Second Year Post-Wildfire Recovery Inhibits Dispersal of Allelopathic, Invasive Forb

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Research Article

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Abstract

The increasing frequency of wildfires in Southern California's Mediterranean-type habitats has been facilitating the displacement of native plants by invasive annuals. Black mustard (*Brassica nigra*) is an abundant, allelopathically harmful, invasive forb, which readily colonizes soil niches following most disturbances. Wildfires, however, are unlike other forms of disturbance because they can fundamental alter plant-soil interactions through both physical and chemical changes in the soil. Here, a comparative field study of burned and unburned sites suggests that the Woolsey Fire – the largest wildfire ever recorded in California's Santa Monica Mountains – inhibited dispersal of *B. nigra* and changed how it interacts with other plant species in the second year of post-fire recovery. More surprisingly, native plants were more likely to replace *B. nigra* than non-native plants in burned sites. These results indicate the possibility of post-fire seeding with specific "fire follower" native plant species may allow native flora to occupy soil niche space until longer-lived, competitive native shrubs establish.

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Introduction

Understanding how plant communities respond to disturbance has been a focus of ecology for over a century (Clements 1916). Resulting succession models from this vein of research informs decisions on land management in protected areas (e.g. Gibson & Brown 1985, Bonet 2004). However, decades of research since Gleason (1926) indicates responses to disturbance are often stochastic (e.g. He & Mladenoff 1999), especially when disturbance changes the abiotic environment (e.g. Moral & Wood 1993). Further complicating the predictive power of succession models is not only the abiotic changes particular to disturbance-type, but also species-specific responses to disturbance and the introduction of invasive species (Brooks et al. 2004).

Wildfires present a special type of disturbance as they may do more than merely remove vegetation. According to the US Forest Service and Bureau of Land Management, both low and high severity wildfires can change both the biotic and abiotic environment. Low-to-moderate severity prescribed fires are a common tool in habitat restoration to remove invasive vegetation, lower pH, mobilize nutrients, neutralize allelopathic effects with active carbon deposits, and facilitate a return of native plants while high severity wildfires result in fundamental alteration of soil properties (see review by Certini 2005). For example, high severity wildfires are often defined by the combustion of nearly all litter and humus in the soil horizon, which can lead to partial or complete incineration of seedbanks, burn roots of regenerative plants, affect N-cycling, and leave behind significantly greater amounts of activated carbon (Collier & Mallik 2010).

In Southern California's Mediterranean-type ecosystems, the increasing frequency of wildfires has been facilitating the establishment of harmful invasive plant species at a loss to the diversity of native flora, despite numerous fire adaptive traits found in native species (e.g. Westman 1981, see review by Rundel et al. 2018). Over the past century, nitrogen deposition from automobile exhaust and edge effects associated with more than a century of nearly unmitigated real estate development have degraded habitat into isolated patches, contributing to the introduction and spread of numerous fast-growing, invasive annuals (Chapin et al. 1986). These fast-growing invasive annuals complete their life-cycle earlier in the year than natives, allowing opportunistic invasive species to outcompete native grasses and forbs for limited water and potentially avoid the fire season all together (D'Antonio & Vitousek 1992). In turn, the fire season fuel load increases earlier in the year as invasives senesce tissues, exacerbating the severity and frequency of wildfire, and increasing the displacement of native grasses and forbs (Talluto & Suding 2008). Wildfires can also disrupt succession by inhibiting the establishment of more competitive long-lived perennial shrubs (Keely et al. 2005) - shrubs which could otherwise inhibit recruitment of invasives (Jacobson et al. 2004, Bell et al. 2018) and even retake territory in the absence of further burning (Freudenberger at al. 1987). However, Wardle et al. (1998) and Certini (2005) emphasize wildfires can affect different species in different ways, especially for species that interact chemically with their soil environments.

Black mustard (*Brassica nigra*) is one of the most harmful invasive annuals in Southern California's Mediterranean-type habitats, often generating near monocultures across entire hillsides (Bell & Muller 1973). The forb's invasiveness is owed partially to its fast growth rate and high fecundity but has also largely been contributed to its root exudates, which kill mycorrhizae and inhibit the germination and growth of other plants (e.g. Turk et al. 2003, Tawaha & Turk 2003). Many forms of disturbance, such as edge effects, erosion along slopes, and low severity fire, may therefore facilitate *B. nigra* dispersal (e.g. Kulmatiski & Beard 2006).

The opportunistic growth behavior of *B. nigra* led to a hypothesis that similar to other invasive plants, wildfire facilitates reestablishment of *B. nigra* during the first year of post-fire vegetative recovery. However, wildfires are well-known to result in chemical changes to soils that reduce the competitiveness of allelopathic species and allow other plant species to compete for soil niches (Wardle et al. 1998, Certini 2005). This latter consideration led to a second hypothesis that despite a general trend of wildfire facilitating the establishment of harmful invasives, wildfire harms *B. nigra* establishment in the second-year of post-fire vegetative recovery. Wildfires also remove vegetation, including the roots of regenerative perennials (see above). Changes to the plant community and abiotic conditions led to a third hypothesis that not only does wildfire change with which species *B. nigra* interacts, wildfire changes how *B. nigra* interacts with other species. Specifically, this study asks: 1.) Did *B. nigra* abundance decrease in the second year of post-fire vegetative recovery following the 2018 Woolsey Fire – the largest wildfire ever recorded in the Santa Monica Mountains National Recreation Area, CA? 2.) Did the Woolsey fire effect a relationship between plant abundance and proximity to *B. nigra* not seen in unburned sites? And 3.) If wildfire does decrease *B. nigra* abundance and how the invasive annual interacts with other species, are invasive or native plants more likely to occupy available soil niches?

Methods

According to National Park Service records, on November 2018, the Woosley Fire jumped the 101 Freeway near the border of Los Angeles and Ventura Counties and burned over 40468.564 ha (88 %) of land in the Santa Monica Mountains National Recreation Area (SMMNRA). The SMMNRA is the largest expanse of protected Mediterranean-type habitats in the world. The integrated parks and nature reserves encompass protected state and federal intertidal zones, beaches, coastal sage scrub, chaparral, coastal woodlands, and grasslands that are home to over 1000 species of plants and 500 vertebrate species. Despite this being the largest wildfire ever recorded in the entire Santa Monica Mountain range, adjacent nature reserves with similar climate, soil, and altitude remained unburned, and were used as reference controls for this observational study.

According to the USDA Web Soil Survey (https://websoilsurvey.sc.egov.usda.gov/), all sites sampled here are composed of up to 30 cm deep gravelly or gravelly silt loams derived from weathered shale and sandstone parent material. Mean annual precipitation is 37.5 – 70 cm with mean annual temperatures 15.6° – 18.9° C and low (11.5 cm) to very low (4 cm) water availability.

In Newton Canyon, *Brassica nigra* and other invasive annuals lined regularly disturbed areas along heavily visited trail-sides and along steep slopes, downhill from Los Angeles County Highway N9. The N9 connects US Highway 101 with scenic beaches along the Pacific Coast Highway US1 in Malibu, CA, and thus is a high traffic area. The introduction of non-native seeds from roadways is well established, and may have reintroduced *B. nigra* and other invasive plants following the fire. Linear regression analysis of distance of *B. nigra* dispersal versus slope grade from uphill hiking trails and Los Angeles County highway N9 indicated slope was a strong driver of the forb's dispersal in burned habitat ($R^2 = 0.44$, $p = 0.035$; *data not shown*). However, the presence of several native plant species as well as leaves on some trees in the immediate vicinity suggested that seedbanks may not have been completely incinerated. To minimize the effects of disturbance associated with hikers, trail maintenance, and especially increased erosion on steeper slopes, 31 m point-intercept transects were randomly laid on relatively level (<5.0 % grade) areas a minimum of 10m from trails on south-facing slopes of canyons and mountains at all sites. Changes in mean percent cover of *B. nigra* from the first to second year of post-fire recovery were determined by comparing the frequency of the desiccated semi-woody shoots from the first year and the living aboveground tissues in the second year in 31 m transects (n = 8 burned, n = 8 unburned) using a two-factor fixed effects ANOVA (year x burned or unburned). Tukey HSD post hoc tests were used to indicate significant differences between treatment means. Species were also identified and characterized into guilds of native or invasive growth forms as indicators of fire's overall effects on community assemblage as a reference point, with special attention on wildfires effects on invasive forbs. Guilds were classified by growth forms: invasive annual grasses, native annual grasses, native perennial grasses, invasive (annual) forbs, native forbs, and native shrubs. To test if burned areas accumulated more native or invasive plant species two-years after a severe fire, percent cover of native and invasive plants as well as intraguild species richness were calculated with the standard point-intercept method and compared using a two-factor random effects ANOVA. Difference between treatment means was tested with Tukey HSD post hoc analysis.

As an indicator of whether the Woolsey Fire affected how *B. nigra* interacted with other plant species, the effect of distance from the nearest *B. nigra* on the abundance of invasives, natives, and all plant species combined were tested with ANCOVAs. Distance from *B. nigra* was the covariate. The mean number of natives and invasives were counted at 5 cm intervals along 1 m point-intercept transects straddling a flowering *B. nigra* (n = 7 burned, n = 7 unburned). Counting began at the point-intercept of the *B. nigra* (0 m) and moved N and S 50 cm.

Finally, if *B. nigra* dispersal was inhibited in the second year, this study sought to find if the open niche is more likely to be filled by native or invasive plants. A series of X^2 Contingency Tests for associations with the previous year's desiccated *B. nigra* were conducted with Bonferroni adjustments for multiple comparisons. In 31 m transects in both burned and unburned sites, the presence of native and invasive plant species were recorded when a living second year *B. nigra* was not present, as strong indication that the first year's *B. nigra* was not able to replace itself in its immediate vicinity.

All statistical analysis was performed in Rstudio v0.98.1062.

RESULTS

In order to test the effect of fire on dispersal of *B. nigra,* percent cover in the 2nd year was calculated with point-intercept transects and compared to the percent cover of the previous year's senesced semi-woody *B. nigra* shoot tissues. Wildfire had an interactive effect with year of post-fire vegetative recovery (ANOVA $F_{1,28} = 7.606, p = 0.01, Fig. 1$). Wildfire decreased *B. nigra* vegetative cover 74.3 % from the first year to second year (Tukey HSD post hoc p = 0.004) while *B. nigra* percent cover remained unchanged in unburned sites (Tukey HSD post hoc p = 0.999). The percent cover of *B. nigra* in burned sites during the second year was a moderately significant 55.8 % lower than *B. nigra* percent cover in unburned sites the same year (Tukey HSD post hoc p = 0.056).

As a reference, percent covers of all invasives and natives were analyzed as well as intraguild species richness and compared between burned and unburned sites. Despite a decrease in *B. nigra* dispersal in the second year of post fire recovery, there was no change in percent covers for invasives or natives (ANOVA $F_{1,28} = 0.236, p = 0.57; Fig. 2A$) between burned and unburned sites. Fire did have an interactive affect with intraguild species richness (ANOVA $F_{4,70} = 3.629, p < 0.01; Fig. 2B$). Tukey HSD post hoc analysis reveals the richness of invasive forbs did not differ between burned and unburned sites (p = 0.972), but in burned sites, invasive forbs were of a weakly significant (p = 0.0815) greater richness than invasive grasses – a difference between means not seen in unburned sites. It is also noteworthy that high severity wildfire reduced the guild species richness of native shrubs by 53.8 % (Tukey HSD post hoc p = 0.044).

As an indicator of whether wildfires can change how *B. nigra* interacts with other species, the abundance of invasives, natives, and all plants were tested as a function of distance from *B. nigra.* Severe wildfire had a moderately significant interactive effect with proximity to *B. nigra* on native abundance (ANCOVA p < 0.055 Fig. 3A). Linear regression analysis showed no relationships between native abundance and proximity to *B. nigra* in unburned sites (R^2 = 0.06, p = 0.493), but there was a strong positive relationship in burned sites (R^2 = 0.82, p = 0.0003).

Wildfire did not interact with proximity to *B. nigra* on invasive abundance (ANCOVA $p < 0.192$), nor did the proximity to *B. nigra* have a significant relationship to invasives in burned ($R^2 = 0.23$, $p = 0.137$) or unburned ($R^2 = 0.03$, $p = 0.606$) sites with linear regression analysis (Fig. 3B). When all plants were analyzed, fire had a moderately significant interactive effect with proximity to *B. nigra* (ANCOVA $p = 0.0567$; Fig. 3C). Similar to native abundance, linear regression analysis showed a strongly significant, positive relationship between the abundance of all plants and proximity to *B. nigra* in burned sites ($R^2 = 0.63$, $p = 0.004$), but not unburned sites ($R^2 < 0.01$, $p = 0.984$). Aligning the results of percent cover in the 31 m transects above, it was apparent that within the entire 1 m transects used in ACNOVAs here, wildfire did not significantly reduce the overall abundance of invasives or natives (ANOVA $F_{1,24} = 2.62, p = 0.119$; *data not shown*).

Finally, if *B. nigra* does not replace itself in the second year of post-fire vegetative recovery, this study sought to answer whether natives or invasives are more or less likely to fill the available niche. The X^2 contingency test analysis showed that in burned sites, natives replaced *B. nigra* 26.9 % more than was anticipated while invasives replaced *B. nigra* 19.5 % less than would be predicted by chance alone (Fig. 4). In unburned sites, natives replaced *B. nigra by* 45.5 % less than expected and invasives replaced *B. nigra* 86.9 % less than was expected (Fig. 4).

Discussion

As hypothesized, this study suggests that the second year of vegetative recovery following a wildfire reduced the abundance of the harmful invasive *B. nigra* (Fig. 1), even as burns generated growing conditions that favor invasive forbs over invasive grasses (Fig. 2B). Wildfire also affected the ways *B. nigra* interacts with other species in a manner consistent with water and nutrient competition, not seen in unburned sites. Wildfire generated a significant positive relationship for abundance of natives and all plants as a function of distance from *B. nigra,* which was not observed in unburned sites (Fig. 3A&C). But most surprisingly, contrary to a general trend of wildfires facilitating the dispersal of invasives, *natives* were more likely to replace *B. nigra* than invasives in burned sites two growing seasons following the largest wildfire on record for the study area (Fig. 4).

Wildfires generally increase the establishment and dispersal of harmful invasive plants in Southern California's Mediterranean-type habitats, but species-specific responses to post-fire vegetative recovery vary (Brooks et al. 2004). This study does not investigate *B. nigra* abundance in burned sites before the Woolsey Fire, and is therefore not a causative study. However, in burned sites, *B. nigra* mean abundance in the first year of post-fire vegetative recovery was equal to both years in unburned sites (Fig. 2), indicating similar levels of propagules from the seedbank, hiking paths, or roadways. The significant loss in invasive forb's abundance in the second year of recovery in burned sites is likely then the result of wildfire's delayed effects – whether indirect effects from changes in soil chemistry, direct effects as *B. nigra* interacts with a different assemblage of species, or both.

Previous studies suggest that if *B. nigra* does not replace itself, then wildfire should facilitate the establishment of other invasives in California's semi-arid coastal plant communities (e.g. Keeley 2001; Arianoutsou & Vilà 2012). While wildfire did not change the mean percent cover of invasives or natives (Fig. 2A), wildfire affected intraguild species richness (Fig. 2B), indicating a change to the assemblage of species. For example, *B. nigra* exhibited a loss in abundance even as post-fire growing conditions favored invasive forbs over invasive grasses. Though the difference in intraguild richness between invasive forbs and grasses was weakly statistically significant in observations here, non-overlap of standard error bars suggests increasing the sampling size slightly would likely result in a lower alpha. More observations are merited, but it is possible that some of the observed increases in establishment of invasives following wildfires in Southern California is really changes to the invasive assemblage. Wildfire corresponded to a significant decrease in the abundance of native shrubs (Fig. 2B). Many of these native shrubs can inhibit the re-establishment of *B. nigra* (Bell et al. 2018). The loss of these shrubs therefore should have made conditions more favorable for *B. nigra,* but it did not.

Not only did fire change which species *B. nigra* interacted with, wildfire changed how *B. nigra* interacts with other plant species (Fig. 3A-C). Here, ANCOVA and linear regression analysis indicate that in burned sites, natives and all plants increase in abundance as a function of distance (Fig. 3A&C), but not in unburned sites. Wildfire's effects on how *B. nigra* interacts with native plants could be explained by changes in intraguild richness and which species of native plants *B. nigra* is interacting with. Or wildfire could change how *B. nigra* interacts. The interactions seen with native plants and all plants is similar to results in other systems produced by competition for water and nutrients (e.g. Ozier-Lafontaine et al. 1998; Hauggaard-Nielsen et al. 2001). If the latter is true here, then *B. nigra* is interacting with other species in different ways in unburned sites, in which no relationship was seen. Either way, wildfire produce an interaction, not seen in unburned sites (Fig. 3A-C).

Most surprisingly here, when *B. nigra* did not successfully replace itself in 31 m transects in burned sites, native plants were more likely to replace *B. nigra,* and invasive plants were less likely (Fig. 4). Thus, the observation of natives germinating and growing at a higher than expected rate in burned sites but not in unburned sites further suggests that the wildfire changed *B. nigra* species interactions.

Wildfire generate fundamental changes to soil chemistry (see Introduction), but active carbon deposits by the Woolsey Fire offers the best explanation as to why the allelopathic invasive *B. nigra* experienced decreased dispersal and changes to its species interactions two years after a massive wildfire. Active carbon deposits from wildfires neutralize several types of allelopathy in several types of habitat, allowing other plant species to grow in soils they otherwise would be excluded from (Wardle et al. 2007). In a thorough review of experimental designs in allelopathy, Inderjit and Callaway (2003) show allelopathy commonly extends up to 4 m and describe three general effect-types of allelopathy: inhibition zones, monocultures, and root segregation. *Brassica nigra* commonly forms large patches of monocultures or near monocultures (Bell & Muller 1973). If *B. nigra* fails to replace itself in burned sites, it is not likely to establish a monoculture. Wildfire favored invasive forbs over invasive grasses, yet wildfire reduced *B. nigra* competitiveness. Here, ANCOVA and linear regression analysis indicate that in burned sites, natives and all plants increase in abundance as a function of distance, but not in unburned sites (Fig. 3A&C). If allelopathy inhibited plant growth in burned sites, other plants would not increase in abundance as a function of distance from *B. nigra*. Rather allelopathy would generally result in a reduction in plant abundance through the exclusion of most other species across a zone. The positive relationship of distance from *B. nigra* to natives and all plant abundance in burned sites is indicative of alternate species interactions, such as competition for water or nutrients (e.g. Ozier-Lafontaine et al. 1998; Hauggaard-Nielsen et al. 2001). Moreover, *B. nigra* allelopathy exhibits legacy effects, which negatively affect soil microbes, insects, and plant growth after the forb completes its lifecycle and may thereby offer its offspring fewer competitors in the following growing season (Lankau & Lankau 2014). In unburned sites, *B. nigra* replaced itself at every point-intercept unless a long-lived dominant shrub was present. In burned sites, dominant shrubs were absent, and *B. nigra* still exhibited decreased dispersal. In the second year, if *B. nigra* allelopathy is neutralized by fire-deposited active carbon, other fast-growing plants - including native species - which do not invest resources in allelopathic compounds may outcompete *B. nigra* for limited rains or take advantage of fire-mobilized nutrients and exclude the forb.

The most common native plant species to replace *B. nigra* was deerweed (*Acmispon glaber*) (Table S1). *Acmispon glaber* seedlings compete poorly for light and water against invasive grasses (Desimone & Zedler 2001), but this native “fire-follower” species is known to commonly dominate Southern California coastal habitat-types two to three years after fires and is eventually replaced by longer-lived, native shrubs (Montalvo 2004). Even without its allelopathy, *B. nigra* may outcompete invasive grasses for water and nutrients in the first year of post-fire vegetative recovery. A loss of allelopathy, however, could allow *A. glaber* to outcompete *B. nigra* in the second year of post-fire vegetative recovery. Nonetheless, *A. glaber* seeds tend not to accumulate in seedbanks dominated by invasive grasses or forbs (Desimone & Zedler 2001). Thus, the potential for *A. glaber* to displace invasive forbs in post-fire recovery may be underappreciated.

CONCLUSION

Further research is needed to more definitively assign drivers of *B. nigra's* loss in abundance in the second year of post-fire vegetative recovery. Still, the data presented here suggests contrary to a general trend of wildfires increasing invasive abundance, severe wildfire reduced abundance of the harmful invasive *B. nigra* in the second year of post-fire vegetative recovery. Intraguild species richness and percent cover of natives or invasives did not differ in burned versus unburned areas, but *natives* were more likely than invasives to fill soil niche spaces when *B. nigra* did not replace itself. Taken together, these results indicate massive wildfire reduces the competitiveness of the harmful invasive *B. nigra* by changing the way it interacts with other species. Surprisingly, removal of *B. nigra* does not open soil niches for other invasive annuals, but instead allows fire-adapted natives to establish. Supplemental data indicates the possibility that some native "fire follower" species may be able to then occupy the open soil niche space. It may be worth investigating if when native "fire followers" are present in the seedbank (or seeded prior to prescribed burning or immediately following wildfires), they can hold the niche until more competitive native shrubs and other perennials establish.

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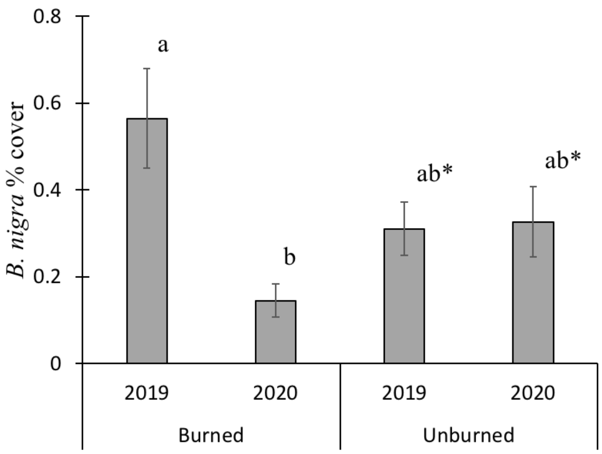
Fig. 1 Mean *B. nigra* percent cover (+/- S.E.) in 31 m transects for 1st and 2nd year post-fire and unburned sites. Unstarred letters indicate significant difference between the means ($p < 0.05$). Starred letters indicate moderately significant difference between the means and unstarred reference letter ($p < 0.057$).

Fig. 2 A.) Mean vegetative percent cover (+/- S.E.) of native and invasive plants in burned and unburned sites. B.) Mean intra-guild species richness (+/- S.E.) Letters indicate significant difference between the means ($p < 0.05$) from Tukey HSD post hoc test on ANOVAs.

Fig. 3 A.) Native abundance B.) invasive abundance and C.) all plants abundance in burned (triangles) and unburned (circles) sites as a function of proximity to *B. nigra.* ANCOVAs revealed a moderately significant interactive effect of fire and proximity to *B. nigra* for native abundance ($p = 0.055$) and all plants ($p = 0.057$) but not invasive abundance ($p = 0.137$). Asterisks indicate significance from regression analyses (* < 0.05, ** < 0.005, *** < 0.0005).

Fig. 4 Observed and expected frequencies of native and invasive plants with first year post-fire *B. nigra* shoots in burned and unburned sites. Statistical results from individual X^2 tests are presented with p-values. Bonnferoni-adjusted for multiple comparisons. All tests had 1 *df.*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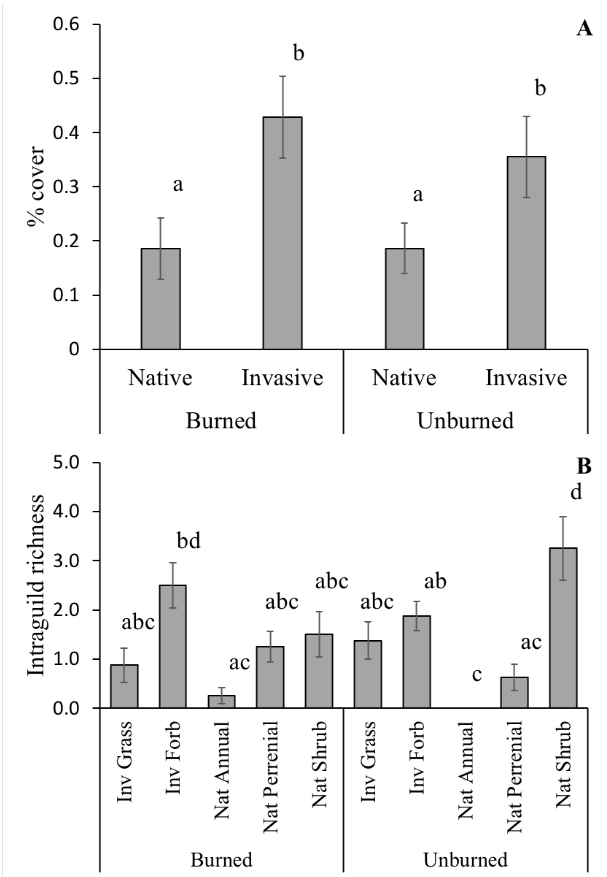
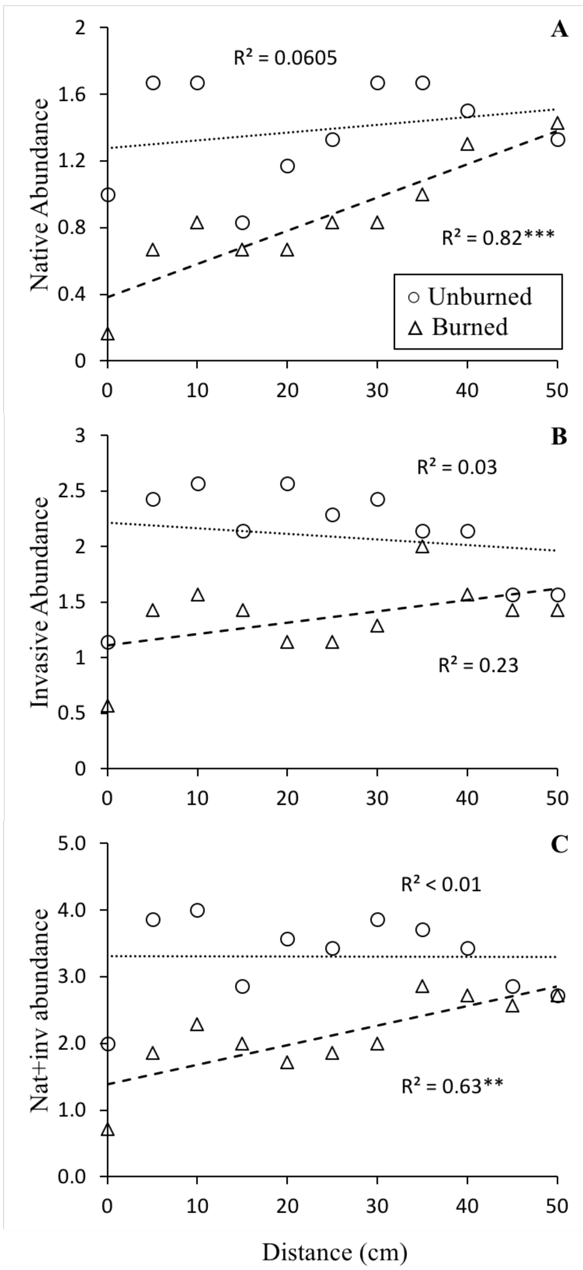
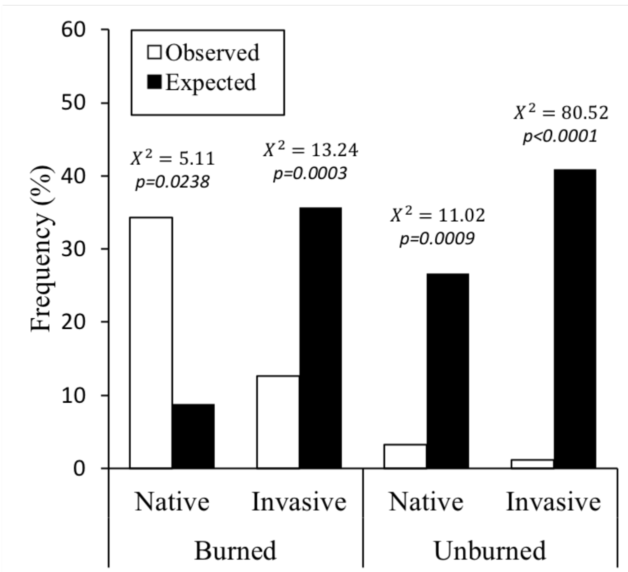
Burned
Unburned


A
% cover
0.6
0.5
0.4
0.3
0.2
0.1
0
a
b
a
b
Native
Invasive
Native
Invasive
Burned
Unburned
B
Intraguild richness
5.0
4.0
3.0
2.0
1.0
0.0
abc
bd
ac
abc
abc
abc
ab
c
ac
d
Inv Grass
Inv Forb
Nat Annual
Nat Perrenial
Nat Shrub
Inv Grass
Inv Forb
Nat Annual
Nat Perrenial
Nat Shrub
Burned
Unburned


A
Native Abundance
R² = 0.0605
R² = 0.82***
Unburned
Burned
B
Invasive Abundance
R² = 0.03
R² = 0.23
C
Nat+inv abundance
R² < 0.01
R² = 0.63**
Distance (cm)


Observed
Expected
Frequency (%)
60
50
40
30
20
10
0
$X^2 = 5.11$
p=0.0238
$X^2 = 13.24$
p=0.0003
$X^2 = 11.02$
p=0.0009
$X^2 = 80.52$
p<0.0001
Native
Invasive
Native
Invasive
Burned
Unburned

Figures

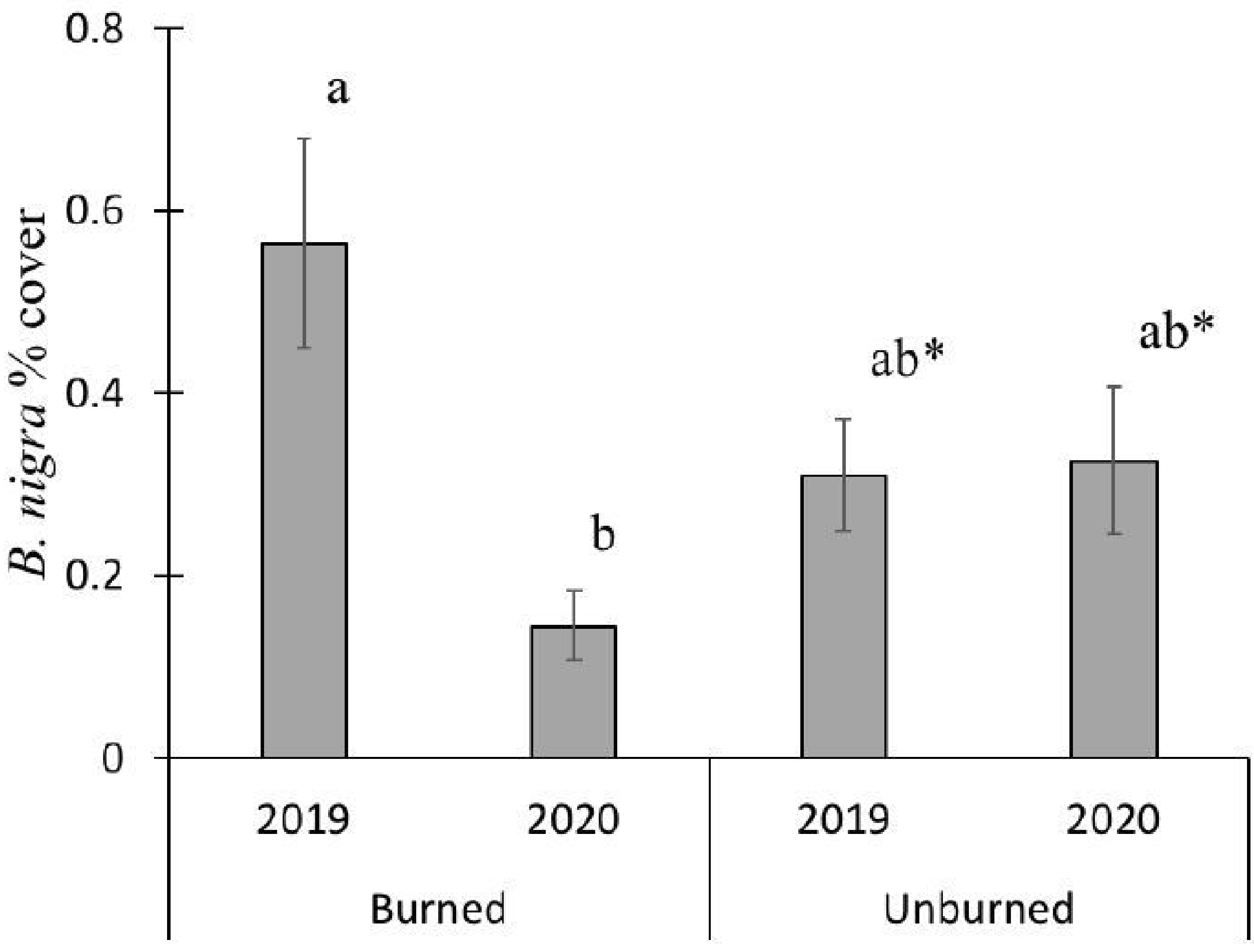


Figure 1

Mean B. nigra percent cover (+/- S.E.) in 31 m transects for 1st and 2nd year post-fire and unburned sites. Unstarred letters indicate significant difference between the means ($p < 0.05$). Starred letters indicate moderately significant difference between the means and unstarred reference letter ($p < 0.057$).

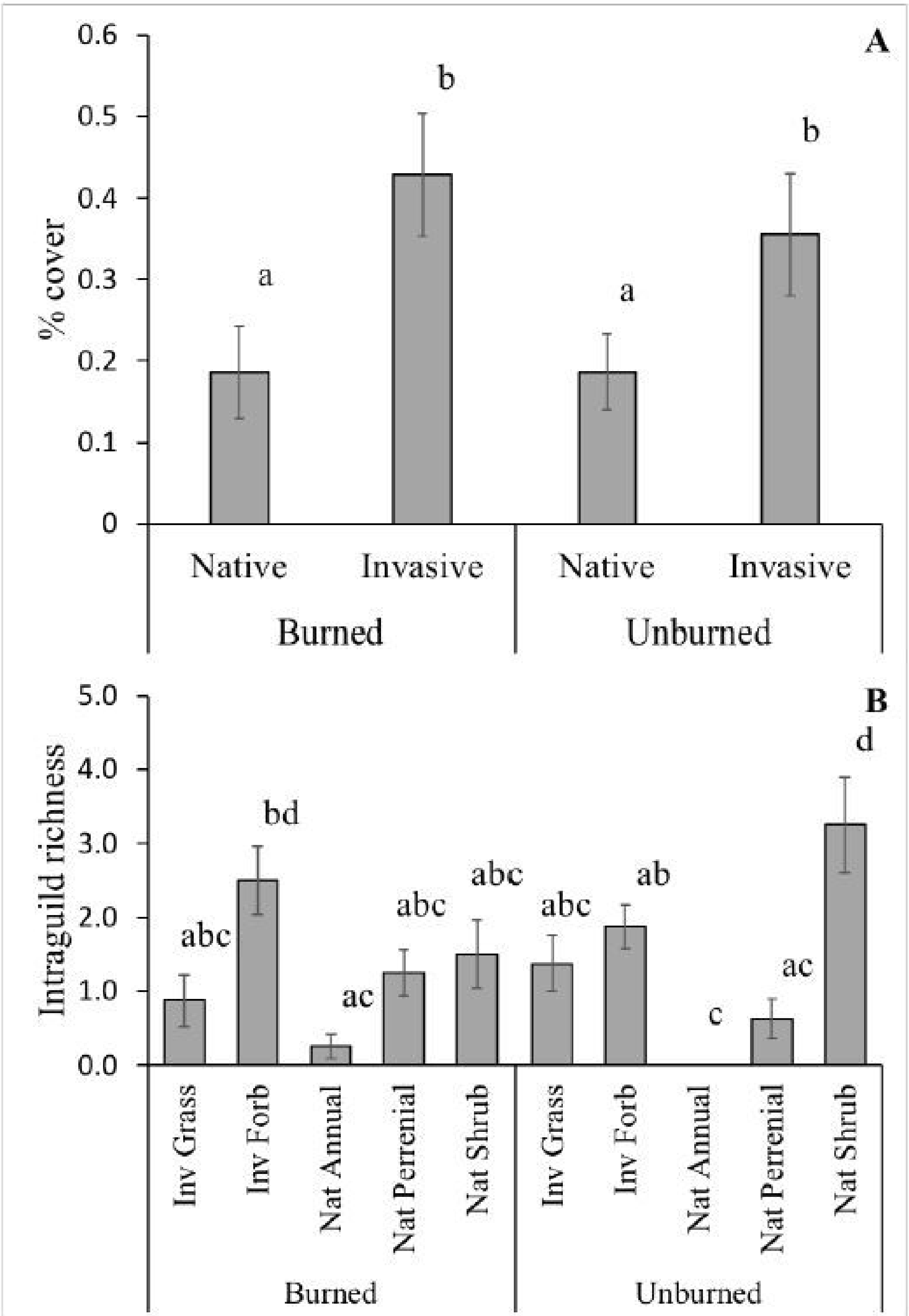


Figure 2

A.) Mean vegetative percent cover (+/- S.E.) of native and invasive plants in burned and unburned sites. B.) Mean intra-guild species richness (+/- S.E.) Letters indicate significant difference between the means ($p < 0.05$) from Tukey HSD post hoc test on ANOVAs.

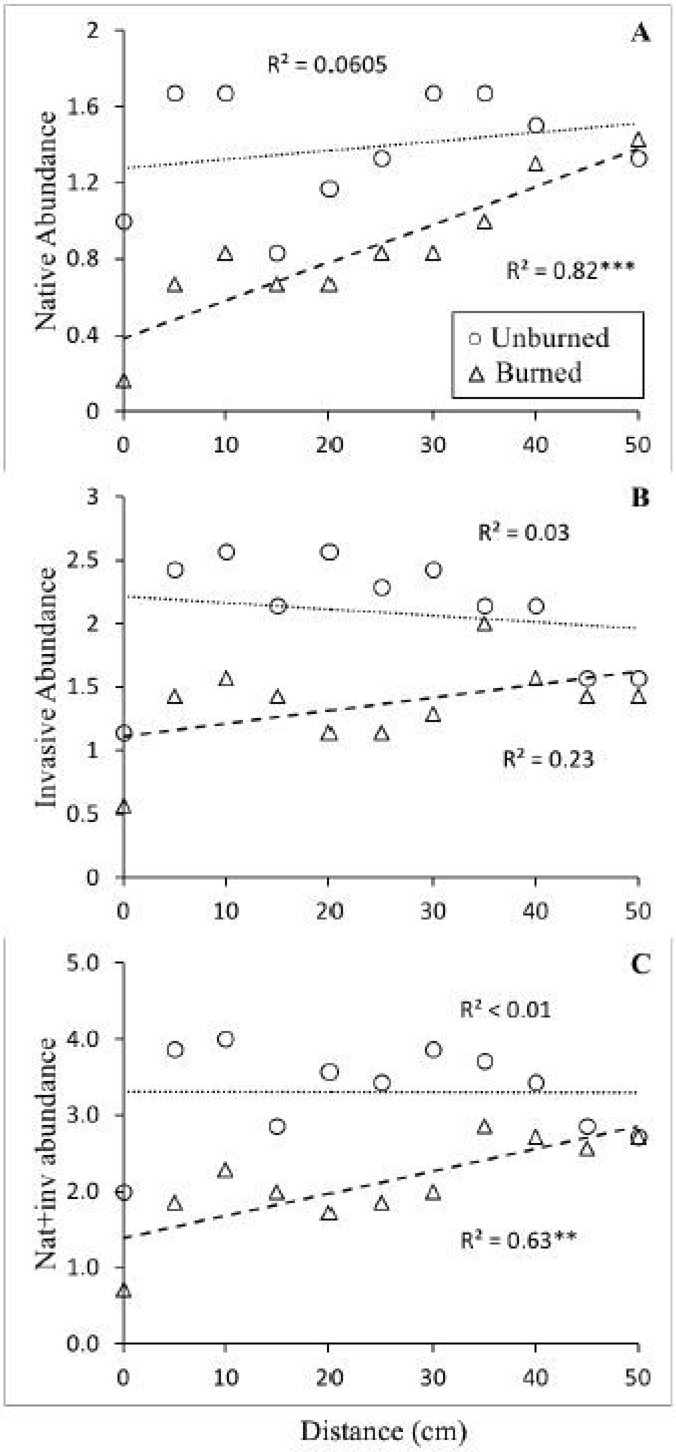


Figure 3

A.) Native abundance B.) invasive abundance and C.) all plants abundance in burned (triangles) and unburned (circles) sites as a function of proximity to B. nigra. ANCOVAs revealed a moderately significant interactive effect of fire and proximity to B. nigra for native abundance ($p = 0.055$) and all plants ($p = 0.057$) but not invasive abundance ($p = 0.137$). Asterisks indicate significance from regression analyses (* < 0.05, ** < 0.005, *** < 0.0005).

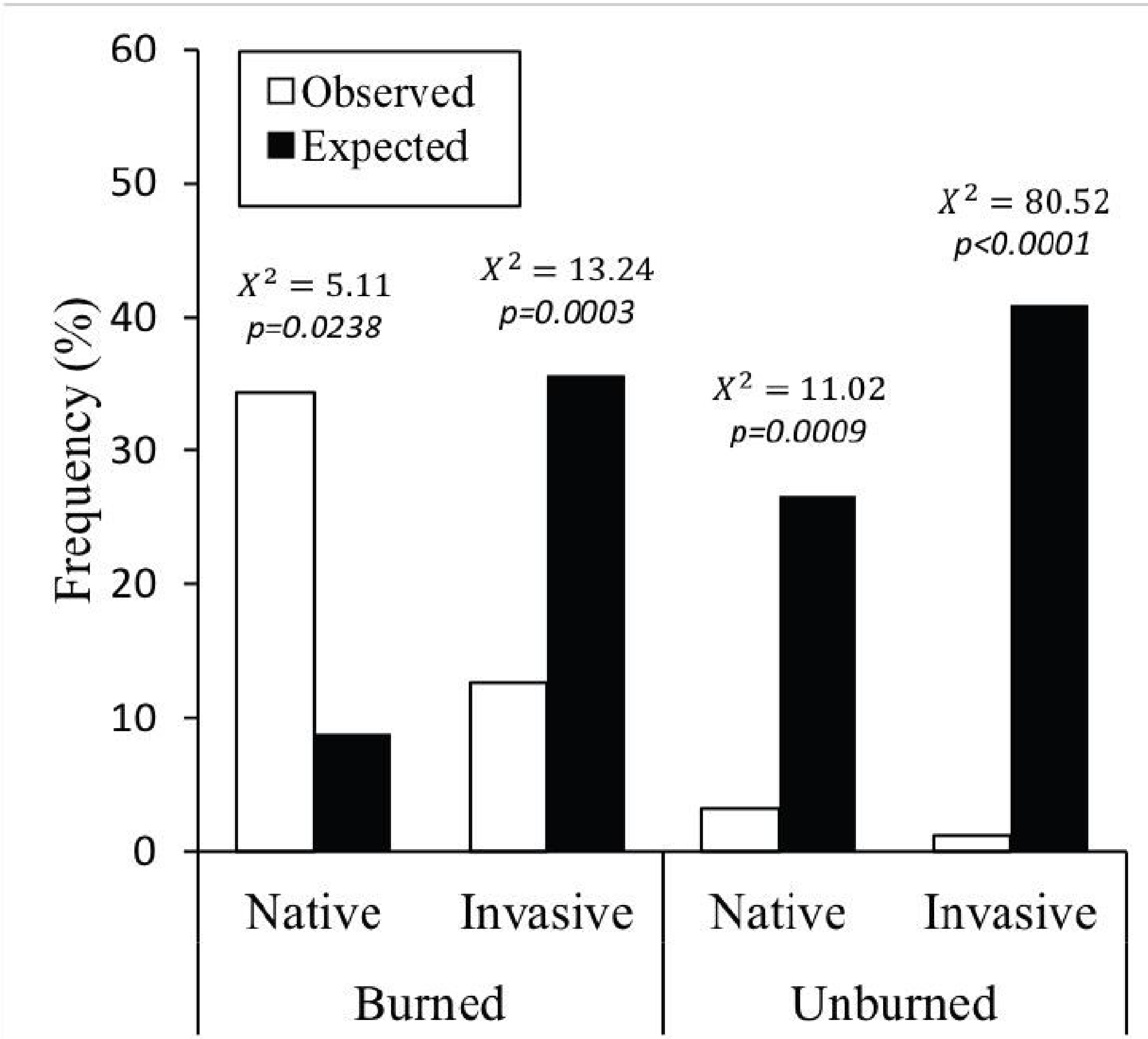


Figure 4

Observed and expected frequencies of native and invasive plants with first year post-fire B. nigra shoots in burned and unburned sites. Statistical results from individual X2 tests are presented with p-values. Bonnferoni-adjusted for multiple comparisons. All tests had 1 df.