# EFFECTS OF BURN SEVERITY ON NON-NATIVE PLANTS: A CASE STUDY IN YOSEMITE NATIONAL PARK, CALIFORNIA

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# ABSTRACT

It is well recognized that exposed soil caused by natural processes such as fire, landslides or by human activities, increase the probability of non-native species establishment in many ecosystems. This study examines the relationship between burn severity and non-native species within an upper montane forest ecosystem. Sixty plots, stratified by burn severity level and landscape position (lowland vs. upland), were sampled three years post-fire. The abundance of non-natives increased with increased burn severity level, and this relationship was modulated by site characteristics such as slope and landscape position. There was a significantly higher abundance of non-natives in riparian areas when compared to upland areas. Our top three negative binomial regression models with interactions indicate that interactions between burn severity and lowland sites, lowland sites and elevation, and aspect and change in tree basal area all affect non-native species abundance. Within the lowland areas non-native abundance increased significantly with increased burn severity. However, within upland sites non-native species abundance did not vary between severities. We suggest that searching for non-natives is

more likely to be successful in lowland areas that have burned with high enough severity to cause a change in tree basal area.

*Keywords*: bull thistle, burn severity, *Cirsium vulgare*, negative binomial regression, non-native plants, wilderness, Yosemite National Park.

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# INTRODUCTION

Fire is a natural part ecosystems, contributing to a mosaic of patches and adding to overall landscape diversity (Pickett and White 1985). However, fire is also known to increase the potential for invasion of non-native species (Hobbs and Huenneke 1992, D'Antonio *et al.* 1999, Lonesdale 1999, Davis *et al.* 2000, Griffis *et al.* 2001). Throughout western ecosystems, fire is an historic and influential ecological process, and native plants have adapted characteristics to allow them to persist with repeated burning (Agee 1993). However, after more than a century of fire suppression and exclusion, resulting in an excess of fuels, fires are hotter and more intense, and burn outside the natural range of variability for that ecosystem (Crawford *et al.* 2001, Keeley *et al.* 2003). Post-fire, this can lead to an increased likelihood of colonization by non-native species (Keeley *et al.* 2003). Crawford *et al.* (2001) found that when fire severity was high in ponderosa pine *(Pinus ponderosa* C. Lawson) stands, exotic species became a more important component of the post-fire understory vegetation. Keeley *et al.* (2003) found that areas that had

high severity fires three years prior to sampling showed an increase of over two times the numbers of overall non-native species.

Fire then presents a dilemma for managers: to maintain current ecosystem types fire is required and should be part of management plans (Hobbs and Huenneke 1992). However, this fire may lead to an alteration of some communities because of the possible invasion of nonnative plants (Hobbs and Huenneke 1992, Mack and D'Antonio 1998, Crawford *et al.* 2001). Studying the relationship between different burn severity levels, spatial extent of burned patches, and subsequent invasive plant presence will lead to a better understanding of the changing dynamics in these ecosystems.

Riparian areas are known to be hotspots for invasive species establishment, and can act as corridors for further invasive species spread (Stohlgren *et al.* 1998, Parendes and Jones 2000, Tickner *et al.* 2001, Katz *et al.* 2005). Although riparian areas can form a break in the fuel continuity from surrounding areas, at the headwaters, they have been found to burn with a similar severity as adjacent upland sites (Agee *et al.* 2002, Dwire and Kauffman 2003). Overall, riparian corridors are extremely variable, containing different vegetation types due to elevational differences and position in the watershed, and this high variability leads to a high variability of fire behavior and effects. Although much work has been done on non-natives in lowland systems, few studies have looked at the interaction of fire and non-natives in these lowland areas.

This study assesses the degree to which non-native species have colonized burned areas in the wilderness of Yosemite National Park, and what relationship exists between burn severity and invasion. We examined the following research question: what is the nature of the relationship between burn severity level and non-native plant abundance, in both upland and lowland sites?

# **METHODS**

# Study Area

Field work for this project took place in the federally designated wilderness of Yosemite National Park, California, USA. Located in the central Sierra Nevada mountain range, the park totals 302 768 ha (3028 km<sup>2</sup>), of which 94 % is wilderness. With an elevation range spanning from 524 m to 3998 m, Yosemite contains over 1400 species of vascular plants (Botti 2001). The lower and middle elevations are characterized by a Mediterranean climate, with cool, wet winters, and hot, dry summers, while the upper alpine areas are characterized by more boreal climate, with long, very cold winters, and short cool summers. Precipitation in the lower and middle elevation zones tends to occur from November through April, averaging about 95 cm per year, with winter months (January through March) averaging 48 cm. Highest temperatures occur in July, averaging 22 ° C, and coldest temperatures occur in January, averaging 3 ° C. There are currently 155 non-native species occurring in Yosemite, with 63 of those species ranked as priority species for management (Gerlach *et al.* 2003).

We chose the Tuolumne Fire of 2003 for our case study (Figure 1). This fire burned a total of 1540 ha, spanning an elevational range from 1890 m to 2560 m. The forest and woodland communities were predominantly mixtures of red fir (*Abies magnifica* A. Murray) and white fir (*A. concolor* [Gord. & Glend.] Lindl. ex Hildebr.), with Jeffrey pine (*Pinus jeffreyi* Balf.), lodgepole pine (*P. contorta* Douglas ex Louden var. *murrayana* [Balf.] Engelm.), western white pine (*P. monticola* Douglas ex D. Don), and sugar pine (*P. lambertiana* Douglas) (van Wagtendonk *et al.* 2002). Burn severity, as determined by the Relative differenced Normalized Burn Ratio (RdNBR) (Thode 2005, Miller and Thode 2007), was heterogeneous throughout the

burn, with approximately 44 % of the site described as a moderate burn, 30 % low severity burn, 17 % high severity burn, and 9 % of the area was unchanged (unchanged sites were classified as unburned sites in this study). Prior to field sampling, we performed an independence analysis to confirm that burn severity level was not correlated with topographical or environmental parameters (K. Kaczynski, Colorado State University, unpublished data).

Several sources of water are present in the burned area: the Middle Tuolumne River and the smaller Long Gulch Creek both cross the study site. There are also unnamed year-round drainages, as well as many seasonal drainages. The terrain is variable, with steeper areas on the south side of Long Gulch, and flatter sites on the north. Visitor use in this area is low, and is estimated to be only a few parties per year (L. Boyers, Yosemite National Park, personal communication; C. Kuvlesky, Yosemite National Park, personal communication).

#### Field Methods

We sampled 64 plots between June and August 2006 (Figure 1) using a stratified random sample based on burn severity level and physiographic location was used to determine sample locations. Twenty plots were sampled in each of the high, moderate, and low severities. Thirty plots each were sampled in upland and lowland areas. We defined lowland sites as any location within a 25 m buffer on either side of a river, creek, stream, seasonal drainage, or wetland.

One 0.1 ha (20 m  $\times$  25 m) enhanced modified Whittaker plot was set up at each randomly located upland point (Stohlgren *et al.* 1995). Lowland plots, due to restricted sampling time frames, were one-quarter the size of upland plots (0.025 ha). We enhanced all plots by adding additional 1 m<sup>2</sup> quadrats (34 in upland plots, 17 in riparian plots). These additional quadrats

were arranged 2 m apart along the central line, as well as along each side, spaced 10 m apart. Upland plots were established with the 50-m side parallel to the slope. Lowland plots were established with the 25 m side parallel to the wet area.

We recorded site characteristics at each plot, including plant species present, tree and snag basal area, and landscape characteristics such as elevation, slope, and aspect. A species list was generated for the entire plot, as the abundance of each invasive species was recorded. Species were identified to the finest taxonomic level using Botti (2001) and Hickman (1993). We recorded diameter at breast height (dbh) of all standing trees and snags in a randomly chosen quadrant of the upland plots and in the full lowland plot.

# Preprocessing of Data and Statistical Methods

Prior to performing statistics, we took a number of processing steps to standardize the data. All lowland plot data were normalized for area, and were converted from 0.025 ha to 0.1 ha. Basal area was calculated on a per hectare basis. Post-burn basal areas were actual basal areas of the plots. Because no pre-fire site data exist for this study area, pre-burn basal area was based on the assumption that trees recorded as snags were alive prior to the burn. A new variable, change in basal area, was defined as the post-burn basal area subtracted from the pre-burn basal area. Prior to fitting regression models, all predictors were standardized by subtracting the mean and dividing by the standard deviation such that  $x_{std} = \frac{x-\bar{x}}{s}$ .

To predict the abundance of non-native species, we examined Poisson and negative binomial regression models in a model selection framework using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). Because the response variable is discrete count data and contains a relatively large proportion of zeros, the normal distribution was not appropriate to describe the data and other families of models were required. Models were fit in R version 2.8 using the MASS and pscl packages (R Development Core team, http://www.rproject.org/). The negative binomial family of models resulted in the lowest AIC scores, and thus only these models are discussed in the following sections.

# RESULTS

Of the 60 plots sampled, 22 (37 %) had at least one non-native species (Table 1). Nonnative species found included bull thistle (*Cirsium vulgare* [Savi] Ten.), prickly lettuce (*Lactuca serriola* L.), spiny sowthistle (*Sonchus asper* [L.] Hill), yellow salsify (*Tragopogon dubius* Scop.), and *Rumex acetosella*. All five species are on the Yosemite priority non-native species list. Bull thistle was the most widely recorded non-native, occurring in 14 (22 %) of the plots.

Bull thistle density was not high, and where it occurred, it averaged five individuals per 0.1 ha. Spiny sowthistle, a much smaller plant, had very high abundance where it occurred, averaging 10.9 individuals per 0.1 ha. Overall, the abundance of non-natives throughout the Tuolumne burn was low.

Abundance of non-natives increased as burn severity increased, although the difference in non-natives per burn severity level does not differ significantly. Mean abundance in high severity patches was 4.8 individuals (SD = 8.42), while within moderate severity patches, mean abundance was 3.1 individuals (SD = 6.44). Low severity patches had a mean abundance of less than 1 individual (SD = 2.68).

Due to the non-normality of the data, as well as over dispersion, we ran several negative binomial and Poisson regression models. The model with the lowest AIC was a negative binomial with 15 parameters, including five interaction terms (Table 2). However, the top three models are indistinguishable among each other and all have similar interaction terms, with all the coefficients of the interaction terms in the same direction (Table 3). The top three models explained an average of 65 % of the variation. Slope was the only variable with a main effect, where sites with higher slopes having lower abundance of non-natives. Other variables were interpreted as interactions (Figure 2). At lowland sites, an increase in burn severity increased the abundance of non-native plants. However, at upland sites, and increase in burn severity had no effect. On north facing slopes, the change in basal area had a negative effect on the abundance of non-natives, however on south facing slopes, the change in basal area had a small positive effect. In addition, in lowland sites, as elevation increases, the abundance of non-natives increases. The final interaction is between aspect and species richness, where on north facing slopes, as species richness increases, the abundance of non-natives increases faster than on south facing slopes.

#### DISCUSSION

#### Patterns of Exotic Plant Establishment after Fires

Studies have demonstrated a relationship in different ecosystem types between burn severity and non-native plants (Keeley *et al.* 2005, Kerns *et al.* 2006), while other studies have shown no effect with burn severity and non-native plant abundance (Kuenzi *et al.* 2008). In addition, studies have shown a positive relationship between riparian sites and non-native plant abundance (Stohlgren *et al.* 1998). Our models demonstrate that there are interacting factors which exhibit strongly negative or positive relationships with non-native plant abundance, with the strongest of the interactions between burn severity and physiographic location. At lowland sites, as burn severity increased, the abundance of non-native plants increased. Lowland sites that burned at a high severity had four times the abundance than low severity burned sites. In contrast, at upland sites, as burn severity increased, there was no effect on the non-native abundance. The presence of surface water during the growing season, even if the water dries up later in the season, created a micro-site which was highly conducive to non-native plants.

Studies have found a positive relationship between species richness and higher nonnative species presence – the rich-get-richer hypothesis (Stohlgren *et al.* 1998, Stohlgren *et al.* 1999). We found that species richness, interacting with the dominant aspect of the site was an important predictor. North facing slopes with higher species richness had a higher abundance of non-native species, likely due to the increase in soil moisture levels on north facing slopes. Our study found a weak relationship between slope and non-native plant abundance, steeper slopes had fewer non-natives than more shallow slopes. Lowland areas had significantly shallower slope than upland sites. Klinger *et al.* (2006) found that invasive species presence was significantly positively correlated with slope, thus as slope increased, abundance of invasives increased. This was the opposite of the case that was found in this study in lowland areas.

# Non-native Species and Riparian Sites

Non-native species were commonly found where surface water was present. The winter of 2005-2006 was a heavy snow year, and as a result, there was greater runoff for a longer period

of time throughout the summer. This study did find a significant difference in the abundance of non-natives in areas classified as lowland when compared to upland areas and this finding is supported by many studies (Stohlgren *et al.* 1998, Tickner *et al.* 2001).

Stohlgren *et al.* (1998) found that at the square meter scale, mean invasive species richness was higher in three of four sites in riparian areas when compared to upland areas. At  $1000 \text{ m}^2$  scale, mean species richness was significantly greater in riparian than in upland areas, and he concluded that these plants could be a possible source of seeds for upland sites. We found that lowland sites averaged overall four more species per  $1000 \text{ m}^2$  than upland sites.

Bull thistle was also found in significantly higher abundance in lowland sites when compared with upland sites. This is in contrast to what Parendes and Jones (2000) found, where bull thistle was found only 20 % of the time along stream corridors, and 80 % of the time along roads. It is likely that there was higher light availability along the roads when compared to along stream corridors (Parendes and Jones 2000). This could help explain why there was an increase in abundance, although not significant, of bull thistle in riparian areas when the burn severity level increased. The increased sunlight, from the removal of the canopy (a higher change in basal area), and the water that is naturally present at these sites, was favorable for the establishment of bull thistle.

#### **Conclusions**

The results from this study show that three years post fire, within the mid-elevation range of the Sierra Nevada, non-natives are only minor constituents of the forest community. Although not highly abundant, the potential still exists for seed dispersal into new sites within the burn area and beyond.

We have demonstrated that burn severity, interacting with physiographic location (lowland vs. upland) is an important predictor of non-native plant abundance. Because early detection is important in combating the spread of non-natives, park managers can use this research to refine their search areas. We would suggest that given limited resources and time, areas which are categorized as high severity burned sites that are in or near a lowland area (including seasonal lowland sites) are ideal sites to examine for non-native plant establishment three years after the burn.

It is important to continue to study the spread of non-natives into mid-elevation forests, because these forests are predicted to have a lower non-native abundance and have historically been studied less than lower elevation forests and shrublands. As the awareness of the importance of fire as a natural process continues to grow, and sites return to fire intervals within their natural range of variability, the dynamics of non-native plant populations will undoubtedly change. This topic will continue to be of major importance to park managers for years to come.

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## LITERATURE CITED

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- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Agee, J. K., C. S. Wright, N. Williamson, and M. H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management 167:57-66.
- Botti, S. J. 2001. An illustrated flora of Yosemite National Park. The Yosemite Association, El Portal, California, USA.
- Burnham, K., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, New York, USA.
- Crawford, J. A., C.-H. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. Journal of Vegetation Science **12**:261-268.
- D'Antonio, C. M., T. L. Dudley, and M. Mack. 1999. Disturbance and biological invasions: direct effects and feedbacks. Pages 413-452 in L. R. Walker, editor. Ecosystems of Disturbed Ground. Elsevier, Amsterdam, Netherlands.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.
- Dwire, K. A., and J. B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western US. Forest Ecology and Management **178**:61-74.
- Gerlach, J. D., P. E. Moore, B. Johnson, D. G. Roy, P. Whitmarsh, D. M. Lubin, D. M. Graber, S. Haultain, A. Pfaff, and J. E. Keeley. 2003. Alien plant species threat assessment and management prioritization for Sequoia-Kings Canyon and Yosemite National Parks. Open File Report 02-170, US Geological Survey Open Survey Report 02-170 Carson City, Nevada, USA.
- Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. H. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. Forest Ecology and Management 146:239-245.
- Hickman, J. C. 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324-337.
- Katz, G., J. Friedman, and S. W. Beatty. 2005. Delayed effects of flood control on a flooddependent riparian forest. Ecological Applications 15:1019-1035.
- Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. Ecological Applications 15:2109-2125.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. Ecological Applications 13:1355-1374.
- Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. Ecoscience 13:44-55.

- Kuenzi, A. M., P. Z. Fule, and C. H. Sieg. 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. Forest Ecology and Management 255:855-865.
- Lonesdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.
- Mack, M., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.
- Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment **109**:66-80.
- Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conservation Biology 14:64-75.
- Pickett, S. T. A., and P. A. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hotspots of native plant diversity. Ecological Monographs 69:25-46.
- Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology **138**:113-125.
- Stohlgren, T. J., M. B. Falkner, and L. D. Schnell. 1995. A Modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.
- Thode, A. E. 2005. Quantifying the fire regime attributes of severity and spatial complexity using field and imagery data. University of California, Davis, California, USA.
- Tickner, D. P., P. G. Angold, A. M. Gurnell, and J. O. Mountford. 2001. Riparian plant invasions: hydrogeomorpholgical control and ecological impacts. Progress in Physical Geography 25:22-52.
- van Wagtendonk, J., K. A. van Wagtendonk, J. B. Meyer, and K. J. Painter. 2002. The use of geographic information for fire management planning in Yosemite National Park. The George Wright Forum **19**:19-39.

Figure 1: Location of the Tuolumne burn, Yosemite National Park, California. Plots where an invasive species was present are shown by triangles and plots where invasive species were absent are shown by circles.



Figure 2: Interactions between parameters which influence the abundance of non-native species. These three interactions were prominent in change in basal area  $(m^2/ha)^*$  aspect (top), species richness\*aspect (middle), and burn severity level\*lowland (bottom).



Severity Level		Plots with non-natives	Total plots sampled	Percent with non-natives
High	Upland	3	9	33 %
	Riparian	8	11	73 %
Moderate	Upland	1	10	10 %
	Riparian	5	10	50 %
Low	Upland	4	10	40 %
	Riparian	1	10	10 %

Table 1: Frequency distribution of plots where non-native species were found. Percent of plots sampled within each category with non-natives present.

Table 2: Top nine models, ranked by AIC. Also included are the log-likelihoods, the number of parameters included in the model, the change in AIC, model weights, residual deviance, and residual degrees of freedom. Model parameter abbreviations are as followed: slope (slope), burn severity (BSlevel; -1 = high, 0 = moderate, +1 = low), lowland (lowland = 1, upland =0), elevation (elev), transformed aspect (asp; -1 = north, +1 = south), species richness (SR), change in basal area (CBA). Slope, elevation, aspect, species richness, and change in basal are all standardized around the mean.

		#		Δ	Model	Residual	Residual
Model	loglike	param	AIC	AIC	weights	deviance	df
slope + BSlevel*lowland + lowland*elev + asp*SR + CBA*asp	101.46	15	131.46	0	0.290	33.12	46
slope + SR + BSlevel*lowland + lowland*elev + CBA*asp	103.75	14	131.75	0.29	0.251	35.43	47
SR + BSlevel*lowland + lowland*elev + CBA*asp	107.28	13	133.28	1.82	0.117	37.32	48
BSlevel*lowland + lowland*elev + SR*asp + CBA*asp	106.03	14	134.03	2.57	0.080	36.39	47
BSlevel*lowland + lowland*elev + SR*asp	110.54	12	134.54	3.08	0.062	37.80	49
asp*CBA + BSlevel*lowland + elev*lowland + SR + lowland*CBA	106.91	14	134.91	3.45	0.052	37.51	47
SR + asp + BSlevel*lowland + lowland*elev	112.98	11	134.98	3.52	0.050	38.63	50
slope + BSlevel*lowland + lowland*elev + asp*SR + CBA+asp	107.19	14	135.19	3.73	0.045	34.99	46
SR + BSlevel * lowland + lowland * elev	115.69	10	135.69	4.23	0.035	36.98	51
asp*CBA + BSlevel*lowland + elev*lowland + SR + BSlevel*asp	106.93	15	136.93	5.47	0.019	36.86	46

Table 3: Parameter directions of the three best models (lowest AICs): negative binomial regression with interactions, predicting the abundance of non-native species abundance. Predictor variables for change in basal area (CBA), slope, elevation, and species richness (SR) were standardized. Lowland is a categorical variable, with 1 representing lowland and 0 representing upland. Burn severity level is categorical, with -1 representing low severity, 0 representing moderate, and +1 representing high.

Predictor	Coefficient			
Intercept	negative			
slope	negative			
change in basal area (CBA)	negative			
BSlevel (moderate)	strongly positive			
BS level (high)	strongly positive			
species richness (SR)	positive			
lowland	strongly negative			
elevation	negative			
BSlevel*lowland	positive			
lowland*elevation	strongly negative			
aspect*CBA	positive			
aspect*SR	negative			