Extended leaf phenology may drive plant invasion through direct and apparent competition

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Invasive plants can inflict great harm, yet drivers of successful invasion remain unclear. Many invaders of North American deciduous forests exhibit extended leaf phenology (ELP), or longer growing season relative to natives. ELP may grant invaders competitive advantages, but we argue that ELP more potently drives invasion in the presence of herbivores. ELP invaders can support herbivores by lessening starvation during winter; consequently, native plants may suffer when attacked later through apparent competition. As modeled here, even short ELP can promote competitive success of invaders, and apparent competition sharply enhances ELP invader dominance. In 'partial enemy escape' scenarios, a less palatable ELP invader nearly excludes a preferred native where an invader without ELP could not. Together, ELP and apparent competition enhance invasion even when biotic resistance should suppress it, i.e. when the invader competes weakly or provides preferred forage. Thus, ELP-apparent competition interactions grant invaders considerable success while challenging core tenets of invasion ecology.

Invasive plant species can inflict significant economic costs (Pimentel et al. 2005) and can alter native communities and ecosystems (Mack et al. 2000, Levine et al. 2003). However, despite immense attention, the causes and consequences of species invasions still remain somewhat unclear (Gurevitch and Padilla 2004, Moles et al. 2012). Ecologists and managers continue to seek deeper insight into factors that drive species invasions. Theory points to focus on traits of interacting species: high impact invaders often differ in key functional traits compared to native species inhabiting the invaded range (MacDougall et al. 2009). Leaf phenology may be one such trait. For example, plant invaders of eastern deciduous forests often exhibit extended leaf phenology (ELP; Fridley 2012, Smith 2013). ELP grants these species longer intervals between leaf budbreak in spring and abscission in autumn relative to co-occurring natives (Fridley 2012). The extent of ELP of invaders varies, though, ranging from a few weeks to several months (Smith 2013).

Extended leaf phenology may drive invasion by conferring invaders with a competitive advantage over native species. By opening access to seasonally underutilized resources, ELP may allow the invader to exploit light and nutrients that are unavailable to dormant natives (Wolkovich and Cleland 2011, Fridley 2012). This access to resources may grant the 'ELP invader' a competitive advantage later in the growing season. Empirical evidence supports this expectation. In forest understories, invaders gain significant carbon before and after native species have lost their leaves (Harrington et al. 1989, Fridley 2012). Furthermore, access to light prior to canopy closure can allow invaders to suppress some native competitors (Smith and Reynolds 2013). Annual plant species with ELP can also gain fitness advantages (Godoy and Levine 2014, Kraft et al. 2015). However, ELP-driven resource competition cannot fully explain invader dominance. Some invaders – even those with ELP – appear to compete weakly with native species (Daehler 2003, Kalisz et al. 2014). Ordinarily, biotic resistance from superior native competitors might suppress these weakly competitive invaders; yet, these invaders continue to dominate native plant communities. For these invaders, additional factors must account for their dominance.

A multi-trophic framework may powerfully explain success of even weakly competitive ELP invaders (Smith 2013). For example, ELP may drive invader impact by altering herbivore population dynamics, with cascading effects on native plant communities. These cascading effects could occur through apparent competition, in which one plant species suppresses another by promoting a shared enemy. Under apparent competition, an introduced species that supports elevated herbivore densities can increase herbivore pressure on natives. Higher herbivory, in turn, suppresses native species more than resource competition alone, in theory (Holt 1977, Holt et al. 1994, Chesson 2013) and empirically in some invasion systems (Smith and Quin 1996, Roemer et al. 2002). ELP invaders may drive stronger apparent competition than non-ELP invaders. For example, ELP invaders may subsidize herbivore density when native plants are scarce, essentially preventing some herbivores from

starving. ELP-supported herbivore density, then, could more strongly suppress native species (Settle et al. 1996, Blitzer and Welter 2011).

However, the importance of ELP-mediated apparent competition may depend strongly on the relative palatability of invaders (Fig. 1). Indeed, herbivore preference could undermine it: invaders might be too inedible or too palatable. For instance, exotic invaders often benefit from 'enemy escape.' Here, native herbivores avoid unfamiliar or unpalatable invaders (Keane and Crawley 2002), perhaps undermining the ELP-mediated, apparent competition-based mechanism of invasion success. However, partial enemy escape of invaders may still boost enemy density (Chaneton and Bonsall 2000), especially when preferred (native) food is scarce. If herbivores exhibit prey-switching, preferentially consuming natives as native density increases, the temporal release from herbivory could enhance invader success. Alternatively, highly palatable invaders may fail to dominate due to 'biotic resistance' from native herbivores (Maron and Vila 2001, Levine et al. 2004). However, if an extended growing season enables palatable invaders to support high herbivore densities while maintaining their own growth, subsequent herbivore pressure on native competitors may still promote high relative abundance of the invader. If this scenario holds, the conventional expectation that native generalist herbivores will suppress palatable exotics may falter for ELP invaders (Fig. 1).

A key case study of ELP invaders and white-tailed deer *Odocoileus virginianus* illustrates these ideas in eastern (USA) deciduous forests. Currently, extreme overabundance of white-tailed deer imposes intense herbivore pressure on natives, powerfully shaping native understory communities (Tilghman 1989, Rooney and Waller 2003, Côté et al. 2004). Seasonal food availability can strongly shape deer dynamics, since starvation during winter can result in high mortality (Pekins et al. 1998). Thus, invaders with ELP might fuel deer overabundance by increasing late season fat reserves and reducing early season starvation. White-tailed deer do consume several ELP invasive shrubs and vines that vary in palatability (Rogers et al. 1990, Schierenbeck et al. 1994, Vellend 2002, Myers et al. 2004, Shelton et al. 2014). The extent of ELP among these grazed invaders ranges from

a few weeks or months for deciduous shrubs such as bush honeysuckle *Lonicera maackii* (McEwan et al. 2009) to evergreen invaders such as the vine purple wintercreeper *Euonymus fortunei* (Smith 2013). It seems possible, then, ELP may enhance invader dominance in these forest ecosystems via apparent competition from deer.

Inspired by this deer-based case study, we developed a mathematical model to address some key uncertainties about ELP-mediated direct and apparent competition. Specifically, we focused on three questions linking ELP to interactions between native and invasive plants and their herbivores. Question 1, extent of ELP: what extent of ELP would enhance an invader's advantage in direct and apparent competition? Question 2, ELP and competitive ability: can ELP and apparent competition maintain invader dominance even when the invader competes very weakly? The interaction of ELP and herbivory may explain success of otherwise competitively inferior invaders. Question 3, herbivore preference: how does herbivore preference for natives versus ELP invaders influence the outcome of apparent competition? ELP-mediated apparent competition may exacerbate partial enemy escape for less palatable invaders. Such an escape would undermine biotic resistance against palatable invaders.

Model

We constructed a model of two plant species (the native, N, and the invader, I) that share one herbivore (H). The plants compete following Lotka–Volterra assumptions, while the herbivore feeds with a type-II multi-prey functional response. We incorporated extended leaf phenology into the model using sinusoidal growth functions, where the maximal growth rate, $r_j(t)$, for each plant varies according to a sinusoidal function over the course of the growing season (sensu Turchin and Hanski 1997). The two plant species exhibit logistic growth due to negative density dependence, where the strength of intraspecific density dependence is c_N or c_I. The plants suppress each other's growth through Lotka–Volterra competition, where α and β are competition coefficients that scale c_N and c_I to reflect the strength of interspecific competition. The two plants share an herbivore with
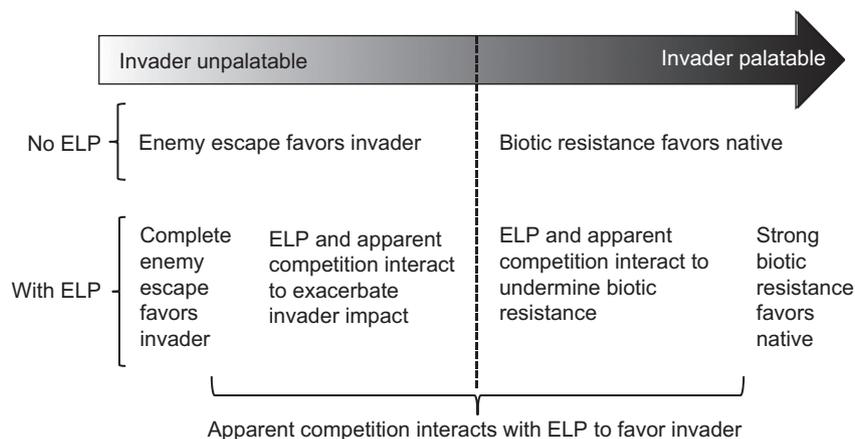
Figure 1. Extended leaf phenology (ELP) and herbivory may interact to exacerbate dominance of unpalatable invaders and but may also undermine biotic resistance towards palatable invaders. The dotted line denotes equal palatability of invader and native.

a species-specific grazing rate f_N or f_I, and with a common half-saturation constant of h. The model is:

$$\frac{dN}{dt} = r_N(t)N - c_N N^2 - c_N \beta IN - \frac{f_N NH}{h+I+N} \tag{1}$$

$$\frac{dI}{dt} = r_I(t)I - c_I I^2 - c_I \alpha NI - \frac{f_I HI}{h+I+N} \tag{2}$$

Seasonal forcing is driven by a sinusoidal growth function, $r_j(t)$, for each of the two plant species. Sinusoidal growth functions are commonly used to model seasonality because they provide mathematically elegant, smooth transitions between growing and non-growing seasons (Turchin and Hanski 1997). For the native species, the growing season is approximately half of the year (Table 1), so one symmetrical cosine function can capture the seasonal forcing (Eq. 3):

$$r_N(t) = r_N\left(1 - \varepsilon\cos\frac{\pi t}{Z_N}\right) \tag{3}$$

Here (Eq. 3), $r_N(t)$ is the growth function for the native, r_N is ½ of the maximum growth rate, and epsilon (ε) is the amplitude of seasonal forcing. The term within the cosine function gives a symmetrical sinusoidal wave with a period of one year ($2Z_N = Y$). A different function represents ELP of the invader, $r_I(\tau)$. It follows a more piece-wise structure, with a longer growing season and shorter winter season (Fig. 2a). If the length of the year is Y, but the growing season of the invasive is Z_I, then density-independent growth rate of the invasive, $r_I(\tau)$, is:

$$r_I(\tau) = r_I\left\{ \begin{array}{ll} \left[1-\varepsilon\cos\dfrac{\pi t}{Y-Z_I}\right] & when \qquad 0 < \tau < \left[\dfrac{Y}{4}-\dfrac{\delta}{2}\right] \\[12pt] \left[1-\varepsilon\cos\dfrac{\pi(\tau+\delta)}{Z_I}\right] & when \qquad \left[\dfrac{Y}{4}-\dfrac{\delta}{2}\right] \le \tau \le \left[\dfrac{3Y}{4}+\dfrac{\delta}{2}\right] \\[12pt] \left[1+\varepsilon\cos\dfrac{\pi(\tau-Z_I)}{Y-Z_I}\right] & when \qquad \left[\dfrac{3Y}{4}+\dfrac{\delta}{2}\right] < \tau \le Y \end{array} \right\} \tag{4}$$

where r_I is half of the maximum growth rate, ε is the amplitude of the season wave, δ is the difference between invasive and native growing seasons, $Z_I - Z_N$, and τ is time scaled between 0 and 12 months. The top row (Eq. 4) models density-independent growth rate from January (month 0) through the start of the growing season; the second row represents the growing season; and the third row captures the end of season. When $\delta > 0$, the invader exhibits ELP; when $\delta = 0$, growth rate collapses back to that of the (symmetrical) native species (Eq. 3). When the two species have identical (half) peak maximal growth rates ($r_I = r_N$), the average growth rate for the invader slightly exceeds that for the native. Higher year-averaged growth of ELP invaders is consistent with field measurements (Rogers et al. 1990, Baruch and Goldstein 1999, Matzek 2011, Heberling and Fridley 2013). During the non-growing season, maximal growth rate, $r(t)$, remains positive but the carrying capacity of the native or ELP plant drops. Hence, the population shrinks (i.e. growth rate becomes negative, $dN/dt < 0$, for some part of the year).

The herbivore (Eq. 5) feeds on both the native and invader at rates f_N and f_I, respectively, with a conversion efficiency of g. The herbivore exhibits a type II functional response with half saturation constant h, and has a constant background mortality rate of m (Eq. 5):

$$\frac{dH}{dt} = \frac{g(f_I I + f_N N)H}{h+I+N} - mH \tag{5}$$

We simulated this model (Eq. 1–5) to understand how ELP influences both direct and herbivore-mediated apparent competition. To answer our three focal questions, we simulated our model across gradients of growing season length (Z_I), relative competitive abilities of the two plant species (α and β), and herbivore preference (f_I and f_n). We simulated using MATLAB (ver. R2013a) and a standard adaptive step integrator (ode45) over ranges of the parameter values (Table 1). In all cases, we simulated the model for 1000 months to eliminate transients, and then another 1200 months (100 years) to calculate annual mean densities or relative invader density ($[I+N]/N$) by integrating through time using the trapezoid rule. Default parameter values (Table 1) were consistent with estimated values for ungulate herbivores eating native and invasive understory vines and shrubs (Supplementary material Appendix 1). Plant and herbivore mass (individuals and growth per individual during the season) were expressed as Mg ha^{-1} (megagrams per hectare). Qualitative results of the model shown here were robust given the ranges of parameter values listed (Table 1).

Results

Extended leaf phenology can grant invaders an advantage in direct competition alone, and apparent competition enhances this advantage. In the latter case, an ELP invader ($Z_I > Z_N$) elevates herbivore density more than an invader without ELP ($Z_I = Z_N$; Fig. 2b), thus increasing grazing pressure on natives. To illustrate, consider a few examples incorporating ELP, competition, and apparent competition incrementally (Fig. 2c–f). Extended leaf phenology slightly elevates invader density without competition and herbivory (because the invader enjoys higher growth rate averaged over the year; Fig. 2c). However, addition of direct interspecific competition (Fig. 2d) or herbivore-mediated apparent competition (Fig. 2e) increases the relative advantage of the invader over the native. Combining both direct and apparent competition (Fig. 2f) further increases the density advantage of an ELP invader over the native species.

The extent of ELP, particularly with grazing, strongly influences competition between plant species and dominance of the invader (Question 1; Fig. 3–4). Without ELP, biotic resistance from the native competitor should prevent invader dominance whenever natives are competitively superior (i.e. $\alpha < \beta$, given other parameters). Without herbivores, longer growing season of the invader (i.e. $Z_I > 6$, up to 9 months) decreases the threshold competition coefficient β required for invader dominance (i.e. more than 50% invader biomass; $I > N$ and $N = 0$ regions, Fig. 3a). The herbivore accentuates this effect, dropping this threshold β even more sharply with increasing invader ELP (Z_I) (Fig. 3b). With

Table 1. State variables and parameters used in the model (Eq. 1–5).

State variables	Definition	Default value	Units	
N	Aboveground (edible) biomass of native	…	Mg ha^{-1}	
I	Aboveground (edible) biomass of invader	…	Mg ha^{-1}	
H	Biomass of herbivore	…	Mg ha^{-1}	
t	Time	…	months	
Parameters	Definition	Default value	Units	Range
r_N	½ of peak maximal growth rate, native	0.3[a]	month^{-1}	0.04–1
r_I	½ of peak maximal growth rate, invader	0.3[a]	month^{-1}	0.04–1
c_N	Strength of intra-specific negative density dependence for native	0.3[a,b]	(Mg ha^{-1})$^{-1}$ month^{-1}	0.04–1
c_I	Strength of intra-specific negative density dependence for invader	0.3[a,b]	(Mg ha^{-1})$^{-1}$ month^{-1}	0.04–1
α	Competition coefficient, effect of N on I	0.5	--	0–1
β	Competition coefficient, effect of I on N	0.5	--	0–1
f_I	Maximum grazing rate on invader	0.7[c,d]	month^{-1}	0–1
f_N	Maximum grazing rate on native	0.7[c,d]	month^{-1}	0–1
h	Half-saturation constant of herbivore	0.4[b]	Mg ha^{-1}	0.3–0.5
g	Conversion efficiency of herbivore	0.5[e]	--	0.4–0.6
m	Mortality rate of herbivore	0.2[f]	month^{-1}	0.15–0.3
Z_I	Length of growing season, invader	8[g,h,i]	months	6–9
Z_N	Length of growing season, native	6[j]	months	6
δ	Extent of ELP ($Z_I - Z_N$)	2	months	0–3
Y	Length of a full year	12	months	12
ε	Seasonal strength (amplitude in Eq. 3,4)	0.7[k]	--	0–1

Sources: a = (Rogers et al. 1990); b = (Vivas and Saether 1987); c = (Wickstrom et al. 1984); d = (Crete and Bedard 1975); e = (Turchin 2003); f = (Voigt et al. 1997); g = (Fridley 2012); h = (Xu et al. 2007); i = (McEwan et al. 2009), j = (Smith and Reynolds 2013), k = (Turchin and Hanski 1997).

large ELP ($Z_I > 8$ months), herbivory enables dominance by an invader with no direct competitive effect on the native at all ($\beta = 0$, Fig. 3b). In contrast, without the herbivore, the invader must always exert some direct competitive impact on the native ($\beta > 0$) in order to dominate (Fig. 3a). Further-more, invaders with larger ELP benefit more from herbivory (Fig. 4). For instance, elevation of grazing rate (f_N and f_I) favors invaders with longer growing season (Z_I). In contrast, with small ELP, increasing grazing rate alters invasive domi-nance little (Fig. 4a). The herbviore becomes most abundant
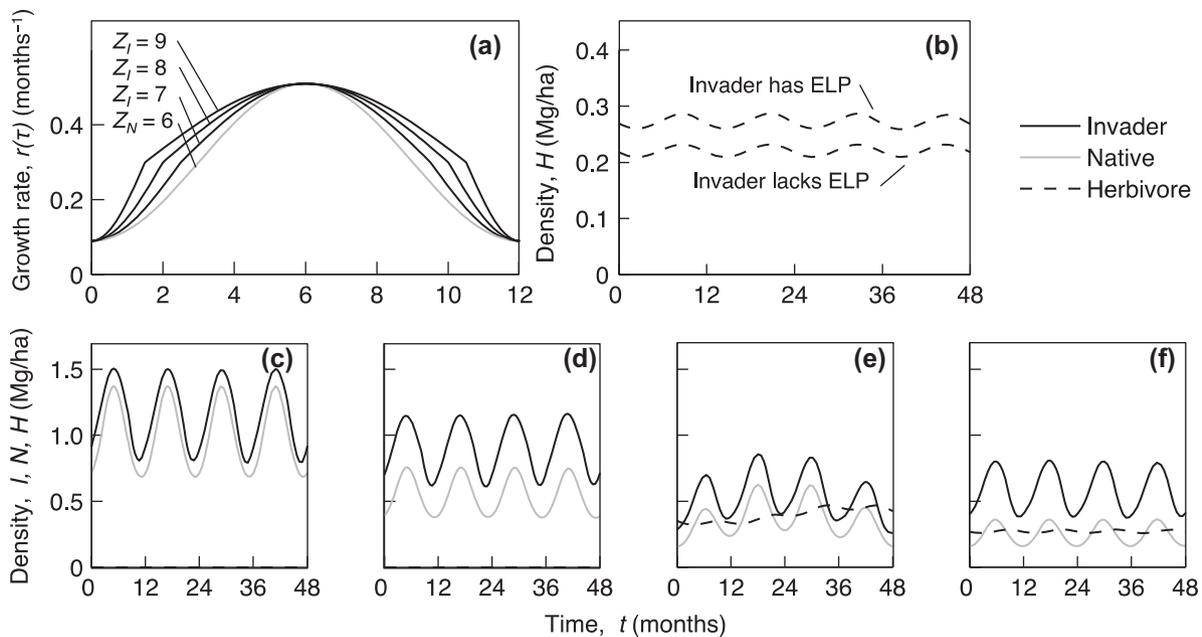
Figure 2. Invaders with extended leaf phenology (ELP) can elevate herbivore density and gain advantage in direct and apparent competi-tion. (a) Maximal growth rate of the ELP invader, $r_I(\tau)$, as a piecewise cosine function (invader: black, with three growing season lengths [Z_I]; native: grey, with six month growing season [Z_N]). (b) Invader ELP elevates herbivore density. Lower dashed line: no ELP ($Z_I = Z_N = 6$ months); upper dashed line: invader with ELP ($Z_I = 8$, $Z_N = 6$). (c–f) Four scenarios with an ELP invader ($Z_I = 8$), the native plant ($Z_N = 6$), and their shared herbivore (grazing rate: $f_N = f_I = 0.6$). (c) No competition (coefficents $\alpha = \beta = 0$), no herbivores ($H = 0$); (d) symmetrical competition ($\alpha = \beta = 0.5$) without grazing; (e) shared herbivory without competition (i.e. pure apparent competition); and (f) grazed plants compete symmetrically ($\alpha = \beta = 0.5$). Default parameters used (Table 1) unless otherwise specified.
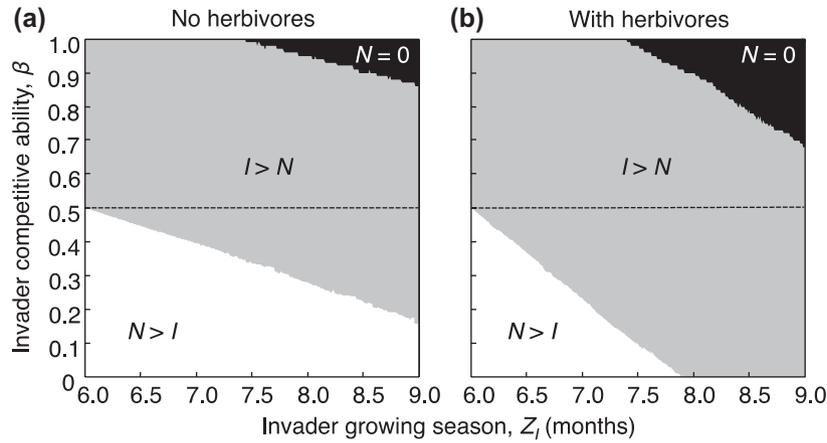
Figure 3. Herbivory combined with extended leaf phenology allows the invader (I) to dominate even when it is a weak competitor compared to the native (N). Contour plots show varying invader competitive ability (β) and invader growing season length (Z_I) (a) with and (b) without the herbivore (H). Three qualitative outcomes are depicted: the native dominates (white region: '$N > I$'), the invader dominates (grey region: '$I > N$'), or the invader excludes the native (black region: '$N = 0$'). Native competitive ability (α) is fixed at 0.5, indicated by the dashed horizontal line; when $\beta < 0.5$, the invader competes inferiorly. Unless otherwise specified, all parameters use default values from Table 1.

as Z_I increases (Fig. 4b), reaching a maximum with long ELP and moderate grazing rate.

Extended leaf phenology interacts with herbivory to alter the relative competitive ability required for invader dominance (Question 2, Fig. 5). Extended leaf phenology (ELP) subtly benefits the invader when the two plant species compete without herbivory (i.e. left and central columns of Fig. 5). However, ELP with herbivory (right column, Fig. 5) confers a much greater advantage to the invader. More specifically, without ELP ($Z_I = 6$) the native and invader have equal density when they are equal competitors ($\alpha = \beta$, Fig. 5a–c). Adding ELP (e.g. $Z_I = 8$) enables invader dominance even when it competes weakly ($\alpha > \beta$, Fig. 5d–f). Then, adding herbivory drastically increases the invader's advantage. In fact, with apparent competition, it possible for the invader

to exclude the native over a range of competitive scenarios (Fig. 5g–i).

Variation in herbivore preference reveals further joint influence of ELP and apparent competition on invasive dominance (Question 3, Fig. 6). Preference for the native species ($f_N > f_I$; above the dashed 1:1 lines) enables the invader to dominate, even without ELP. However, ELP strongly exacerbates this effect. When the invader has the same growing season length as the native (no ELP, $Z_I = 6$), preference for either species reduced its abundance - the results were symmetrical (around the 1:1 preference line; Fig. 6a). Neither plant species could exclude the other when both shared equal growing seasons (at least over the parameter range examined). But, with ELP, invaders can dominate even if the herbivore exerts slight preference for the invader, i.e. when we might
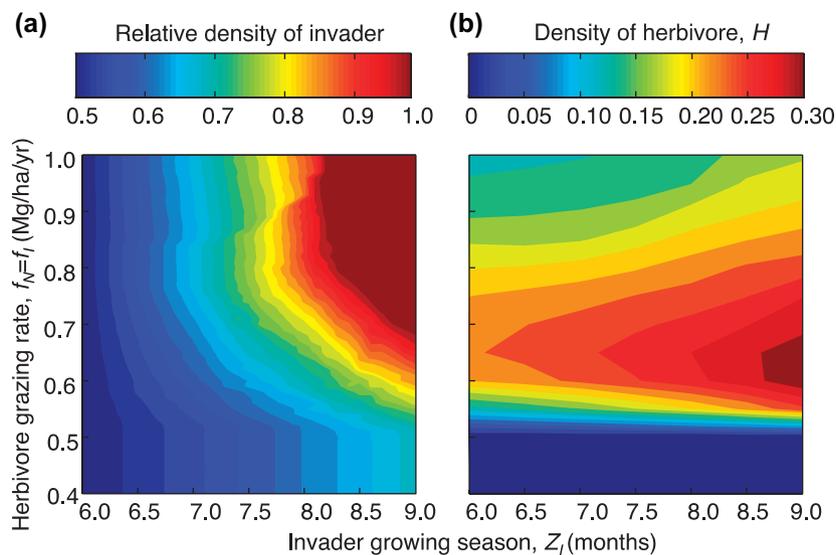
Figure 4. Herbivory increases dominance (relative density > 0.5) of an invader with extended leaf phenology. Contours show (a) relative density of the invader (I), and (b) density of the herbivore (H, Mg ha^{-1}) as herbivore grazing rate and length of invader growing season (Z_I) vary. Native growing season (Z_N) is fixed at six months. Herbivores exert symmetrical grazing rate on both plants ($f_N = f_I$); additionally, both plants compete symmetrically ($\alpha = \beta$). Unless otherwise specified, all parameters use default values from Table 1.
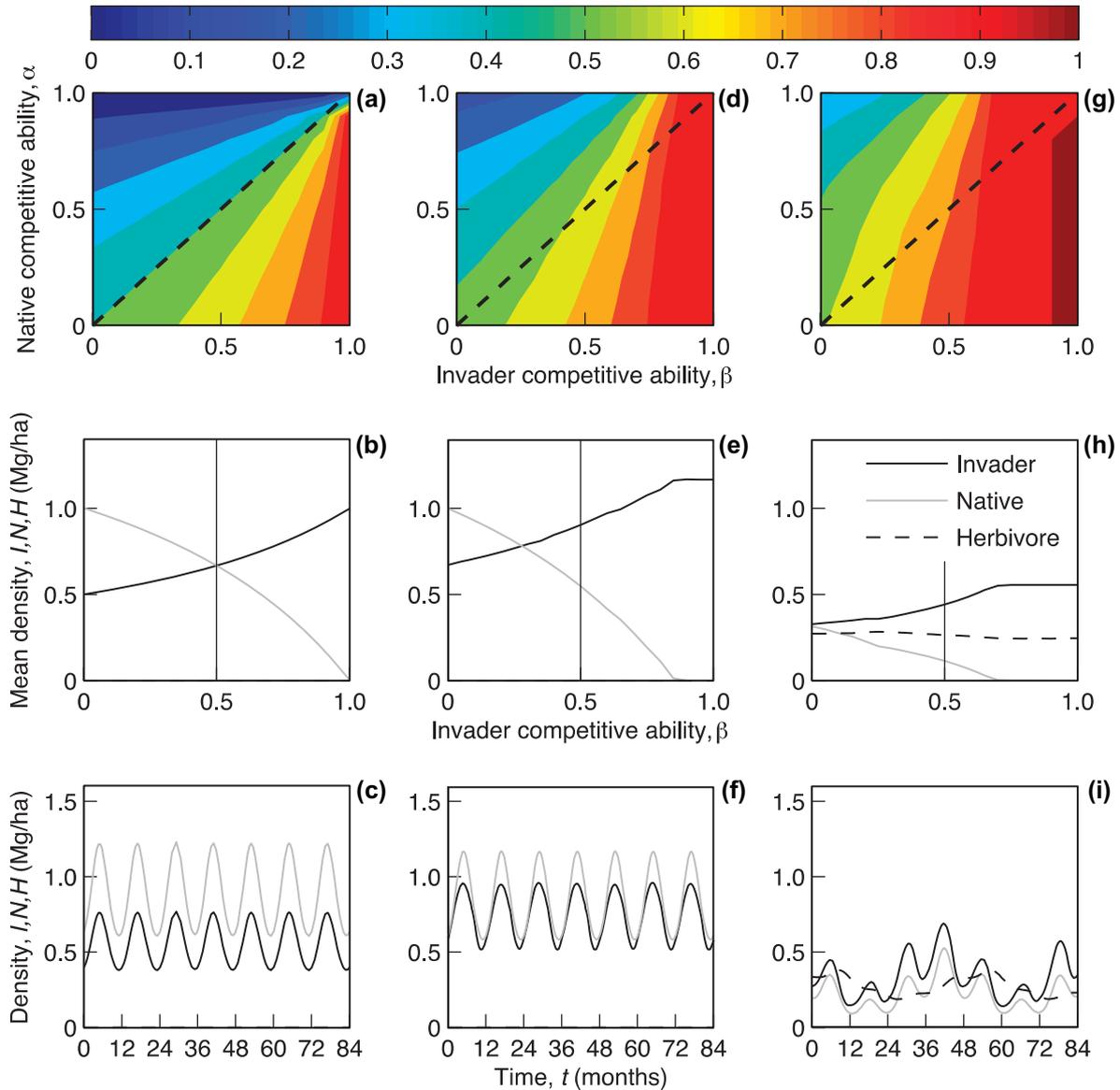
Figure 5. Links between competition coefficients (α, β) and dynamics of the native plant (N), the invader (I) with extended leaf phenology (ELP), and their shared herbivore (H). First column (a–c): no ELP ($Z_I = Z_N = 6$ months), no herbivore; middle column (d–f): invader has ELP ($Z_I = 8$ months), no herbivore; third column (g–i): ELP with herbivory (but $f_N = f_I$). Top row (a, d, g): relative density of the invader (see top bar for scale) with varying competitive strengths. The dashed (1:1) line indicates competitive equivalence ($\alpha = \beta$). Below the line, the invader competes superiorly. Middle row (b, e, h): mean (annual) species densities as the invader's competition coefficient (β) varies but the native's remains fixed ($\alpha = 0.5$). These can be viewed as a 'slice' of the figures in the top row. Bottom row (c, f, i): dynamics with a competitively weak invasive ($\beta = 0.2$) relative to the native ($\alpha = 0.5$). All other parameters use default values (Table 1).

expect biotic resistance from herbivory to suppress invasion ($f_I > f_N$; below the dashed 1:1 line; Fig. 6b). When the herbivore prefers the native species (i.e. 'partial enemy escape' for the invader), herbivores enable the invader to strongly dominate and even exclude the native over a wide range of parameter values (Fig. 6b.vi). Herbivores must strongly prefer the invader to undermine the advantages granted by ELP to the invader (Fig. 6b.iv).

Discussion

In our model, even moderate levels of extended leaf phenology (ELP) enabled the invasive plant to dominate the native through direct and apparent competition. ELP

elevated herbivore density, enhancing apparent competition. As a result, ELP can allow an invader to dominate over the native species - even when the invader is an inferior competitor compared to the native species (Question 2; Fig. 3). Furthermore, ELP-enhanced apparent competition acted potently with partial enemy release to secure invader dominance (Question 3). More specifically, when herbivores preferred the native species (the common scenario: Keane and Crawley 2002), ELP drastically increased the advantage the invader gained through apparent competition (Fig. 6b). ELP-enhanced herbivory could even promote invader dominance when the herbivore slightly preferred the ELP invader (Fig. 6b). This counter-intuitive result required ELP: without ELP, the herbivore would suppress the invader through biotic resistance (Fig. 6a).
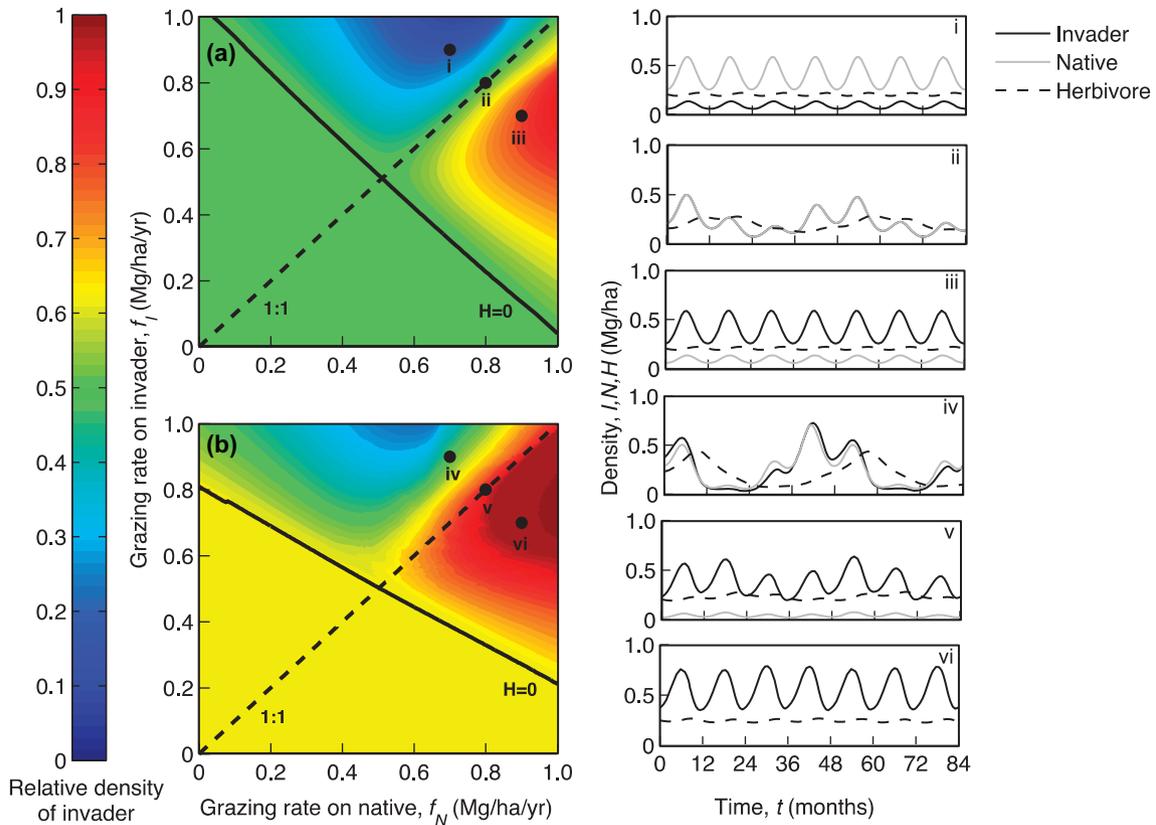
Figure 6. Extended leaf phenology (ELP) gives the invader (*I*) a strong advantage in apparent competition when the herbivore (*H*) prefers the native (*N*; i.e. when $f_N > f_I$). Contour plots and select simulations link relative herbivore preference to relative density of the invader (scaled by colored contours) when plants compete equally. Below the solid line (denoted as 'H = 0'), the density of the herbivore is zero. The dotted 1:1 diagonal line denotes no preference by the herbivore ($f_I = f_N$). Roman numerals in contour plots pair parameter values (dots) with illustrative simulations on the right. Top row (a): the invader does not have ELP ($Z_I = Z_N = 6$); bottom row (b): invader has ELP of eight months ($Z_I = 8$) versus the native's six months ($Z_N = 6$).

Questions 1 and 2: extent of ELP and relative competitive ability

While invaders often show extended leaf phenology, the extent of ELP can vary widely, from a few weeks to several months (Kloeppel and Abrams 1995, Rodgers et al. 2008). Can short periods of ELP can influence invader dominance at all? Our model shows that, without herbivores, longer ELP lowers the competitive ability required for invader dominance (almost proportionally with ELP: Fig. 2a). A phenological advantage of two months – typical for several deciduous shrub invaders (Supplementary material Appendix 1) – allows an invader which competes inferiorly to dominate ($\alpha > \beta$; Fig. 4b). Herbivores greatly enhance this ELP-mediated advantage. Thus, ELP with apparent competition can promote invader dominance even with very small phenological difference between competitors. These results suggest that, all else being equal, invaders with longer ELP should dominate natives more than those with shorter ELP; yet, with apparent competition, even slight ELP can grant invaders considerable advantage.

Question 3: ELP and herbivore preference

The model also shows that 'partial enemy escape' and ELP-mediated apparent competition can interact potently. 'Partial

enemy escape' describes many systems in which herbivores prefer natives but still eat invaders (Pearson et al. 2011, Burghardt and Tallamy 2013). The model confirms that partial enemy escape should benefit the invader, even without ELP (Fig. 5a). However, ELP drastically enhances invader dominance: the invader nearly excludes the native when the herbivore shows any preference for the native species (i.e. when there is any 'partial enemy escape'; Fig. 5b). The herbivore can even elevate relative density of an ELP invader that it slightly prefers, as when defended natives compete with more palatable invaders. However, the invader must have ELP to produce this scenario. Thus, ELP enables dominance of invaders which herbivores would otherwise suppress (i.e. ELP can undermine biotic resistance, Levine et al. 2004). Instead of preventing invasion through biotic resistance, the herbivore could promote invasion of palatable ELP plants through apparent competition.

Conservativeness of parameterization

Our model realistically but conservatively grants higher year-averaged maximal growth rate to ELP invaders. Consider our default trait values (Table 1). Both native and ELP-invader species have identical (half) peak maximal growth rates ($r_N = r_I$). Thus, the invader has higher (ca 13% when $Z_I = 8$) maximal growth rate when averaged over

a year. This difference reflects the biology of extended leaf phenology, which generally grants invaders elevated year-averaged growth compared to native species. In fact, our parameterization is likely conservative for many ELP invaders, which exhibit elevated maximal growth rates throughout the growing season. For example, invaders commonly exhibit elevated maximum photosynthetic rates compared to native congeners (Heberling and Fridley 2013, Zinnert et al. 2013), in addition to elevated carbon gain due to ELP (Harrington et al. 1989, Schierenbeck and Marshall 1993, Fridley 2012). The invader *Lonicera japonica* fixes carbon 40–450% faster that its native competitors, depending on the season (Schierenbeck 2004). In our model, such an elevated peak maximal growth rate for the invader (i.e. $r_I > r_N$) only accentuates herbivore-mediated advantages gleaned by ELP-invaders. Therefore, for many important invasive species problems, our model may underestimate the role of apparent competition in ELP systems.

Relevance to the case study

Our model helps to explain how ELP can simultaneously drive invader dominance and deer overabundance in the focal case study. Deer densities have reached record highs in many Eastern deciduous forests, unleashing devastating consequences for native vegetation (Tilghman 1989, Rooney and Waller 2003, Côté et al. 2004). Elevated deer density may reflect release from predation via culling and extirpation of predators such as wolves, although recent work challenges this conventional wisdom (Côté et al. 2004, Kauffman et al. 2010, Marshall et al. 2013). Nonetheless, the present model shows how even moderately palatable, ELP invaders could also bolster high deer densities from the bottom up. By providing relatively high quality food during starvation periods, ELP invaders could elevate deer carrying capacities. Field patterns are consistent with this hypothesis. For example, deer reach higher densities in landscapes with the ELP invader bush honeysuckle *Lonicera maackii*; (Allan et al. 2010), and deer do consume honeysuckle throughout eastern deciduous forests (Vellend 2002, Myers et al. 2004, Shelton et al. 2014). Both lines of evidence support our key prediction that ELP invaders can dominate by elevating herbivore densities. However, confirmation of this prediction requires large scale studies of white-tailed deer dynamics in areas invaded by ELP species versus areas where management actions exclude them (assuming equal predation of deer across both environments).

Enhancing the herbivore model

Although parameterized for a white-tailed deer example, our general model could incorporate more relevant biology of this or any other system. For example, focusing on the case study again, deer experience increased metabolic demands and elevated starvation rates during winters, particularly fawns and females undergoing gestation (Pekins et al. 1998). This phenomenon could be modeled within our framework by making the per capita loss rate of the herbivore (*m*) vary seasonally but also as a function of food density. An age-structured dynamic energy budget (DEB) model could more accurately predict deer dynamics, too. The DEB framework accounts for fat reserves and for seasonal variation in metabolic demand associated with gestation, lactation, and maintenance (sensu Illius and O'Connor 2000, De Roos et al. 2009). However, adding this realism (seasonal/resource dependent mortality, energy storage) would likely enhance the patterns produced from the generalized model. An invader that provides high quality food during times of very high metabolic demand would elicit even greater effects on population sizes of herbivores. Our current model, then, may even underestimate the importance of ELP as a force modulating apparent competition between natives and invaders.

Applications to climate change

Although focused on ELP invaders, this model can also anticipate outcomes of competition (direct and apparent) between co-occurring native species with different phenologies, particularly in response to climate change. For instance, early spring green-up due to inter-annual variation in spring temperature, which increases food during times of a scarcity, can increase the carrying capacity of large herbivores (Pettorelli et al. 2005, Garel et al. 2011). Increased herbivory should elicit cascading consequences for vegetation density and community structure (Schmitz et al. 2000, Estes et al. 2011). Within any deciduous system, native species vary in their leaf phenologies (Lechowicz 1984, Polgar and Primack 2011), as well as in their phenological plasticity in the face of climate change (Morin et al. 2009). By supporting more herbivores, species that respond to climate change by leafing out early may indirectly intensify grazing on more conservative species that leaf out later, altering vegetation dynamics amongst native species. Furthermore, in a seasonally fluctuating environment, natives with ELP could gain advantage from ELP even if they sustain higher herbivory due to their phenology. This prediction contradicts expectations for plants sharing similar phenologies (Fig. 6a).

Conclusions

This seasonal model of extended leaf phenology provides significant insight into several key questions in invasion ecology. First, ELP can promote invader dominance through both direct and apparent competition. ELP grants invaders an advantage even with small phenological differences between native and invasive plants. Furthermore, ELP combined with apparent competition can drive invader dominance even when the invader competes relatively weakly. Combined, these two results may explain surprising dominance of ELP invaders in the field, even of those competing inferiorly in more controlled experiments. Second, partial enemy escape can accentuate the advantage invaders gain through combined ELP and apparent competition. This finding challenges the conventional wisdom that enemy escape and apparent competition are mutually exclusive invasion mechanisms. Third, ELP undermines biotic resistance as a mechanism that deters invasion. Because they fuel herbivore growth at key times seasonally, highly palatable invaders with ELP can suffer intense herbivore pressure and still dominate natives. Thus, due to ELP, native communities with generalist herbivores that attack exotics may repel invaders less effectively than previously hoped.

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