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Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern USA forest[1]

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Abstract: Severe wildfires often facilitate the spread of exotic invasive species, such as Dalmatian toadflax (*Linaria dalmatica*). We hypothesized that toadflax growth and reproduction would increase with increasing burn severity in a ponderosa pine (*Pinus ponderosa*)-dominated forest. We measured toadflax density, cover, flowering stalks, and native species richness and cover on 327 plots for 3 y after a 2001 wildfire. Toadflax stem density, cover, and flowering stalks increased in 2003, then decreased in 2004 in all burn severity classes, but remained higher than initial 2002 values. Toadflax spread to previously uncolonized areas, though stem density decreased in unburned plots. Transition matrices showed that more plots on moderately (73%) and severely (74%) burned areas classified as high toadflax density in 2002 remained high density in 2004. Deterministic matrix modeling using 2002 to 2004 transition probabilities projected that the percentage of high-density plots would stabilize on moderately and severely burned sites at 41 and 61%, respectively. In contrast, 20-y rates of change (λ) for unburned and low-severity burn sites were < 1.0, and stabilizing at 2% for unburned plots and 19% for low-severity burn plots. Post-wildfire conditions in high-severity burned areas favour increased density, cover, reproduction, and spread of Dalmatian toadflax, while native species richness was reduced, suggesting that the invasive species would persist, at least in the short term, at the expense of natives.
Keywords: Arizona, disturbance, exotic, invasive, *Pinus ponderosa* forest, transition matrices, wildfire.

Résumé : Les feux de forêt sévères facilitent souvent la propagation d'espèces envahissantes exotiques, telle que la linaire à feuilles larges (*Linaria dalmatica*). Nous avons formulé l'hypothèse que la croissance et la reproduction de la linaire augmenteraient avec un accroissement de la sévérité du feu dans une forêt dominée par le pin ponderosa (*Pinus ponderosa*). Après un feu en 2001, nous avons mesuré la densité des linaires, leur couverture, le nombre de tiges en fleurs, ainsi que la richesse et la couverture en espèces indigènes dans 327 parcelles durant 3 ans. La densité des tiges de linaires, leur couverture et le nombre de tiges en fleurs ont augmenté en 2003 et ensuite diminué en 2004 dans toutes les classes de sévérité de feu, mais les valeurs sont demeurées plus élevées qu'initialement en 2002. Les linaires se sont propagées dans des secteurs auparavant non colonisés, quoique dans les sites non brûlés la densité de tiges était plus faible. Des matrices de transition ont démontré que plus de parcelles des secteurs modérément (73 %) et sévèrement (74 %) brûlés s'étant classées dans la catégorie de densité élevée de linaires en 2002 le sont demeurées en 2004. Un modèle matriciel déterministe utilisant les probabilités de transition de 2002 à 2004 prévoyait que le pourcentage de parcelles possédant une haute densité de linaires se stabiliserait à 41% dans les sites modérément brûlés et à 61 % dans ceux brûlés sévèrement. À l'opposé, les taux de changement sur 20 ans (λ) pour les sites non brûlés et ceux brûlés légèrement étaient < 1,0 et les pourcentages se sont stabilisés à 2 % pour les parcelles non brûlées et à 19 % pour celles brûlées légèrement. Les conditions après feu dans les secteurs brûlés sévèrement ont favorisé une augmentation de la densité, couverture, reproduction et propagation des linaires à feuilles larges alors que la richesse en espèces indigènes a été réduite, suggérant que l'espèce envahissante persistera, du moins à court terme, aux dépens des espèces indigènes.
Mots-clés : Arizona, envahissante, exotique, feu, forêt de *Pinus ponderosa,* matrices de transition, perturbation.

Nomenclature: USDA NRCS, 2007.

Introduction

The frequency of large wildfires has increased in recent decades in some dry coniferous forest types of North America. Increases in the number and size of stand-replacing fires is often attributed to fuel buildups and dense stand conditions resulting from past management practices and fire exclusion, in combination with drought and warm temperatures (Covington & Moore, 1994; Swetnam, Allen & Betancourt, 1999; Korb & Springer, 2003; Schoennagel *et al.,* 2005; Westerling *et al.,* 2006). Large stand-replacing wildfires can leave behind areas of exposed mineral soil that are quickly colonized by opportunistic species, either native or exotic (Crawford *et al.,* 2001; Griffis *et al.,* 2001; Sieg, Phillips & Moser, 2003; Wolfson *et al.,* 2005). Many colonizing exotic species are ephemeral or apparently benign, but a subset are invasive and spread over a considerable area, and some are considered "transformer species" (Wells *et al.,* 1986), which persist over large areas and can greatly alter ecosystem structure or function (Richardson *et al.,* 2000). Ecosystem alterations may include replacing native vegetation, displacing wildlife, out-crossing with native flora, and altering nutrient-cycles, hydrology, and disturbance regimes (Vitousek *et al.,* 1997; Walker & Smith,

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1997; D'Antonio & Meyerson, 2002). Such alterations can profoundly impact biodiversity (Richardson *et al.,* 2000).

A number of previous studies have reported an increase in exotic species invasion following fire (D'Antonio, 2000). The degree to which exotic species dominate post-fire communities as well as what species appear following wildfires depends on a number of factors. Individual abilities of species to tolerate fire or colonize burned areas, pre-fire population levels, and degree of competitiveness are important attributes affecting invasive species response to fire in grasslands (Grace *et al.,* 2001). In coniferous forests, severity of the fire, which influences availability of resources such as light and nutrients, propagule pressure, time since fire, and past management history can also influence post-fire community composition. Increased populations or richness of exotic species are associated with high-severity burns in some studies (Keeley, Lubin & Fotheringham, 2003; Hunter *et al.,* 2006; Kerns, Thies & Niwa, 2006), but others report relatively low levels of exotic species cover on severely burned areas (Huisinga *et al.,* 2005; Kuenzi, Fulé & Sieg, 2008). Propagule pressure of individual species as well as time since the burn can affect post-fire plant community composition (Floyd *et al.,* 2006). Past management history, including seeding practices and livestock grazing, may influence post-fire plant communities and the contribution of exotic species (Keeley, Lubin & Fotheringham, 2003; Hunter *et al.,* 2006). For many exotic species, we have a poor understanding of the mechanisms involved in their establishment and spread following disturbances (Stohlgren *et al.,* 1999; Grace *et al.,* 2001).

Dalmatian toadflax (*Linaria dalmatica*) (hereafter "toadflax") was introduced to North America in 1894 as an ornamental plant from the Mediterranean region, where it is native from Croatia to Iran (Alex, 1962). It has since become widespread in the western United States and Canada, where it is considered highly invasive, replacing native forage species for domestic and wild animals (Vujnovic & Wein, 1996; Lajeunesse, 1999). Toadflax is legally designated as a "noxious weed" or "regulated non-native plant" in 12 western US states (USDA NRCS, 2007) and 3 Canadian provinces (Rice, 2007). Toadflax is a polycarpic, short-lived perennial member of the Scrophulariaceae family. Plants produce large numbers of seeds that likely disperse only a short distance from the parent plant (Lajeunesse, 1999). Germination occurs mostly in the spring, but seeds can remain dormant for 10 y or more (Robocker, 1970). Thus, while individual plants may survive 3 to 5 y, patches of toadflax may persist 13 y or longer due to germination of seeds from the seedbank. High seed production, vegetative reproduction, an extensive root system and carbohydrate reserves, plus a long active growing period allow toadflax to compete with native species and flourish in disturbed areas (Robocker, 1970; Lajeunesse, 1999). Toadflax might be considered a transformer species, as it has been credited with disrupting ecosystem composition and structure by replacing native plant species in some settings (Robocker, 1974; Lajeunesse, 1999) and even out-competing other non-natives (Lange, 1958). Toadflax is not considered allelopathic, but alkaloids found in the leaves and stems make it unpalatable to most animals (Vujnovic & Wein, 1996; Lajeunesse, 1999).

Few quantitative studies have explored toadflax response to fire. In a Montana study, biomass and seed production of toadflax increased dramatically after a prescribed burn, compared to an unburned area (Jacobs & Sheley, 2003). Toadflax cover also increased in burned plots but was not significantly different from unburned plots (Jacobs & Sheley, 2003). In a northern Arizona study, toadflax density increased after a low-severity prescribed burn, threatening a rare species (Phillips & Crisp, 2001). It is a common exotic species in seedbanks in this area (Korb *et al.,* 2005) and is a successful colonizer of severely burned areas where slash piles were burned (Korb, Johnson & Covington, 2004). Hunter *et al.* (2006) reported spread of a related species, *Linaria vulgaris*, at 2 severe wildfire sites in Colorado.

We took advantage of a wildfire in which detailed fire severity measurements had been completed (Cocke, Fulé & Crouse, 2005a) to address the response of toadflax and interaction with the native plant community. We measured the response of toadflax for 3 y post-fire at 4 burn severity levels and 4 toadflax density levels, asking the following questions: 1) How do toadflax density, cover, and reproduction vary with burn severity? We hypothesized that toadflax would respond favourably under increasing burn severity. 2) Is the response of toadflax dependent on its density? We hypothesized that toadflax would increase the most in areas with higher initial toadflax density. 3) How do cover and density of toadflax relate to changes in native species richness? We hypothesized that native species richness would increase over time since fire but that areas with high toadflax cover and density would be associated with decreased native richness.

Methods

Study area

This study was conducted in areas burned in the Leroux wildfire on the San Francisco Peaks, Kachina Wilderness Area, of the Coconino National Forest, approximately 10 km north of Flagstaff, Arizona (Figure 1). In June 2001, the human-ignited wildfire burned 486 ha on the south-facing slope of Agassiz Peak, between 2490 and 3145 m in elevation. The Leroux fire burned a ponderosa-pine–dominant forest in a mosaic pattern, leaving a patchwork of burn severity ranging from unburned to high-severity crown fire (Cocke, Fulé & Crouse, 2005a). Typical understory is dominated by the perennial native grasses *Festuca arizonica*, *Muhlenbergia montana*, *Poa fendleriana*, and *Elymus elymoides*, numerous annual and perennial forbs, and some exotic species (Korb & Springer, 2003; Fisher & Fulé, 2004). The Kachina Wilderness has experienced extended fire exclusion, which contributed to the development of dense forests (Cocke, Fulé & Crouse, 2005b). The area was heavily utilized historically for logging and livestock grazing and is currently used for a variety of recreation activities. These activities introduced exotic species, including toadflax, to the wilderness area prior to the Leroux fire (L. Moser, US Forest Service, pers. comm., 2002; Fisher & Fulé, 2004).

Soil parent materials are andesite and basalt, and common soils are Inceptisols, Mollisols, and Alfisols (USDA

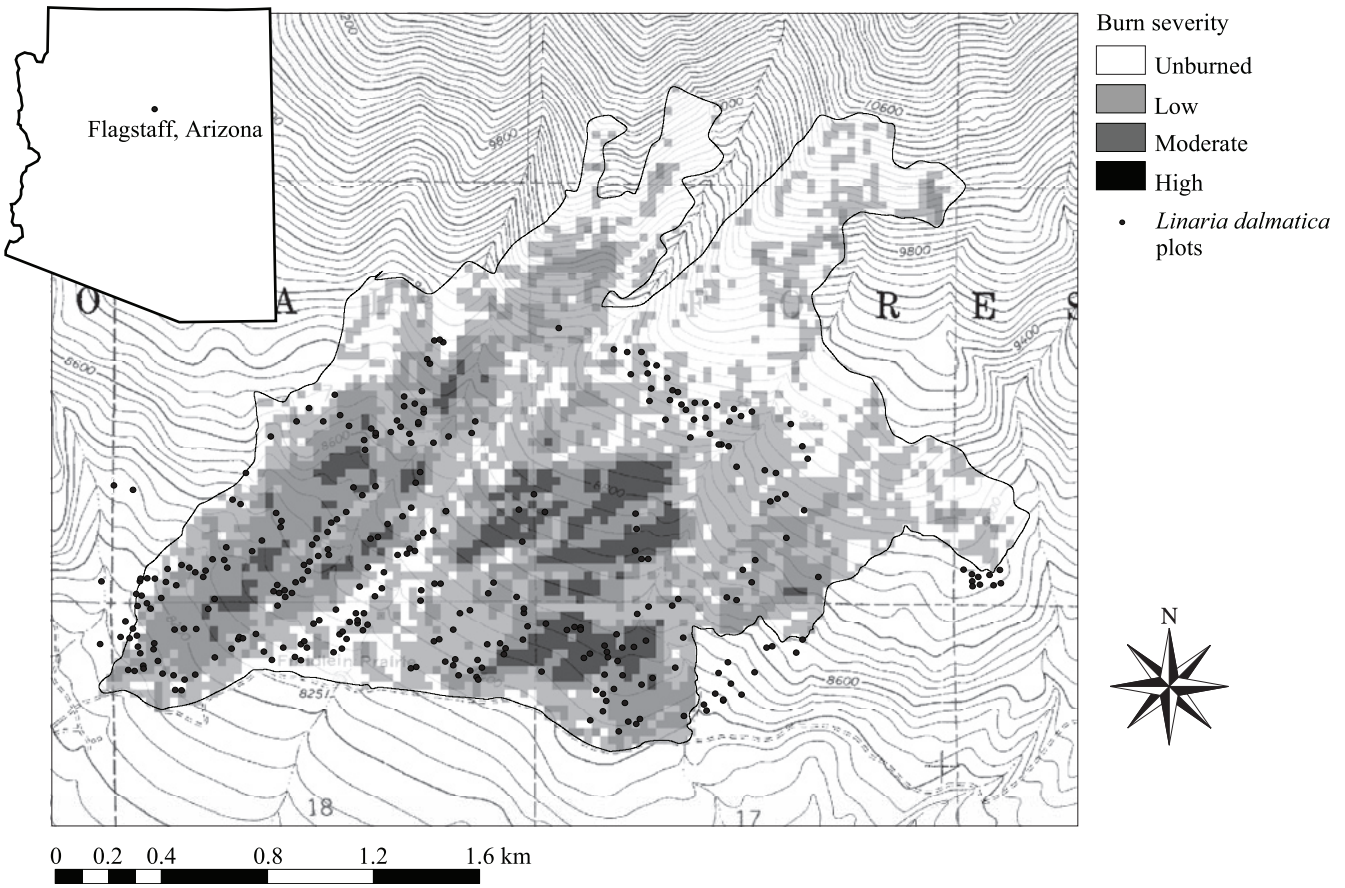

FIGURE 1. Area burned by the Leroux wildfire in 2001, fire severity, and locations of sampling plots.

Forest Service, 1995). Precipitation patterns are bimodal, characterized by periodic snow and rainfall in winter, followed by a pronounced drought in May and June, with monsoon rains occurring in July and August (Sheppard *et al.,* 2002). Average annual precipitation is 53.9 cm in the Flagstaff area, and the monthly mean temperature ranges from –0.8 to 16.2 °C (54-y average) (Western Regional Climate Center, 2004). Annual precipitation from 2001 to 2004 was usually less than the long-term average: 44.7 cm (2001), 32.8 cm (2002), 45.2 cm (2003), and 59.9 cm (2004).

FIELD METHODS

We established 327 permanent research plots distributed within and adjacent to area burned in the Leroux fire. Plots were plant-centred, *i.e.,* each plot was centred around 1 or more plants (Travis & Sutter, 1986), chosen based on burn severity and toadflax stem density in 16 burn severity × plant density categories: 4 burn severity categories and 4 toadflax stem density categories. As is the case in most wildfire studies, pre-existing fuel and topographic characteristics may have influenced fire severity and Dalmatian toadflax response. However, we tried to control variability by limiting sampling to the lower elevations (pine forest) on relatively consistent slopes and aspects and interspersing plots representing all the sampling categories. Burn severity was determined using a landscape burn severity map with 4 severity levels based on differenced Normalized Burn Ratio (dNBR) analysis (unburned, dNBR ≤ 50; low, 51–240; moderate, 241–570; high, ≥ 571) (Cocke, Fulé & Crouse, 2005a). Severity assessment was confirmed by field plots according to NPS-USGS Burn Severity Mapping Project guidelines (NPS-USGS, 2002; Cocke, Fulé & Crouse, 2005a). Field measurements used the Composite Burn Index, in which qualitative severity levels are assigned to vegetation, woody debris, and soil variables (NPS-USGS, 2002). When landscape- and plot-level burn severities differed, the plot-level burn severity was used for plot classification in order to more accurately describe the growing conditions affecting understory species. Density categories were based on the number of toadflax stems (ramets) within the plot frame: (1) none, (2) low: 1–10, (3) medium: 11–29, and (4) high: ≥ 30 stems. These categories represented approximately equal divisions of Dalmatian toadflax density observed at the onset of sampling.

We selected 19 to 28 plots per category, except in the unburned severity class, where only 11-17 plots were established per toadflax density class because fewer toadflax plants were present in unburned areas. Plots with no toadflax plants were selected by walking in a random direction from toadflax plots until an area of similar environmental attributes (aspect, overstory cover, elevation, understory community type, burn severity) was identified where toadflax was absent but was still within the defined study area. This method ensured that the control plots were located in areas with habitats similar to those of non-control plots. A 10-m toadflax-free buffer was required for the establish-

ment of control plots ("no-toadflax" category). All plots were measured in summer months of 2002, 2003, and 2004 after onset of the rainy season in mid-July, when growth of many native species begins.

Plots were 1 m^2 (2 × 0.5 m) and permanently marked with 2 iron stakes at diagonal corners. To minimize visual impact in the Wilderness Area, stakes were placed flush with the forest floor and nearby reference trees were tagged near the base facing the tagged corner stakes; tags were painted brown to conceal them. We recorded distance and direction from the reference tree to the tagged corner stakes and noted UTM coordinates, slope, azimuth, aspect, and elevation of each plot.

Each plant rooted in a plot was identified to species or genus where species was undetermined, and classified as native or exotic to Arizona (Kearney & Peebles, 1960). For toadflax, we counted the number of stems and flowering stalks, and estimated percent foliar cover. Counting the actual number of flowers per plant was not feasible given the resources available for the study, so we counted flowering stalks, defined as a primary, secondary, or tertiary branching stalk with multiple flowers. The primary stalk is the one rooted in the ground, from which secondary and then tertiary stalks branch off. We counted the number of plants for other exotic plant species.

DATA ANALYSIS

Plots were classified by plot-level burn severity and toadflax density class for statistical analysis. The statistical package SPSS version 12.0 was used for all analysis (SPSS, 2003). Assumptions of normality and equal variances were tested using Shapiro–Wilk's and Levene's tests, with $\alpha = 0.05$, for toadflax stem density, cover, flower stalks, and native species richness. Data met parametric assumptions, except for a departure from normality for 3 variables: stems, flower stalks, and native richness (Shapiro–Wilk $P < 0.002$). Normal probability plots indicated that departures were minor, and we concluded that robust parametric methods were the best way to test for burn effects, density effects, time, and burn by density interaction, so we accepted the non-normal data (Steel & Torrie, 1980). Statistically significant differences in toadflax stem density, cover, flower stalks, and native species richness were assessed using the repeated-measures general linear model, with year as the time variable and burn severity and density as between-subject factors.

A significant interaction between year × burn severity × density was followed by a univariate ANOVA of the change between years (2002–2003 and 2003–2004), with a Bonferroni correction of α/2. Tukey's HSD *post hoc* test was used to compare individual means following a significant ANOVA. Pearson's correlation coefficient was calculated to examine the relationship of native species richness between years, native species richness, and toadflax density and cover, and native species cover and toadflax density and cover. We calculated the percentage of control plots without toadflax whose buffer zone became infested with toadflax.

We used matrix modeling (Lefkovitch, 1965; Burgman, Ferson & Akcakaya, 1993) to explore how the proportion of plots classified as high density varied through time among fire severity classes. Stage-based models are commonly used to assess population rates of change (λ) for plant species with discrete life-history stages. Such models have been used to model population growth rates of invasive species under varying stages of invasion (Parker, 2000) or in response to control efforts (Drayton & Primack, 1999). Matrix models can also be used to compare transition rates among plant community types (Scanlan & Archer, 1991; Hibbard *et al.,* 2003). We developed transition matrices for each fire severity class to track annual changes in the proportion of plots classified in a given density class (none, low, moderate, or high) between 2002, 2003, and 2004. We then used a Visual Basic for Applications macro in Excel (Sieg, King & Van Dyke, 2003) to calculate the rate of change (λ) of the proportion of plots initially classified as high density in 2002 that remained classified as high density in 2004, by fire severity class. We used the number of plots in each density class in a given fire severity class as initial values for the models and ran the deterministic models for 20 y or until λ converged (Burgman, Ferson & Akcakaya, 1993). We then compared relative differences in projected λ's, as this often provides insights into underlying causes for changes in λ (Beissinger & Westphal, 1998).

Results

TOADFLAX RESPONSE

Toadflax stem density, percent cover, and flowering stalks in burned plots increased in 2003, then decreased slightly in 2004 in most density classes, but remained greater in 2004 compared to 2002. Averaged across all density classes, total toadflax stem density increased by 38–221% from 2002 to 2003 and decreased by 13–22% from 2003 to 2004 (Figure 2a). Toadflax cover increased by 65–109% from 2002 to 2003 and decreased by 2–45% from 2003 to 2004 (Figure 2b). Similarly, flower stalk density increased by 16–147% from 2002 to 2003 and decreased by 11–46% from 2003 to 2004 (Figure 2c). In contrast, in the unburned plots toadflax stem density decreased consistently each year ($P = 0.04$), percent cover increased insignificantly each year, and flower stalk density remained similar.

There were significant time × burn severity × density interactions for toadflax stem density, % cover, and flower stalks ($P < 0.001$). The change in stems from 2002 to 2003 differed significantly among burn severity classes ($P < 0.001$) but not among density classes ($P = 0.2$), while change in stems from 2003 to 2004 differed by density class ($P < 0.001$; Figure 3a) but not burn severity ($P = 0.8$; Figure 2a). The increase in toadflax stem density between 2002 and 2003 was greater on high burn severity plots than all other burn severity classes (Tukey's HSD, Figure 2a).

From 2003 to 2004, the change in stem density also differed significantly among density classes (Tukey's HSD, High = Medium > Low; Figure 3a). The change between 2002 and 2003 for toadflax cover and flowering stalks showed a significant burn severity, density, and interaction effect ($P < 0.001$) with a separation between the high burn severity and other severity classes, as well as a separation between the no-toadflax class and other density classes (Tukey's HSD). These same variables

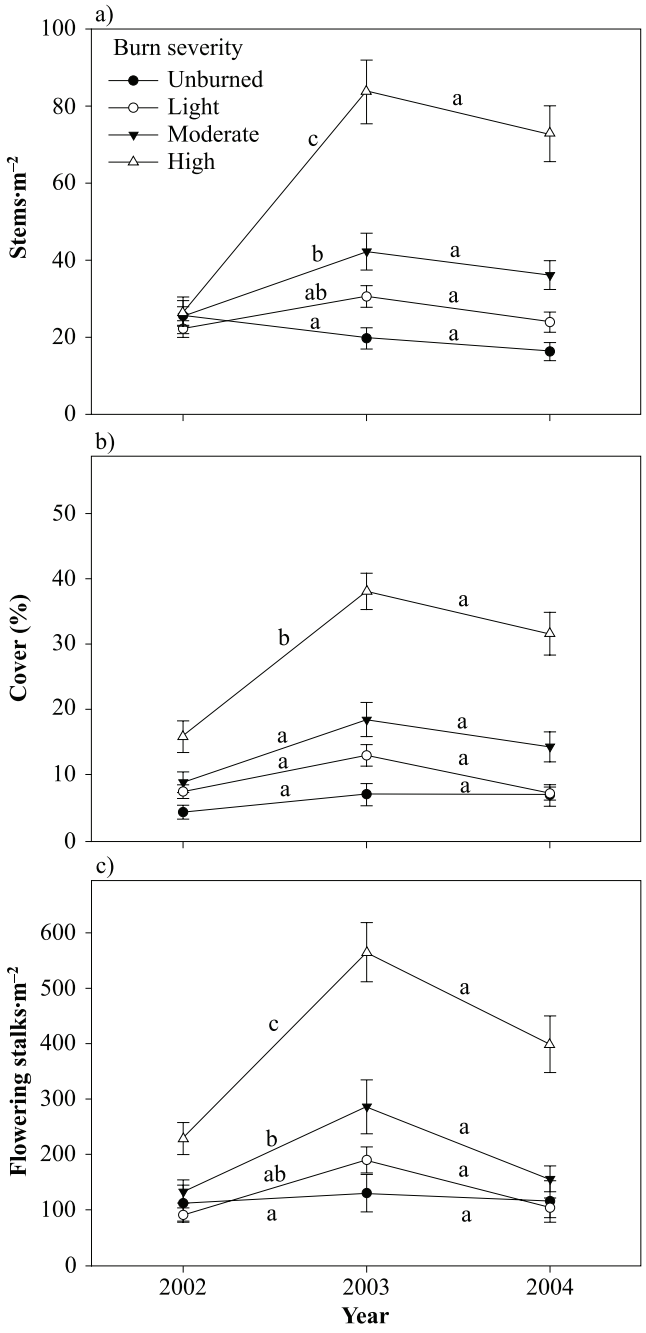

FIGURE 2. Average Dalmatian toadflax (a) density (stems·m^{-2}), (b) plant canopy cover (%), and (c) flowering stalk density (flowering stalks·m^{-2}), by year and burn severity class. Line segments within each time step labelled with the same letter did not differ significantly among burn severity classes (Tukey's HSD, $P > 0.025$).

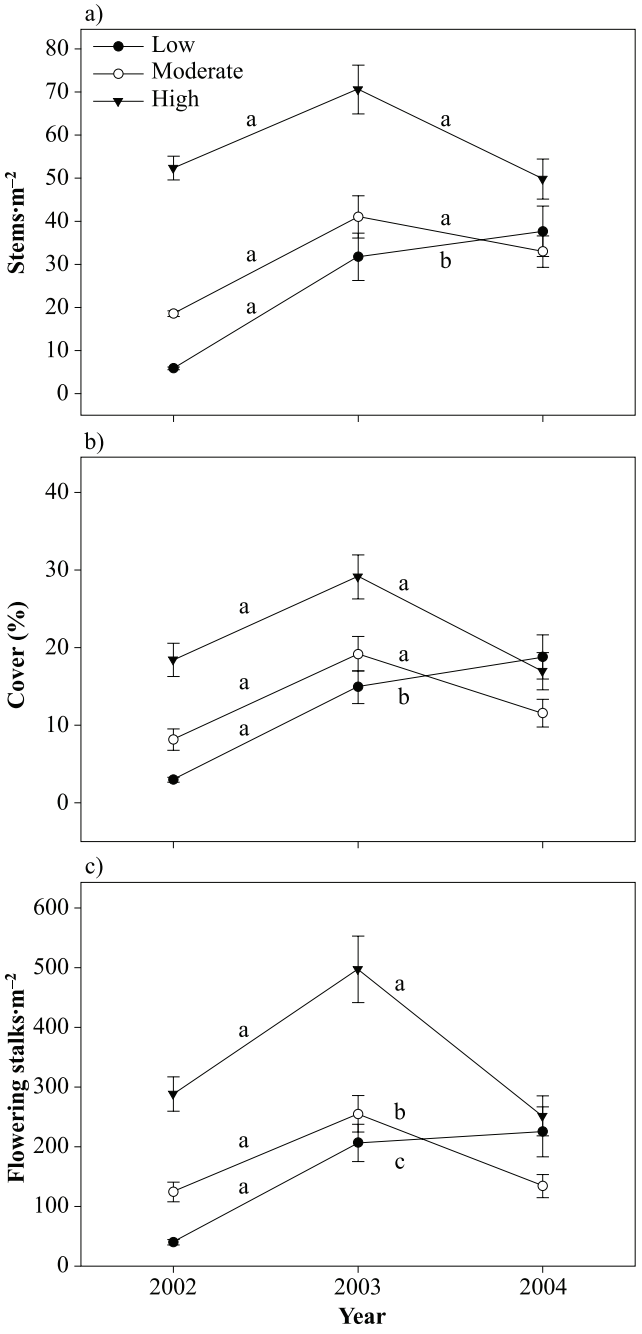

FIGURE 3. Average Dalmatian toadflax (a) density (stems·m^{-2}), (b) plant canopy cover (%), and (c) flowering stalk density (flowering stalks·m^{-2}), by year and toadflax density class. Line segments within each time step labelled with the same letter did not differ significantly among density classes (Tukey's HSD, $P > 0.025$).

between 2003 and 2004 differed only among toadflax density classes ($P < 0.001$). The decrease in cover from 2003 to 2004 was significantly less for the low density class (Tukey's HSD), and similar between the moderate and high density classes. The change in flowering stalk density between 2003 and 2004 differed significantly (Tukey's HSD) among density classes with the low and none classes being the only similar pair. Neither stem density nor percent cover of Dalmatian toadflax was significantly correlated with future toadflax stem density, or with native or exotic plant species richness. The number of flowering stalks in 2002 was positively correlated with flowering stalks in 2003 ($r = 0.66$, $P < 0.001$), and 2003 flowering stalk density was positively correlated with flower stalks in 2004 ($r = 0.52$, $P < 0.001$). The correlation of 2002 and 2004 flower stalks was weaker ($r = 0.26$, $P = 0.01$).

NATIVE AND EXOTIC SPECIES RESPONSE

Average richness of native plant species was generally highest in low burn severity plots (6.5 ± 0.2) and lowest

in the high burn severity (4.8 ± 0.1) over the 3 y. Native species richness increased each year, except for the high burn severity class, which did not show an increase until 2004 (Figure 4a). The time × burn severity interaction was significant for native species richness ($P < 0.001$), with no significant difference among toadflax density classes ($P = 0.09$). The change in native species richness from 2002 to 2003 and 2003 to 2004 was significantly different among some burn severity classes ($P < 0.001$ and $P < 0.01$) (Figure 4a). In contrast to our hypothesis, richness of exotic plant species did not differ significantly among burn severity classes, density classes, or time, and there was no interaction effect ($P > 0.09$), although relatively few exotics other than Dalmatian toadflax were encountered (Figure 4b). The most frequently occurring exotic species other than toadflax was *Verbascum thapsus*. Other less frequent exotic species included *Cirsium vulgare, Erodium cicutarium, Bromus tectorum, Trifolium repens,* and *Thinopyrum ponticum*.

As expected, native species richness was positively correlated with native plant species richness of the previous year (2003: $r = 0.70$, $P < 0.001$ and 2004: $r = 0.74$, $P < 0.001$), although this relationship was slightly weaker across 2 y ($r = 0.62$, $P < 0.001$). We chose 6 of the most frequent native plant species to test for an effect of Dalmatian toadflax stem density or percent cover on native species cover: *Elymus elymoides*, *Festuca arizonica*, *Muhlenbergia montana*, *Cirsium wheeleri, Erigeron flagellaris,* and *Lupinus argenteus*. In contradiction to our hypothesis, we did not observe a significant negative correlation between density or cover of Dalmatian toadflax and cover of any one of these 6 native species ($P > 0.05$ for all tests).

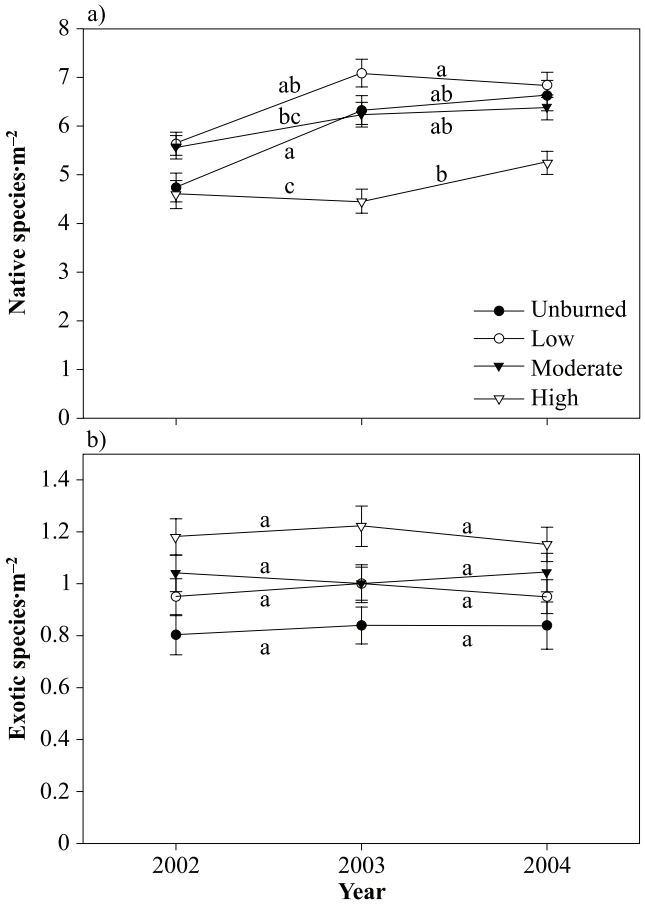

FIGURE 4. Average (a) native species richness (species·m^{-2}) and (b) exotic species richness (species·m^{-2}) by burn severity class and year. Line segments within each time step labelled with the same letter did not differ significantly among burn severity classes (Tukey's HSD, $P > 0.025$).

TRANSITION MATRICES

None of the Dalmatian toadflax control plots (no-toadflax) was invaded by toadflax in 2003, and only 2 plots were invaded in 2004. However, the 10-m toadflax-free buffer zone was invaded by toadflax in 31.5% (24) plots by 2004. Of these plots, 58% were categorized as high burn severity, 17% were moderate severity, 21% were low severity, and 4% were unburned. Dalmatian toadflax disappeared from 6 plots in 2004 in which it had been present in the previous 2 y; 3 of the plots were unburned and the other 3 were burned, one in each burn severity class.

The 4 transition matrices for the 2002 to 2004 transitions corresponding to the 4 classes of burn severity showed that the majority of burned plots either remained in their original toadflax density class or moved to a higher density class in 2004 (Table I), and the percentage of plots moving into or remaining in the high density class increased with increasing burn severity. A greater proportion of plots on moderately (73%) and severely (74%) burned areas classified as high density in 2002 remained as high density in 2004. In contrast, 58% of plots classified as high density in low burn severity areas in 2002 remained as high den-

TABLE I. Transition matrices of the probability (proportion) of plots classified in a given toadflax stem density class in 2002 that remained in that density class or changed to another density class in 2004, by burn severity class. Values represent the proportion of plots that remained in or changed density classes from 2002 to 2004.

	Density class 2002			
Density class 2004	None	Low	Medium	High
UNBURNED				
None	1	0.059	0.077	0.091
Low (1–10)	0	0.471	0.308	0.364
Medium (11–29)	0	0.471	0.538	0.182
High (30+)	0	0	0.077	0.364
Total plots	15	17	13	11
LOW BURN SEVERITY				
None	1	0	0	0.053
Low (1–10)	0	0.571	0.222	0.053
Medium (11–29)	0	0.333	0.481	0.316
High (30+)	0	0.095	0.296	0.579
Total plots	19	21	27	19
MODERATE BURN SEVERITY				
None	0.952	0	0.045	0
Low (1–10)	0	0.391	0.091	0
Medium (11–29)	0.048	0.391	0.500	0.269
High (30+)	0	0.217	0.364	0.731
Total plots	21	23	22	26
HIGH BURN SEVERITY				
None	0.95	0	0.045	0
Low (1–10)	0.05	0.107	0.091	0.130
Medium (11–29)	0	0.143	0.227	0.130
High (30+)	0	0.750	0.636	0.739
Total plots	20	28	22	23

sity in 2004, and only 36% of high toadflax density plots in unburned areas in 2002 remained in that category in 2004. In the unburned class, more low-density plots shifted to a greater density class (47%), while 39% of medium-density plots shifted to lower density classes and half remained as medium. Since only 2 control plots became invaded over the 3 y, the "none" density class remained similar in the matrices.

Rate of change (λ) of plots classified as high density in 2004 compared to 2002 was stable (λ = 1.0) for moderate- and high-severity burns, but was < 1.0 for both low-severity burns (λ = 0.98) and unburned (λ = 0.93) plots. That is, when transition probabilities from 2002 to 2004 were held constant for 20 y, projected λ's indicated an initial increase in the proportion of high-density plots on moderate- and high-severity burns and then stabilized. In contrast, on low burn severity and unburned plots, projected λ's for plots classified as high density decreased dramatically, and then stabilized at a decreasing rate of < 1.0. The projected percentage of high-density plots ranged from < 2% for unburned sites to > 61% on high-severity burn sites (Table II).

Discussion

Our findings suggest that wildfire areas in northern Arizona may be susceptible to the colonization and spread of Dalmatian toadflax. The size and frequency of stand-replacing fires observed in recent years in the southwestern US is expected to continue (Swetnam & Baisan, 1996; Covington *et al.,* 2001; McKenzie *et al.,* 2004; Schoennagel *et al.,* 2005; Westerling *et al.,* 2006), which can facilitate forest invasion by exotic species.

Dalmatian toadflax growth and reproduction on areas burned by the Leroux Fire were strongly related to burn severity and were greatest in high burn severity areas, supporting the first research hypothesis. Toadflax density, cover, and flowering stalks increased in all burned plots, but there was a disproportionately high response in severely burned areas. These findings were similar to other studies in northern Arizona that documented increases of other exotic species on high-severity burns (Crawford *et al.,* 2001; Griffis *et al.,* 2001; Wolfson *et al.,* 2005) and reduced native species richness (Griffis *et al.,* 2001). The lack of competition from native species and overstory and subsequent increased availability of soil moisture and nutrients may have contributed to the increased growth of toadflax at higher burn severities.

TABLE II. Rate of change (λ) in proportion of plots classified as high density that remained as high-density plots, years to convergence, and percentage of high-density plots at convergence using 2002–2004 transition probabilities (Table I), by burn severity class. Lambda values > 1 indicate an increase in the proportion of plots classified as high density, and values < 1 indicate a decrease in the proportion of plots classified as high density.

Burn severity	λ	Years to convergence	% of high density plots at convergence
Unburned	0.93	6	1.75
Low	0.98	6	18.6
Moderate	1	6	41.3
High	1	9	61.29

The second research question, addressing toadflax density-dependence, had a more complex outcome. Unexpectedly, we found that toadflax plants reached a critical maximum density on the study plots by the second year, leading to a decrease in Dalmatian toadflax growth and reproduction in the third year. Field observations showed that the decline in toadflax density and cover within plots in 2004 did not necessarily reflect a decline in toadflax infestation, but rather that toadflax colonized the area outside of the plots. The change in interaction between burn severity and density over time revealed that burn severity was the driving factor for increases in toadflax in the first year and that stem density was the factor driving the decrease of toadflax growth and reproduction in 2004. Toadflax may have increased to a density higher than normally found under unburned conditions, reached a critical density threshold, and then declined to a more sustainable level for the species. This may explain why toadflax disappeared from 6 previously infested plots in 2004 but was present immediately outside the plot frame. Fire effects such as a nutrient pulse, litter removal, removal of competing plants, increased soil moisture, and increased soil temperature can be short-lived, and it is possible that the rapid growth of toadflax and subsequent decline was a reflection of these transient effects (DeBano, Neary & Ffolliott, 1998). A similar increase in toadflax biomass 1 y post-fire was described by Jacobs and Sheley (2003) and was attributed to a nutrient pulse after fire. Similar responses in native species have also been attributed to a nutrient release by fire (Vose & White, 1991; Phillips & Crisp, 2001). Though initial fire effects can be short-lived, they give Dalmatian toadflax a long-term competitive advantage that is maintained in following years by the higher plant density and seed bank established after the fire.

Lambda values, assessing longer-term trends in the projected portion of high-density plots, also indicated that the proportion of plots in our study population remaining at or moving to high density categories was relatively higher on moderately and severely burned sites compared to low-severity burned sites and unburned areas 3 y post-fire. Pauchard, Alaback, and Edlund (2003) found similar results in a multi-scale study on invasion patterns of common toadflax (*L. vulgaris*): high-density patches tended to disperse rather than aggregate, and younger stands tended to be clumped while older stands were dispersed, similar to the spread observed in our study. Thus, while wildfire burn severity patterns can indicate where the greatest initial growth and spread of Dalmatian toadflax can occur, longer-term population increases are determined more by stem density. This may cause "hot-spots" for toadflax infestation to change over time, requiring flexible management and monitoring strategies as time since fire increases.

Since our study design focused on the response of plants at a small scale, we could not quantify an increase in patch size or actual spread across the landscape. The plant-centred plots we used provided efficient and accurate measurement of the response of toadflax plants to fire severity. However, future studies could employ a nested plot design

to capture both plant- and patch-level responses (Pauchard, Alaback & Edlund, 2003).

Native plant species richness increased over time in low and moderate burn severity classes, as we hypothesized in the third research question, but unexpectedly native richness was not significantly negatively correlated with Dalmatian toadflax density, indicating that fire severity influenced native plant richness to a greater extent than the density of toadflax plants. In general, understory species in northern Arizona ponderosa pine forests are adapted to a low-severity fire regime, which enhances growth, and many species rely on fire to reproduce (Vose & White, 1991; Griffis *et al.,* 2001; Korb & Springer, 2003). Contrary to our expectations, exotic species richness did not change significantly over time (averaging near $1 \cdot m^{-2}$) and was not significantly correlated with burn severity. This trend is not consistent with other studies in northern Arizona (Griffis *et al.,* 2001; Crawford *et al.,* 2001) and other regions (*e.g.,* Kerns, Theis & Niwa, 2006) that have noted an increase in exotic species richness in severely burned sites. Instead, we found exotic species well distributed across our plots, and the list included species designated as "noxious" in one or more southwestern states (Sieg, Phillips & Moser, 2003): *Verbascum thapsus, Cirsium vulgare, Erodium cicutarium,* and *Bromus tectorum,* plus a number of species used in seed mixes in this region, such as *Thinopyrum ponticum* and *Trifolium repens*. Although our study took place in a designated Wilderness area, extensive logging, seeding, and livestock grazing had occurred before the site was set aside as wilderness, presumably leaving a legacy of toadflax and other exotic species seeds in the soil seed bank. In contrast, exotics did not dominate after a fairly severe fire at Grand Canyon National Park, possibly because of the lack of a previous history of logging and livestock grazing (Huisinga *et al.,* 2005). Stohlgren *et al.* (1999) reported that native and exotic species richness were positively correlated across a broad geographic region, suggesting that invasion may be favoured in areas of high native diversity. Our results showed no relationship between Dalmatian toadflax variables and native species richness, but our plant-centred plot methods were focused on toadflax and therefore were not the best suited for measuring native plant presence across the larger landscape, in contrast to the randomly located plots of Stohlgren *et al.* (1999).

Management implications

Concerns over severe wildfire and exotic species invasion are increasingly common in pine and pine–oak ecosystems worldwide, not only in the USA and Canada (Vujnovic & Wein, 1996) but also in Mexico (Rodríguez-Trejo & Fulé, 2003), Central America, and the Mediterranean Basin (Leone & Lovreglio, 2004). Fire occurrence and severity have increased with climate and fuel changes in recent decades (Pausas, 2004; Westerling *et al.,* 2006). For managers and ecologists engaged in treatments to reduce forest vulnerability to severe fire or to rehabilitate post-wildfire ecosystems, the patterns of Dalmatian toadflax that we observed in Arizona may be relevant in other areas with the same species (western North America), other toadflax species such as *Linaria vulgaris*, or other invasive plants in the Scrophulariaceae (*e.g., Verbascum thapsus*).

Our results indicate that severe fire may facilitate Dalmatian toadflax spread in the first 2 y after fire, and that control efforts should be focused on high and moderate burn severity areas. Although toadflax increases were highest on high burn severity plots, toadflax stem densities also increased over the 3 y on low-severity burn plots; thus, even low-severity fires can promote toadflax invasion. Other disturbances can also promote Dalmatian toadflax spread, including fuel reduction treatments, which can disturb soils through tree thinning; prescribed burning; and slash pile burning (Jacobs & Sheley, 2003; Wolfson *et al.,* 2005; Korb, Johnson & Covington, 2004). Our results show that even at lower fire severities typical of prescribed fires, Dalmatian toadflax is capable of spreading.

Stem density is another factor for prioritizing toadflax control efforts. Since toadflax density appears to self-regulate by spreading outward after reaching a maximum critical threshold, the treatment of lower density areas along the periphery of a toadflax patch or satellite plants may be effective at reducing spread. This approach would reduce the amount of land area being directly treated while still treating the overall infested area, therefore alleviating time and cost constraints faced by land managers.

While toadflax control *priorities* are supported by data on the spread of this species, there is a great need for research on the *effectiveness* of different treatment methods, timing of treatment on toadflax production, and timing of treatment on carbohydrate root reserves in order to treat toadflax infestations more efficiently. Research is also needed to see if conducting weed control (pulling, chemical, or clipping) before initiating prescribed fire would reduce the amount of stored resources available for resprouting and minimize seed dispersal. Additional post-fire control might be useful to remove seedlings that are stimulated by the disturbance and resprouting adults. Other studies have found that Dalmatian toadflax seedlings are susceptible to competition before roots become established, so establishment of cool season native plants may provide sufficient competition to prevent toadflax seedling survival (Lajeunesse, 1999). The effectiveness of weed control treatments and toadflax population response should be monitored annually or more frequently (spring and fall), if possible. The failure of managers to treat any exotic species prior to fuel reduction or restoration treatments and after wildfire can result in trading one undesirable condition for another (Sieg, Phillips & Moser, 2003).

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