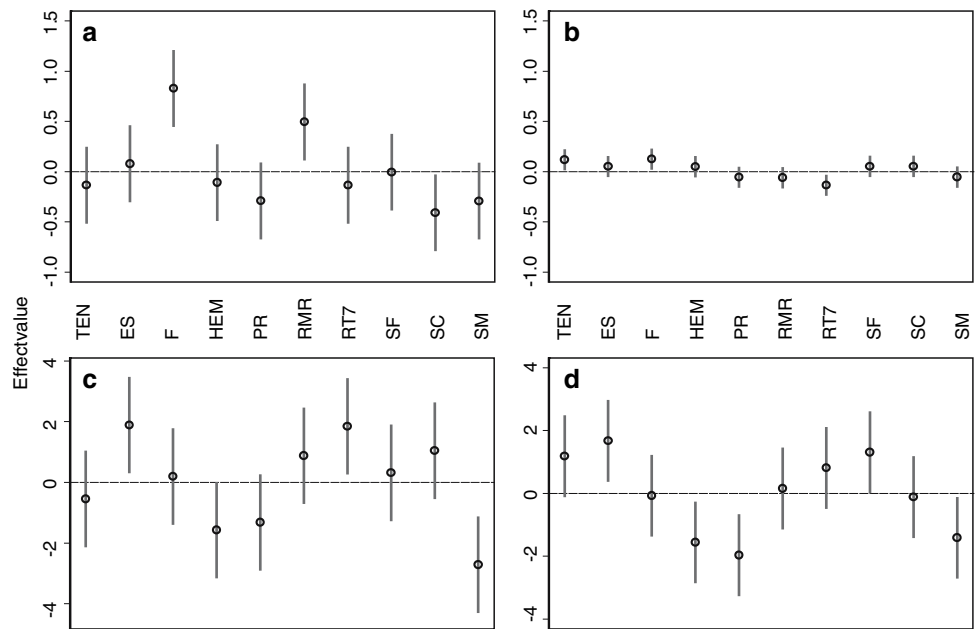
Fig. 4a–b Percent mortality in each habitat for *C. orbiculatus* and *C. scandens*. **a** Sites ordered by moisture; **b** sites ordered by light. The *letter codes* listed along the *x*-axis simply reference the ten different transplant sites. *Celastrus orbiculatus* is represented by the *gray bars* and *C. scandens* by the *white bars*
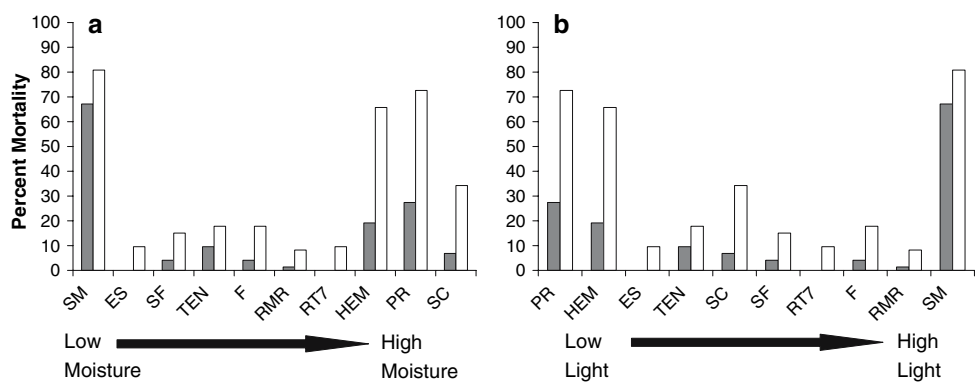
Table 3 Results of linear mixed-effects logistic regression model of the effect of moisture and light on the mortality of *C. orbiculatus* (df = 697) and *C. scandens* (df = 697)

Predictors	Celastrus orbiculatus			Celastrus scandens		
	Value	Standard error	*t*-value	Value	Standard error	*t*-value
Intercept	0.439	1.620	0.271	−1.631	1.337	−1.220
Moisture	14.202	7.191	**1.975**	11.527	5.818	**1.981**
Moisture^2	−17.281	7.963	**−2.170**	−12.070	6.418	**−1.881**
$\sqrt{\text{Light}}$	0.300	1.358	0.221	1.428	1.155	1.236

Bold values indicate significance at the $P \leq 0.05$ level

successfully establish. Extreme light or moisture conditions can prevent establishment, while high plasticity or ecological amplitude can greatly enhance the probability that a species will successfully naturalize. Both species of *Celastrus* show poorer survival in extremely dry and saturated habitats, although some seedlings did survive and grow over the course of the study in these extreme

environments. *Celastrus scandens* tolerated very wet conditions less well than *C. orbiculatus*, suffering much higher mortality (58 vs. 18%). Our results are thus consistent with those in a recent study on invasive dayflowers (Commelinaceae), which have also been shown to have greater biomass and node production (one proxy for height) than noninvasive congeners across varying water and nutrient

availabilities (Burns 2006). In both cases, then, the invasive species has shown greater plasticity in its ability to tolerate a greater range of moisture conditions.

Some of the mortality in dark conditions for *C. scandens* could have resulted from a species-specific fungus, *Marsonina thomasiana*, that caused the leaves to wilt and die (Boothroyd 1951; Jenkins and Jehle 1951; Sinclair et al. 1987). Overall, we observed approximately 17% of all *C. scandens* with lesions from this fungus. However, certain sites (RT7 and ES) had higher percentages of infection, with up to 32% of the plants affected. Despite the high incidence of infection in these sites, there was no apparent environmental causal effect in common. That is, neither site was both dark and wet nor otherwise apparently resource-limited. *Celastrus scandens* can grow back the following year after losing its leaves to this pathogen, but subsequent infections from year to year may be a cause of mortality (Leicht 2005). Interestingly, this fungus was not found to infect *C. orbiculatus* in this study (S. Leicht-Young, personal observation), which may add to its successful spread across the landscape.

Our study illustrates the importance of examining invasive species across environmental conditions. By observing their responses across gradients, we were able to identify characteristic differences in relative performance under different conditions, and also to directly compare the ecological plasticity or generality of the two species. Critically, this kind of experimental assay allows us to interpret current distributions of invasive species and predict their potential distributions across a region. This information allows for better predictions of where an invasive species will or will not be located in a given region, how it will perform there, and the mechanisms driving its performance.

From a practical perspective, this case study provides the first comparisons of relative habitat tolerances of *C. orbiculatus*, one of the most abundant and rapidly increasing invasive species in North America, with its native congener *C. scandens*. It shows clearly that invasive *C. orbiculatus* has the ability to colonize a wide range of environments, while the native *C. scandens* was more limited in its ecological amplitude. The status of *C. scandens* in the Northeastern United States needs to be more formally evaluated, going beyond just anecdotal evidence for its decline, so that appropriate conservation plans can implemented. Many rare and threatened species of the Northeastern United States are those of more open landscapes that have vanished over the past 100 plus years as a result of natural reforestation processes (Mitchell and Sheviak 1981; Zielinski 1993; K. Skogen and J. Barrett, personal communication). Thus, the situation of *C. scandens* may mirror that of other threatened species. Areas with existing populations of *C. scandens* should be monitored for

encroachments of *C. orbiculatus* and other invasive species to prevent the further decline of this species.

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