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Role of multiple invasion mechanisms and their interaction in regulating the population dynamics of an exotic tree

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ABSTRACT

1. Understanding the mechanisms that allow exotic species to have rapid population growth is an important step in the process of controlling existing invasions and preventing future invasions. Several hypotheses have been proposed to explain why some exotic species become invasive, the most prominent of which focus on the roles of habitat disturbance, competitors and consumers. The magnitude and direction of each of these mechanisms on population dynamics observed in previous studies is quite variable. It is possible that some of this variation results from interactions between mechanisms.
2. We examined all of these mechanisms and their interactions on the population dynamics of the Asian exotic tree *Ailanthus altissima* (Simaroubaceae) in fire-suppressed oak-hickory forests in Missouri, USA. We experimentally reduced herbivory (using insecticide), reduced interspecific competition (plant removals), and manipulated disturbance with prescribed fire. We projected the effects of these treatments and their interactions on population dynamics by parameterizing an integral projection model.
3. The lowest population growth rate is found where fire is absent and biotic interactions are present. Fire increased population growth rate, likely through the suppression of interspecific competitors, since competitor removal treatments increased population growth rate in the absence but not presence of fire.
4. These results indicate that biotic resistance from interspecific competitors, more so than consumers, is important for slowing the invasion of *A. altissima*. Furthermore, disturbances that weaken biotic interactions, such as fire, should be used with caution when restoring habitats invaded by *A. altissima*.
5. *Synthesis and applications*. Examining the main and interactive effects of disturbance, competition and herbivory on the population dynamics of exotic species provides a comprehensive understanding of the role of these factors in the invasion process and provides guidance for exotic species management.

Keywords: *Ailanthus altissima,* fire, biotic resistance hypothesis, invasive species, enemy release hypothesis, competition, herbivory, population growth, integral projection model, exotic species

INTRODUCTION

An understanding of the mechanisms that allow exotic species to have rapid population growth is an important step in the process of controlling existing invasions and preventing future invasions. Several hypotheses have been proposed to explain why some exotic species become invasive, the most prominent of which are: (1) disturbance—habitats pushed away from their historic disturbance regime (disturbances have either become more frequent or less frequent compared to the past) are more easily invaded (Mack et al. 2000, Brooks et al. 2004, Stevens and Beckage 2009, Moles et al. 2012, Juani et al. 2015), (2) biotic resistance—some exotic species are suppressed by competition with resident species whereas others have traits that allow competitive superiority (Levine & D'Antonio 1999, Maron & Vilà 2001, McGlone et al. 2011), and 3) enemy release—exotic species are regulated by enemies more strongly in their native compared to their invaded ranges (Maron & Vilà 2001, Keane and Crawley 2002). There is experimental support for these hypotheses in isolation (e.g., Jacquemyn et al. 2005, Lowry et al. 2013), but no single hypothesis provides a universal explanation for all plant invasions. It is likely that these hypothesized mechanisms (i.e., enemies, competition, disturbance history) interactively influence the success of exotic species, and that these interactions create variability in our understanding of the main effects of any one hypothesis.

To determine the effect of an environmental factor on population dynamics, it is necessary to quantify the effect of that factor on vital rates across the entire life cycle of the focal species. For plants and animals, which are typically stage-structured, matrix population models provide an excellent tool for this analysis (Caswell 2001, Burns 2008, Crone et al. 2011, Burns et al. 2013, Ramula 2014). There is a small but growing literature examining the effect of disturbance, biotic resistance and herbivory on population dynamics of exotic species (Ramula et al. 2008, Williams et al. 2010, Rose et al. 2011, Eckberg et al. 2014, Stevens and Latimer 2015). Disturbances have been shown to increase and to decrease the population growth rates of exotic species (Emery and Gross 2005, Williams et al. 2010, Emery et al. 2013, Stevens and Latimer 2015). The direction of the effect depends on the context of the disturbance for both the focal exotic plant and the community it invades, including the disturbance history of the environment, the traits of the exotic plant, the season, frequency, and duration of the disturbance (Crandall and

Knight 2015). Fewer studies have examined the role of competition with resident species (biotic resistance) in regulating population growth of exotic species, but those that have report that resident species may facilitate or compete with exotics (Crooks and Soulé 1999, Griffith 2010, Prevéy and Seastedt 2015). Finally, studies examining the enemy release hypothesis have found significantly greater effects of herbivory on population growth rates of plants in their native compared to the invasive range (e.g., Jongejans et al. 2006, Williams et al. 2010), and that generalist enemies can significantly decrease demographic vital rates and population growth rates of exotic plants (e.g., Schutzenhofer et al. 2009, Tenhumberg et al. 2015).

Plant matrix population models tend to examine the effects of single environmental drivers on plant population growth (reviewed by Ehrlén et al. 2016). This is the case for exotic plants as well, as only one study has considered multiple drivers (Williams et al. 2010), and none have considered interactions among drivers in their effects on population growth. However, we expect that the importance of herbivores and competitors in regulating the population growth rate of exotic species might depend on disturbance history. For example, if native competitors are adapted to persist and quickly recruit following disturbances, then exotic species that are not adapted should have less success in the post-disturbance environment. Conversely, if disturbances reduce the vital rates of native competitors, then disturbance-tolerant exotics should have high post-disturbance population growth rates (e.g., Cavallero and Raffaele 2010, Williams et al. 2010, Roy et al. 2014). Furthermore, herbivores have been shown to be both less abundant (e.g., Knight and Holt 2005) and more abundant (Lopes and Vasconcelos 2011, Massad et al. 2013) after large scale disturbances such as fire, and thus the effect of herbivory on exotic individuals may be weaker or stronger in the post-disturbance environment.

Here, we examine the main and interactive effects of disturbance, competitors and herbivores on population dynamics of an exotic tree species. *Ailanthus altissima* invades forest ecosystems that contain a moderate density of native, resident vegetation that might provide biotic resistance. Further, a specialist insect enemy to *A. altissima* is present in the invaded range, providing us with the opportunity to assess the effect of this enemy on population growth rate. Finally, *A. altissima* is actively invading fire-suppressed habitats. Land managers are considering restoring these ecosystems using prescribed fires, but it is currently not known if the presence of fire would facilitate or hinder the invasion of *A. altissima.*

MATERIALS AND METHODS

Study Site and Species

This study was conducted at Tyson Research Center near St. Louis, Missouri, U.S.A. (38.526578 N, -90.560322 W), a deciduous, oak-hickory forest within the Missouri Ozarks. The regional climate is characterized by approximately 104 cm of annual precipitation, hot summers (21-32°C), and cold winters (-6.0-5.5°C; <150 frost-free days) (NWS 2017). Historically, Native Americans used widespread fires every 4-6 years throughout large portions of the Ozarks region to maintain savanna-like conditions (Cutter and Guyette 1994). Although forests of the Tyson Research Center have been fire suppressed for more than five decades, recently the use of fire for restoration of the property has gained interest. We identified five patches of *A. altissima* at the Tyson Research Center, each near a roadside. We focused on the three largest patches for this research. *Ailanthus altissima* has been present at the Tyson Research Center for more than 10 years (but probably less than 30 years) and patches have expanded over the past 10 years (personal observation). Our three focal patches were chosen because they contained a mixture of individuals at large and small size classes. Each patch was relatively small and contained just enough spatial spread of individuals for 12-18 4 m^2 plots including buffers.

Ailanthus altissima (P. Mill.) Swingle (Simaroubaceae) (tree-of-heaven) is native to central China. It was introduced to North America by gardeners in the late 1700s and then again by Chinese laborers during the California gold rush in the mid-1800s. It is now considered invasive across most of the United States and parts of Canada, where it often produces monospecific stands (Lawrence et al. 1991). This flood- and shade-intolerant species is particularly common in disturbed gaps along forest edges and in forest clearings (Knapp and Canham 2000). It invades a range of habitats from mesic lowlands to dry, upland forests, all of which historically experienced fires, albeit the fire frequency and intensity likely varied within and between habitats (e.g., Crandall and Platt 2012, Myers et al. 2015). Its success is partially attributed to its tolerance for pollutants, allelopathic chemicals, and lack of generalist herbivore enemies (Carter and Fredericksen 2007; Gómez-Aparicio and Canham 2008). It is difficult to know what the historical and current fire frequencies are for *A. altissima* in its native range. Currently, fires are infrequent across much of Asia (Page et al. 2009). Some habitats (e.g., lowlands) historically experienced frequent natural and human-induced fires (Stott et al. 1990). *Ailanthus altissima* has a broad Asian distribution, and it is therefore likely that this species experienced fire during its evolutionary history.

Ailanthus altissima is a dioecious tree that reproduces both vegetatively and sexually

(Fig. 1). Late in the growing season, mature females produce an abundant crop of seeds with samaras that are wind-dispersed and thus able to travel long distances (Landenberger et al. 2007). Seeds benefit from indirect (reduced competition, increased light attenuation, etc.), but not direct (heat, smoke) effects of fire (Guthrie et al. 2016). They may remain in the soil seed bank for at least a year or germinate the spring after dispersal. Both small and large individuals of *A. altissima* are capable of vigorous clone production and resprouting from root crowns (Kowarik 1995). The time necessary for *A. altissima* to transition from seedling to reproductive tree varies by habitat (Hunter 1995). The greatest seed production occurs between 12 and 20 years of age (Miller 1990).

Larvae of an exotic specialist herbivore, *Atteva aurea* Fitch (Attevinae) (Ailanthus webworm moth), builds communal nests in *A. altissima* by pulling leaves together with webbing. This herbivore is native to Mexico and Central America where it is associated with closely related plant species in the same family (Simaroubaceae) that have a similar chemical composition as *A. altissima* (Becker 2009). They track the invasion of *A. altissima* across the United States and Canada, but they are not adapted to cold temperatures and thus die each winter. The following spring, a new generation of *A. aurea* follows warm weather as far north as Canada. The life cycle of *A. aurea* is completed in four weeks and thus it has more than one generation per year. Generations often overlap so trees are affected during most of the growing season from mid-Spring until the first hard frost. *Atteva aurea* consumes leaves, flowers, and seeds of *A. altissima*, often leaving only naked branches and stems, before building their cocoons within the shelter of their webs (Powell et al. 1973). These herbivores have little impact on large, adult trees, but can devastate small individuals, removing every leaf (Kok et al. 2008).

Ailanthus altissima produces defense chemicals (Lawrence et al. 1991), which should limit herbivory by mammals or generalist herbivores. For instance, Carter and Fredericksen (2007) observed that deer preferentially browse on native saplings over those of *A. altissima*. However, other researchers noted that moles and invertebrates consume leaves of seedlings, but have little influence on seedling survivorship, and that rodents predate seeds (Ostfeld et al. 1997, Cadenasso and Pickett 2000). *Ailanthus altissima* alters soil and litter communities, reducing the abundances of generalist herbivores, such as Coleoptera and Gastropoda (Motard et al. 2015).

Data Collection

We designed an experiment to examine the main effects of herbivory (and seed predation), interspecific competition, and fire; as well as the interactive effects of fire*herbivory and fire*competition on the population dynamics of *A. altissima*. We measured demographic rates of mapped individuals of *A. altissima* from 2012-2013. Within two oak-hickory forest gaps invaded by *A. altissima*, 18 plots of 2 x 2 m were established. In a third, similar gap another 12 plots were established for a total of 48 plots. Each plot had approximately the same number of *A. altissima* seedlings (cotyledons present) and nonreproductive trees, 3 and 8 individuals respectively, prior to treatments and was located less than 65 m from a female, reproducing tree and greater than 50 m from a road. Few plots contained reproductive-sized trees (main stem > 100 cm diameter at 1.37 m height); so, all reproductive-sized trees within 65 m of any study plot (i.e., within the invasion patch) were also tagged and included in this study. In all patches, *A. altissima* was the dominant tree with occasional *Acer* spp., *Carya* spp., and *Ulmus alata* in the overstory. *Ageratina altissima*, *Galium circaezans*, *Muhlenbergia sobolifera*, *Parthenocissus quinquefolia*, *Sanicula canadensis*, and woody seedlings were abundant in the understory.

Each patch was divided into burned and unburned treatments (each approx. 4000 m^2) in a split-block design. Half of each patch was burned using prescribed fire during the dormant season (February 15) of 2013. After creating a black line, plots were burned using a head fire, which resulted in a slow-moving surface fire typical of mesic, deciduous forests. Within each burned and unburned treatment, plots were randomly assigned to a second treatment: control, competitor removal, or herbivore removal. Competitors (mainly understory species listed above as abundant) were removed from plots by clipping and removing aboveground biomass of heterospecific plant species within plots and 0.5 m surrounding each plot. Although we call these competitor removal plots, it is possible that some of *A. altissima*'s neighbors are facilitating rather than competing. Competitor removal treatments were initiated in early spring of the second year (2013) and maintained once per month over the growing season. Herbivore removal treatments focused on insect herbivores and seed predators (see Appendix S1 for details on seed predation experiment); we did not observe damage from mammal herbivores. Applications of this treatment began in early spring of 2013 using Spectricide Malathion, a broad-spectrum organophosphate insecticide. Malathion is an ideal for manipulative experiments because it is a contact cholinesterase inhibitor insecticide with low toxicity for small mammals. Furthermore, it has no effect on plant community biomass (Pfleeger and Zobel 1995) or the natural soil community (Brown et al. 1987). Individuals of *A. altissima* were selectively sprayed every two weeks and after rain events. Treatments were not applied to reproductive-sized individuals (described below) because we had a low sample size of these individuals and most were not present in our demographic plots. Their demographic data were thus pooled across treatments in the model.

Pre-treatment and post-treatment demography data were collected during August 2012 and 2013, respectively. Individuals were mapped and identified as a seedling, new clone, nonreproductive tree, or female/male reproductive tree. The number of stems originating from the base of each individual was recorded. Each stem was measured separately at either 0.5 cm or 1.37 m above ground level for plants; the latter for individuals larger than 45 cm. If an individual had multiple stems, they were added to calculate a total diameter. Individuals ranged from having 1 to 8 stems and ranged in total diameter from 1 to 210 cm. *Ailanthus altissima* fecundity was estimated by counting the number of inflorescences on reproductive individuals, and then multiplying the number of inflorescences by the average number of seeds per inflorescence. We determined the average number of seeds per inflorescence (517) from two inflorescences from each of 10 trees (n=20).

We examined the post-treatment response of plant demography to our treatments in a single year (August 2012 – August 2013). Because we consider a single year, we cannot model the effects of temporal environmental stochasticity on demography, which could be due to a variety of factors (e.g., annual fluctuations in the abundance of herbivores, climate variability). However, we note that the weather in our year of study was typical for this region (NWS 2017). In other systems, fire has been shown to have effects on plant demography that last multiple years, particularly when fire resets the successional trajectory of the of the ecosystem (e.g., Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004, Menges et al. 2006). We expect that the effects of fire in our system will be relatively short-lived, since fire does not reset the successional trajectory of the ecosystem; the overstory vegetation remains intact after our fires, and the understory vegetation quickly re-grows in the post-fire environment. We monitored plants at one of our sites for an additional year and found that vital rates in the post fire-treatment are similar to those in the control treatment (see Figures S8-S10).

Data Analysis

We used integral projection models (IPMs) including both discrete and continuous stages to calculate population growth rates (λ) and to conduct life-table response experiments. Integral projection models are similar to size-based demographic matrix models, but they use continuous relationships between size and vital rates rather than dividing the population into discrete size classes (Easterling et al. 2000; Ellner and Rees 2006), which more appropriately describes the plants in our study. The parameters of the model are described in Table 1 and we provide a detailed description of our models, including methods and calculations for the discrete stage (i.e., seed demography, seed predation experiments), in Appendix S1 in Supporting Information. We also provide the functions used in the IPM (Appendix Table S1) and demographic functions showing the relationship between size and vital rates for each treatment (Appendix Fig. S1-S6). We conclude that treatments have significantly different population growth rates or vital rates if they do not have overlapping 95% confidence intervals. The main purpose of our model was to summarize demographic responses to treatments across the entire life cycle of the focal plant species, and not to forecast population size.

RESULTS

Seed viability and the proportion of viable seeds that germinate did not differ between treatments with and without the exclusion of seed predators, indicating seeds were not consumed or damaged by mammals or other herbivores ($P > 0.2$ for all comparisons). Thus, all data were combined to calculate seed viability ($v = 0.025$) and germination ($g = 0.146$).

Ailanthus altissima populations were persisting and expanding regardless of treatments manipulating fire, competitors, and herbivores (i.e., all λs greater than 1; Fig. 1A). Competitor removal, but not herbivore removal, significantly increased the population growth rate of *A. altissima* in unburned treatments. Fire increased population growth rates (unburned controls vs. burned controls), but this difference was not significant. Within the burn treatment, the absence of biotic interactions did not significantly change the population growth rate. Burned and unburned herbivore removal treatments were not significantly different.

A comparison of individual vital rates indicated that the treatments did not significantly influence the survivorship curves of *A. altissima* ($P = 0.98$; Fig. 1B; Appendix Fig. S1), but they did alter clone production (i.e., number of clones produced per tree) and seedling number (Fig. 1C-D). Fire and competitor removal treatments interactively influence the number of clones produced. Clone production was high in the competitor removal treatment, especially where fire was absent (Fig. 1C). Finally, the average change in number of seedlings in plots from pre-treatment to post-treatment (Fig. 1D) was greatest in burned plots ($P = 0.02$), indicating that the combination of direct and indirect effects of fire (q_a) had a net positive effect on early seedling survival. The number of seedlings per plot was 4.7 times greater post-fire than in the same plots pre-fire, but the biotic interaction treatments did not influence seedling numbers (i.e., no difference between control, competitor removal, and herbivore removal plots; $P = 0.28$). In unburned plots, the average number of seedlings per plot was approximately 1.5 regardless of competitor and herbivore removal treatments ($P = 0.60$).

The LTRE identifies the contributions of each vital rate to observed difference in population growth rate between pairwise treatments. A demographic vital rate has large contribution if it changes dramatically across treatments and/or if the population growth rate is sensitive to changes in that vital rate (Caswell 2001). We show all vital rates here because even nonsignificant results are informative to management. Our LTRE indicated that clone production drives the observed changes in λ between treatments (Fig. 2A-B). In both comparisons, clone production ($c(y,x)$), which had high sensitivity (Appendix Fig. S7), contributed disproportionately to changes in λ between treatments, indicating that burning and removing competitors increased λ primarily because these treatments increased clone production.

DISCUSSION

The disturbance, biotic resistance, and enemy release hypotheses are often invoked to explain the success or failure of exotic introductions (Mitchell et al. 2006, Moles et al. 2012). In our study, we found that fire and competition interactively affect population growth rate; the removal of competitors only significantly increases population growth rate where fire is absent. Although competition significantly affects the population dynamics of *A. altissima*, the presence of competitors was not enough to decrease the population growth rate below one. However, we note that *A. altissima* is not typically found in more mature forest stands (Knapp and Canham 2000), so it is possible that its population growth rate declines as forests reach later stages of succession. Herbivores and seed predators do not cause detectable changes in population growth rates even though a specialist exotic herbivore is present in our system.

We found that the presence of interspecific competitors suppresses population growth of *A. altissima*, especially when unburned (Fig. 1A). Competitor removal and fire have similar effects on the availability of resources (Tyler and D'Antonio 1995, Boerner 2000, Keeley and Fotheringham 2000), such as light and nutrients, and thus both create an ideal environment for a shade-intolerant species like *A. altissima* to geminate and recruit into the population (Knapp and Canham 2000, Radtke et al. 2013). Competitor removal, in the absence of fire, results in large increases in clone production (i.e. number of clones produced per tree). Burning increases the establishment of seedlings (Fig. 1). Since the population growth rate is highly sensitive to perturbations in clone production but relatively insensitive to perturbations in seedling establishment (Fig. 2; Supplemental Fig. S7), the removal of competitors in the absence of fire results in the most significant increase in population growth rate. Clone production was greatest in unburned habitats where competitors were removed because, after fire, *A. altissima* is likely allocating energy reserves to resprouting from preexisting stems, and therefore achieves smaller increases in clone production (i.e., Burch and Zedaker 2003). *A. altissima*, like other invasive species, benefits from the post-fire environment (i.e., Kuppinger et al. 2010, Juani et al. 2015).

The presence of an exotic enemy had no effect on the population growth rate of *A. altissima* regardless of the presence of fire. Although we observed high levels of herbivory by the specialist herbivore, *Atteva aurea*, we did not see effects of our herbivore removal treatment on plant vital rates. We observed most of the damage taking place late in the Fall, just prior to the natural senescence of these individuals. Such late-season herbivory is expected to have limited effects on the fitness of plants, since most individuals have already accomplished most of their photosynthesis for the growing season prior to the herbivory (e.g., Knight 2003). While many other studies find that invasive plants accumulate enemies in their invaded range (Liu and Stiling 2006), it is rare that an exotic specialist enemy is present without purposeful introduction (but see Chang et al. 2011, Morrison and Hay 2011, Stricker and Stiling 2012). Typically, specialist herbivores, such as *A. aurea*, are introduced as biological control (DeWalt 2006, Maines et al. 2013). In our study, a specialist herbivore does not significantly decrease population growth rate. Such results indicate that biological control could fail to successfully reduce the growth rate and abundance of target weed populations, even if the control agent causes significant damage to individual plants (see also Schutzenhofer and Knight 2007).

Our results indicate that applied management of this invasive tree should be carefully monitored. *Ailanthus altissima* has significantly positive population growth even in its least favorable treatment (no fire, presence of herbivores and competitors). Fires are a natural feature of the ecosystems invaded by *A. altissima*, and restoration of the native fire regime is often the first step in restoring invaded habitats. However, here we show that *A. altissima* benefits from the post-fire environment by increasing seedling recruitment. It would be difficult to target killing seedlings with management actions, and seedling recruitment would continue as long as female, reproducing trees are present in the population and the seed bank persists. We show that a single fire increases population size. If there are a few years before the subsequent fire, the new individuals would have sufficient time to gain a foothold in the community and grow to a size that would be resistant to fire. Biological control should be carefully evaluated since the specialist enemy already present in this system does not significantly decrease the population growth rate (i.e., Dewalt 2006, Schutzenhofer and Knight 2007). We would suggest that managers that thin hardwood trees prior to burning should proceed with caution when *A. altissima* is in the system, since it performs best in high light environments.

We quantify the effect sizes of treatments and their interactions on population growth rate of *A. altissima* using a single transition year (but see Appendix Figs. S8-S10). However, temporal variability in many factors, such as the abundance of herbivores and climate could influence the magnitude of these effect sizes, and could even influence which treatment is most important for population growth. Climate change is expected to increase both the mean and variability in abiotic conditions experienced by plants around the world, and both native and exotic species will respond to this change. We currently lack consensus on whether or not climate change will favor exotic species, and under which conditions this is expected (Buckley and Csergö 2017). Future studies that consider multiple invasion hypotheses and also consider multiple climate conditions, either through long-term observations or through experiments that manipulate temperature and precipitation, would contribute much to our ability to forecast the response of exotic plants to both disturbances and climate change.

For many land managers, the dominance of exotic species in habitats of conservation interest is a significant problem; they spend much of their time and financial resources removing exotic species and creating conditions that favor native species (Epanchin-Niell and Hastings 2010, Rout et al. 2014). Population models of the focal exotic plant species can help identify phases in the life cycle that have high sensitivity, and thus should be the focus of management (Burns 2008, Ramula 2008, Ramula et al. 2014). Because detailed demographic information is rare for most exotic plant species, managers must make decisions without information from a population model. Recent reviews, however, suggest that knowledge of the life history (Ramula et al. 2008) and functional traits (Adler et al. 2014) of an exotic plant can predict which phases in its life cycle have high sensitivity. The outcomes of management on the growth rate and abundance of the exotic plant population will also depend on the context in which the management is applied. For example, disturbances (e.g., re-introducing fire) are well known to influence the densities of herbivores and competitors (Knight and Holt 2005, Massad et al.

2013), but the magnitude and direction of these results may differ between systems. Further, local knowledge on the key herbivores and competitors in a system, and how these species and the focal exotic plant species are expected to respond to disturbances, should guide land managers to make informed decisions on the likelihood of different management practices to achieve desired results.

Understanding the mechanisms that allow some exotic species to establish and become invasive while others fail to do so is an active field of study. This is of interest for applied scientists that strive to manage current invasive species and prevent future invasions, as well as for a more general understanding of how communities assemble and disassemble in nature. Despite a voluminous literature on the topic, syntheses on which mechanisms are of primary importance in invasions has not been forthcoming. In a recent review, only 4% of the studies examining the causes of invasiveness of plants and animals considered more than two mechanisms (Lowry et al. 2013), and only one of these considered the entire life cycle of the focal invasive species. The broad message from our research is that understanding the effects of environmental factors on the success of focal invasive species requires consideration of multiple mechanisms and a quantitative population framework. Studies such as this should help build towards a synthetic understanding of the mechanisms that allow for high population growth and dominance of invasive species.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository. DOI: 10.5061/dryad.pr686 (Crandall & Knight 2017).

AUTHORS' CONTRIBUTIONS

RMC and TMK conceived the ideas and designed methodology; RMC and TMK collected the data; RMC and TMK developed the models and RMC analyzed the data; RMC and TMK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article.

Appenidix S1. Supplemental methods describing seed demography and development of integral projection model.

Table S1. Model components used by the IPM.

Fig. S1. Demographic function showing the relationships between size at time *t* and survival at time *t+1*.

Fig. S2. Demographic function showing growth between successive years.

Fig. S3. Demographic function showing the relationship between number of female seeds produced by individuals of size *x* at time *t+1*.

Fig. S4. Demographic function showing the probability of individuals of size y at time t+1 being classified as reproductive individuals at time t+1.

Fig. S5. Demographic function showing size distribution of seedlings.

Fig. S6. Demographic function showing size distribution of new clones.

Fig. S7. Change in population growth rate (Lambda) resulting from a 5% increase for each vital rate in the unburned control treatment.

Fig. S8. Probability of survival 1 year to 2 years post-treatment.

Fig. S9. Average number of clones produced per tree pre-treatment and 1 and 2 years post-treatment

Fig. S10. Number of seedlings per plot pre-treatment and 1 and 2 years post-treatment.

Table 1. Descriptions of model components used in the integral projection model. See Appendix S1 for the model summary.

Model Components	**Vital Rates**	**Description**
Survival and Growth $p(y,x)$	$s(x)$	Probability of survival
	$g(y,x)$	Probability surviving individuals grow from size x to size y
Fecundity $f(y,x)$	q_a	Direct and indirect effects of fire on seed and early seedling survival
	q_d	Direct effects of fire on seed survival
	$f_n(x)$	Number of seeds produced by individuals of size x
	$f_d(y)$	Size distribution of seedlings
	$f_r(x)$	Probability of individuals of size x producing seeds
Clonality $c(y,x)$	$c_d(y)$	Size distribution of clones
	$h_n(x)$	Number of clones produced at time t+1 by a

		tree at time t
Seedbank Dynamics		
$B(t+1)$	See Appendix S1	Probability that a seed at time t will remain in the seedbank at time t

FIG. 1. Demographic projections and vital rates for *Ailanthus altissima*: (A) population growth rates (λ), (B) dependence of survival in 2013 on plant size (total diameter (cm) of all stems/individual at 0.5 cm aboveground) in 2012 ($s(y,x)$), (C) average number of clones produced per tree ($h_n(x)$), (D) difference in the average number of seedlings between 2013 (post-treatment) and 2012 (pre-treatment) for unburned (black) and burned (gray) treatments, which was used to calculate q_a, the net direct and indirect effects of fire on seed and early seedling survival. Error bars represent 95% confidence intervals from bootstrapping. See Table 1 and Appendix S1 for descriptions of model components.

FIG. 2. Life table response experiments (LTRE) decompose the contribution of vial rates to observed changes in population growth rate for pairwise treatments. (A) LTRE of the Control-Burned vs. Control-Unburned and (B) LTRE of the Competitor Removal-Unburned vs. Control-Unburned. In both instances, clone production contributed most to the observed difference in population growth rate. See Table 1 and Appendix S1 for detailed descriptions of vital rates.

FIGURE 1

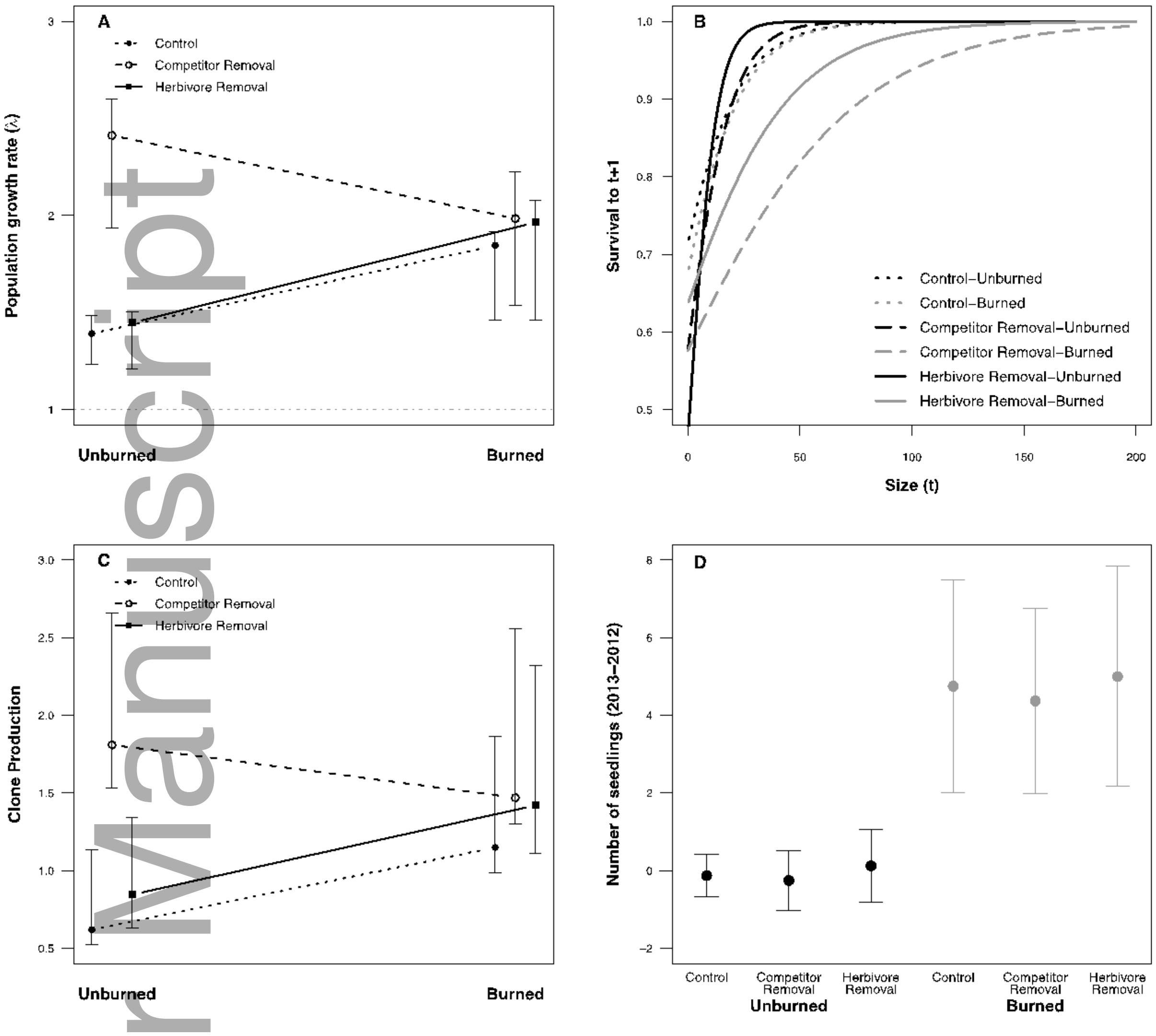
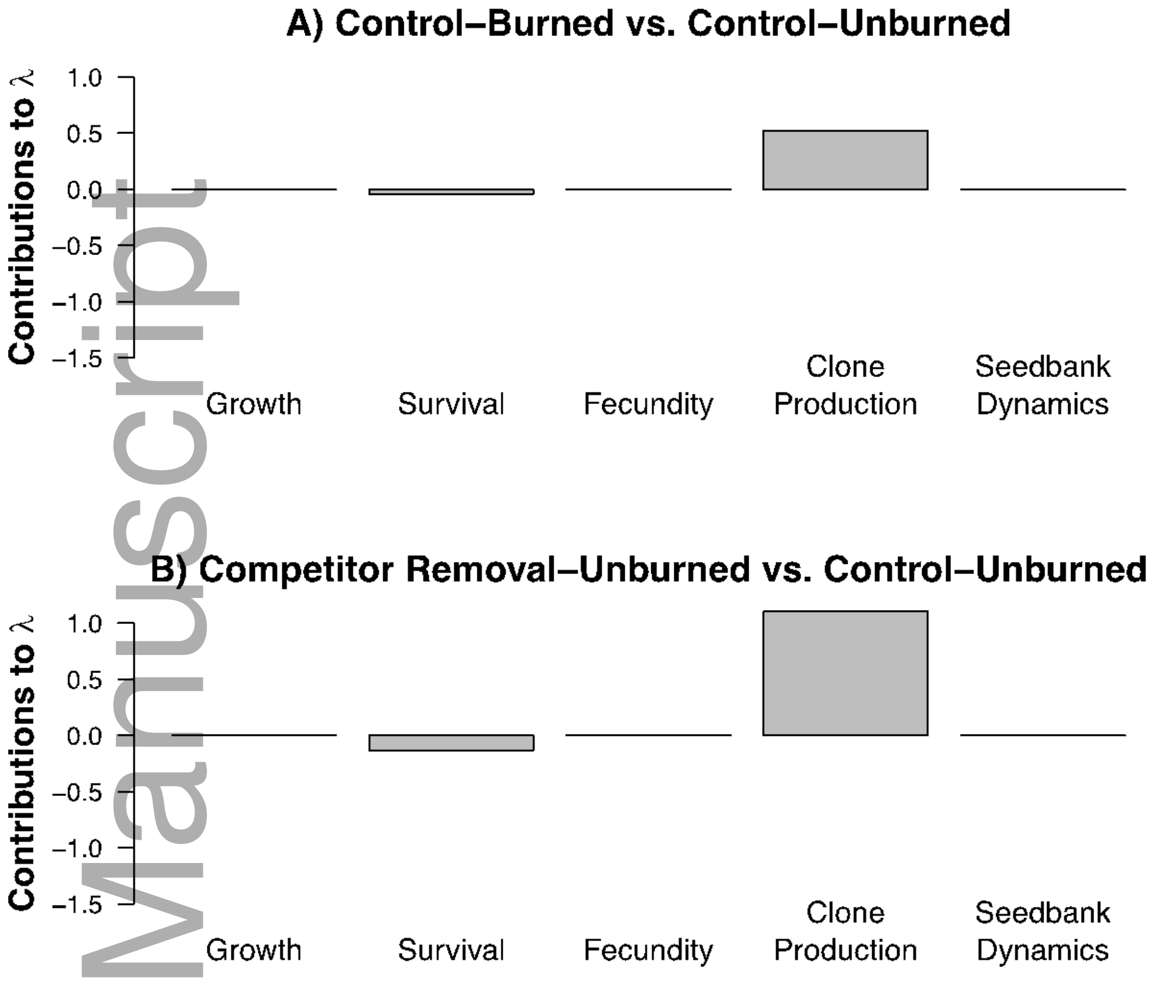

A
Control
Competitor Removal
Herbivore Removal
Population growth rate (λ)
1
2
3
Unburned
Burned
B
Survival to t+1
0.5
0.6
0.7
0.8
0.9
1.0
0
50
100
150
200
Size (t)
Control–Unburned
Control–Burned
Competitor Removal–Unburned
Competitor Removal–Burned
Herbivore Removal–Unburned
Herbivore Removal–Burned
C
Control
Competitor Removal
Herbivore Removal
Clone Production
0.5
1.0
1.5
2.0
2.5
3.0
Unburned
Burned
D
Number of seedlings (2013–2012)
−2
0
2
4
6
8
Control
Competitor Removal
Herbivore Removal
Control
Competitor Removal
Herbivore Removal
Unburned
Burned

FIGURE 2


A) Control–Burned vs. Control–Unburned
Contributions to λ
1.0
0.5
0.0
−0.5
−1.0
−1.5
Growth
Survival
Fecundity
Clone Production
Seedbank Dynamics
B) Competitor Removal–Unburned vs. Control–Unburned
Contributions to λ
1.0
0.5
0.0
−0.5
−1.0
−1.5
Growth
Survival
Fecundity
Clone Production
Seedbank Dynamics