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Topographic Context of the Burn Edge Influences Postfire Recruitment of Arid Land Shrubs☆

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ABSTRACT

Although fire is becoming frequent in arid lands throughout the world, little is known about the recruitment pattern of many arid land shrub species after fire. We explored topographic and edaphic correlates of postfire recruitment for four shrub species 6 years following wildfire in central Nevada, United States. We hypothesized that the spatial pattern of shrub recruitment varies with fire-related species traits according to the topographic position of the burn edge, which correlated with postfire seed sources. Where the burn edge fell on a ridge, the frequency of the colonizing shrub, *Artemisia tridentata* ssp. *vaseyana,* decreased with distance from the burn edge, whereas the frequency of facultative resprouting species was independent or increased with distance. Where the burn edge fell behind a ridge, there were fewer shrubs overall and a greater proportion of resprouting species. Most individuals of resprouting species were adults, suggesting immediate, fire-stimulated recruitment. Interactions among topographic position and distance from the burn edge influence the recruitment patterns of shrub species and have implications for the postfire species assemblage that are predictable on the basis of fire-related plant traits. We demonstrate how the topographic position of the burn edge influences postfire recovery trajectories of the shrub community.

Changes in climate and anthropogenic disturbances have resulted in the alteration of many fire regimes (Brooks et al., 2004; Pausas, 2004). Understanding how vegetation responds to changing fire regimes is important for predicting the distribution of ecosystems (Pausas, 1999). Due to overgrazing, plant invasion, and other pressures resulting in an altered fire regime, the sagebrush steppe of the Great Basin of the United States has become one of the most threatened ecosystems in North America (Noss et al., 1995). Many species of conservation concern depend on a resilient and unfragmented sagebrush ecosystem, including the Greater Sage-Grouse, a sagebrush-obligate bird species that is threatened as a result of habitat loss (Wisdom et al., 2011). An improved understanding of the various influences on the rate and trajectory of sagebrush ecosystem recovery from fire is critical for guiding landscape-level restoration efforts (Chambers et al., 2014).

Adaptations of shrub species to fire regimes are well studied for fire-prone environments (Keeley et al., 2011). Obligate seeding species escape fire with seed burial, and colonizers reestablish into burned areas via wind-borne seeds (Keeley and Zedler, 1978; Ooi et al., 2007). Resprouters regrow from belowground organs following fire (James, 1984). Fire can lead to greater relative cover of resprouting species versus seeding species, as observed in Australia (Clarke, 2002), South America (Galíndez et al., 2009), southern California (Keeley and Zedler, 1978), and Spain (Ojeda et al., 1996). However, fires that result in patches of seed-producing individuals may favor the dominance of colonizing species, which are capable of more rapid growth than resprouting species that must allocate more resources into storage organs (Pausas et al., 2004).

In less fire-prone environments such as pinyon-juniper woodlands and sagebrush steppe, we have a more limited understanding of how native shrub species respond to fire. Functional traits related to postfire survival and establishment provide a framework for exploring this question. We examined the spatial patterns of establishment for four common Great Basin shrub species of varying fire-related responses in central Nevada, United States. Species were classified into functional groups on the basis of resprouting capability and propagule persistence (Pausas et al., 2004). This division resulted in four fire-related functional groups: facultative resprouters, which resprout and survive via seed; obligate resprouters, which resprout but do not survive via seed; obligate seeders, which do not resprout but persist via seed; and colonizers, which do not persist following fire and must arrive onsite from neighboring populations. We hypothesized that proximity to seed source,

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topography, and fire-related functional traits interact to influence the spatial patterns of postfire shrub establishment. Shrubs outside the burn edge provide a seed source, suggesting that the frequency of colonizer shrubs decreases with increasing distance from the burn edge. We predicted that this decrease will be most apparent where the burn edge fell on the ridge, because the ridge itself can effectively block seed dispersal where the burn extends beyond the ridge. Resprouting species were predicted to show no effect of distance from the burn edge as

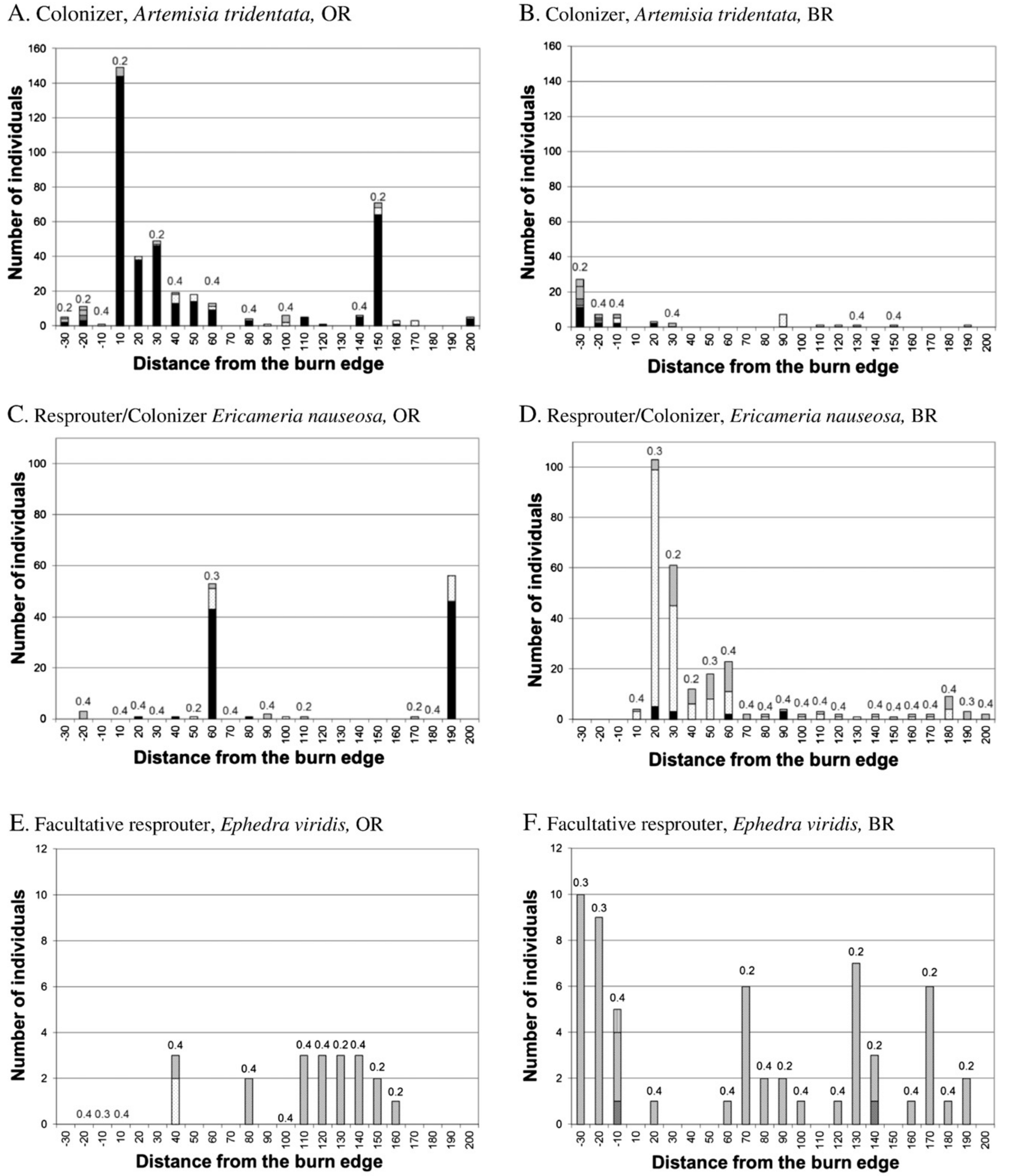
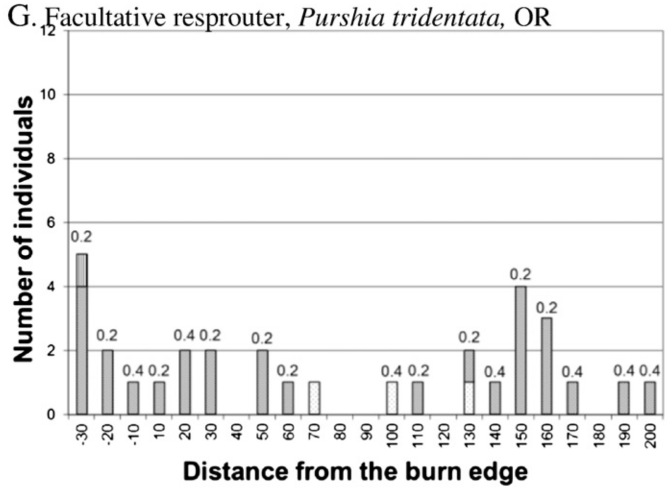


Fig. 1. Stacked bar graphs of total abundance of shrubs by life stage: ■ seedling, □ juvenile, ▩ dead, ▧ adult mature, ▯ adult decadent. Plots where the burn edge was behind the ridge **are** denoted as BR. Plots where the burn edge was on the ridge **are** denoted as OR. Distance from the burn edge is in meters. Abundance of the colonizer species, *A. tridentata* ssp. *vaseyana* on **A,** OR plots and **B,** BR plots. Abundance of resprouter/colonizer *E. nauseosa* on **C,** OR plots and **D,** BR plots. Abundance of facultative resprouter, *E. viridis* on **E,** OR plots and **F,** BR plots. Abundance of facultative resprouter, *P. tridentata* on **G,** OR plots and **H,** BR plots. Seedlings are defined as <5 cm in height. Juvenile shrubs are <15 cm in height. Dead shrubs show no sign of live tissue. Adult mature shrubs have >50% dead tissue and adult mature shrubs have <50% dead tissue. Numbers above the bars indicate the standard error in the number of adult mature individuals of that species by transect, when greater than zero.

G. Facultative resprouter, *Purshia tridentata,* OR



H. Facultative resprouter, *Purshia tridentata,* BR

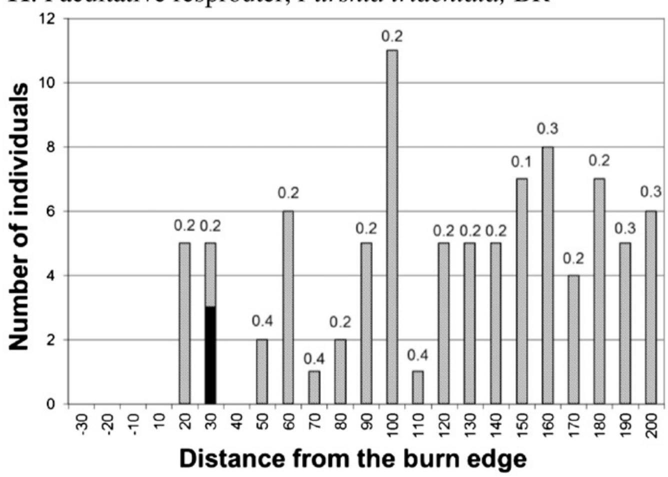


Fig. 1. (*continued*)

they are not dependent on external seed rain for postfire seedling establishment. At our study site, the dominant colonizer species is mountain big sagebrush, *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle. Postfire regeneration of *A. tridentata* is influenced by a short-lived seedbank (Wijayratne and Pyke, 2012) and the spatial distribution and density of unburned individuals (Ziegenhagen and Miller, 2009) that produce wind-dispersed seeds like other members of the Asteraceae family. Antelope bitterbrush, *Purshia tridentata* (Pursh) DC. (family Rosaceae), a facultative resprouter, is a prolific seeder that commonly resprouts following low-intensity fire. Mormon tea, *Ephedra viridis* Coville (family Ephedraceae), is also a facultative resprouter that can resprout after fire or survive in the seedbank. Rubber rabbitbrush, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird (family Asteraceae), produces numerous, wind-dispersed seeds and is more likely to behave as a resprouter or a colonizer than a facultative resprouter or an obligate seeder.

This study was conducted in Wall Canyon of the Toiyabe Range in central Nevada (lat 38°41'N, long 117°13'W). In July of 2000, 2822 ha burned as the result of a lightning strike. Before the fire, the vegetation was predominantly pinyon-juniper woodland and sagebrush steppe. In the summer of 2006, we sampled two qualitatively different types of sites, where the burn edge was on a ridge (OR) or fell behind a ridge (BR) in otherwise comparable environments. The position of the burn edge dictated the topographic position of the unburned seed source. In total, 15 linear transects, a minimum of 100 m apart, were established along a northwest- by west-facing slope spanning 2.4 km in length. Seven transects originated on the burn edge behind the ridge and eight were on the edge that ended on the ridge. Transects ran 30 m into the unburned area from the burn edge and 200 m into the burned area, perpendicular to the burn edge. A 5×2 m plot oriented parallel to the slope contour was sampled every 10 m, for a total of 339 plots, 294 of which were burned. Six burned plots that showed evidence of different environment conditions because of either a mesic drainage or all-terrain vehicle (ATV) traffic were left out of the analysis.

Universal Transverse Mercator coordinates (Trimble Geo Explorer 3 unit, Sunnyvale, CA, USA), slope, aspect, soil depth, percent rock, and gravel cover were recorded for each 10-m^2 plot. Soil depth was calculated as the average of three readings taken with a metal probe hammered into the soil until hitting rock (Harner and Harper, 1976). Percent covers of rock (fragment >7.5 cm in length) and gravel (fragments 1–7.5 cm) were estimated ocularly.

The number of individuals of each species was counted and recorded at each plot. Age classes were recorded for each individual as seedling (≤5 cm tall), juvenile (between 5 cm and 15 cm tall), adult mature (>15 cm tall and <50% of its canopy as dead branches), adult decadent (>15 cm tall and ≥50% of its canopy as dead branches), and dead. Most individuals that were >15 cm tall showed evidence of flowering, justifying their adult status.

A mixed-model analysis of covariance design was used to evaluate the relative influences of topographic and environmental effects on number of individuals for each species. Models included fixed effects of plot type with respect to position of burn boundary (OR or BR), distance from burn edge (m), their interaction, and all measured environmental variables. Transect was included as a random effect to account for spatial variation not otherwise represented by measured environmental variables. Models were weighted to allow for heterogeneous variances of the response variable in each plot type to meet assumptions of symmetrical variance. In the case of *E. viridis,* the exponent of the number of individuals was used so that all models met assumptions of normality. Statistical analyses were conducted in R version 3.0.2, using the package *nlme* (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Unburned reference locations within 30 m of the burn edge were comparable in terms of functional groups. On reference OR sites, *P. tridentata* was more abundant as opposed to reference BR sites where *E. viridis* was dominant (Fig. 1). Both species are facultative resprouters. The colonizer species, *A. tridentata,* was common in both unburned conditions.

Species had varying relationships with topographic factors that were predictable by fire response functional group (see Fig. 1). Plot type, distance from the burn edge, and their interaction were significant predictors of *A. tridentata* (Table 1, Fig. 2). Total counts revealed that the colonizing species, *A. tridentata,* was more abundant in OR plots than BR plots (7:1 ratio of occurrences) decreasing with increasing distance from the burn edge only for the OR plots (Fig. 1A and 1B, 2). *A. tridentata* was found in 59% of 160 OR plots and 35% of 134 BR plots. More sagebrush individuals were found in the unburned area adjacent to BR plots (41 vs. 17 individuals in unburned OR plots), suggesting that the observed effect of position of burn edge relative to the ridge is not due to inherent variability in *A. tridentata* seed source availability.

In contrast, obligate resprouting and facultative resprouting species (*E. nauseosa, E. viridis,* and *P. tridentata*) were more abundant in BR plots compared with OR plots (occurrence ratios of 2.1:1, 2.9:1, and 3.6:1 for each species, respectively). *Ericameria nauseosa* abundance was greater on BR sites, more gradual slopes and more northerly aspects, and decreased with distance from burn edge (see Table 1, Fig. 2). The occurrence of *E. nauseosa* was patchier when the burn edge was on the ridge (see Fig. 1C). Facultative resprouting species, *E. viridis* and *P. tridentata,* were more abundant on BR sites with relatively even abundance with distance from the burn edge (see Fig. 1E—H). Throughout the study, *P. tridentata* showed the highest frequency of

Table 1

Mixed-model analysis of covariance of topographic and surface cover environmental variables, plot type (burn edge on the ridgeline vs. burn edge behind the ridgeline), distance from burn edge, and the interaction of plot type and distance from burn edge, on the abundance of adult mature individuals of the following species: colonizer, *Artemisia tridentata* ssp. *vaseyana* ($n = 39$), resprouter/colonizer *Ericameria nauseosa* ($n = 79$), facultative resprouter, *Ephedra viridis* ($n = 73$), facultative resprouter, *Purshia tridentata* ($n = 108$). *P* values ≤ 0.10 are in bold

	Numerator df	Denominator df	*A. tridentata*		*E. nauseosa*		*E. viridis*		*P. tridentata*	
			F value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Intercept	1	272	**32.20**	**<0.0001**	**4.99**	**0.0262**	**18.78**	**<0.0001**	**25.23**	**<0.0001**
Distance from burn edge	1	272	**5.69**	**0.018**	**9.41**	**0.002**	0.08	0.782	**3.76**	**0.053**
Plot type	1	13	**11.29**	**0.005**	1.57	0.232	0.27	0.612	**7.37**	**0.018**
Percent rock	1	272	0.28	0.599	0.03	0.865	0.15	0.698	0.20	0.653
Percent gravel	1	272	0.13	0.724	1.64	0.201	0.09	0.770	0.08	0.780
Average soil depth	1	272	0.27	0.603	0.31	0.579	0.30	0.585	0.00	0.980
Aspect	1	272	0.24	0.624	**6.73**	**0.010**	0.79	0.375	1.90	0.169
Slope	1	272	0.34	0.559	**2.85**	**0.093**	**7.36**	**0.007**	0.08	0.779
Distance from burn edge × plot type	1	272	**3.50**	**0.0625**	2.44	0.120	0.63	0.429	**6.44**	**0.012**

adult mature individuals ($n = 108$) followed by *E. viridis* ($n = 73$). Topographic factors including plot type, distance from the burn edge, and their interaction, had a significant effect on *P. tridentata* abundance but not *E. viridis* abundance, which showed a positive relationship with slope (see Table 1, Fig. 2).

The interactions among proximity to seed source, topography, and functional trait response to fire strongly influenced survival and recruitment of shrub species. The influence of topographic position of the burn edge on postfire establishment of colonizing shrub species was more apparent when considering differences among age classes because colonizing species did not survive the fire as mature individuals. Six years after the fire they were still colonizing the site and were therefore dominated by younger age classes (see Fig. 1). The observed effect of proximity to burn edge on *A. tridentata* distribution

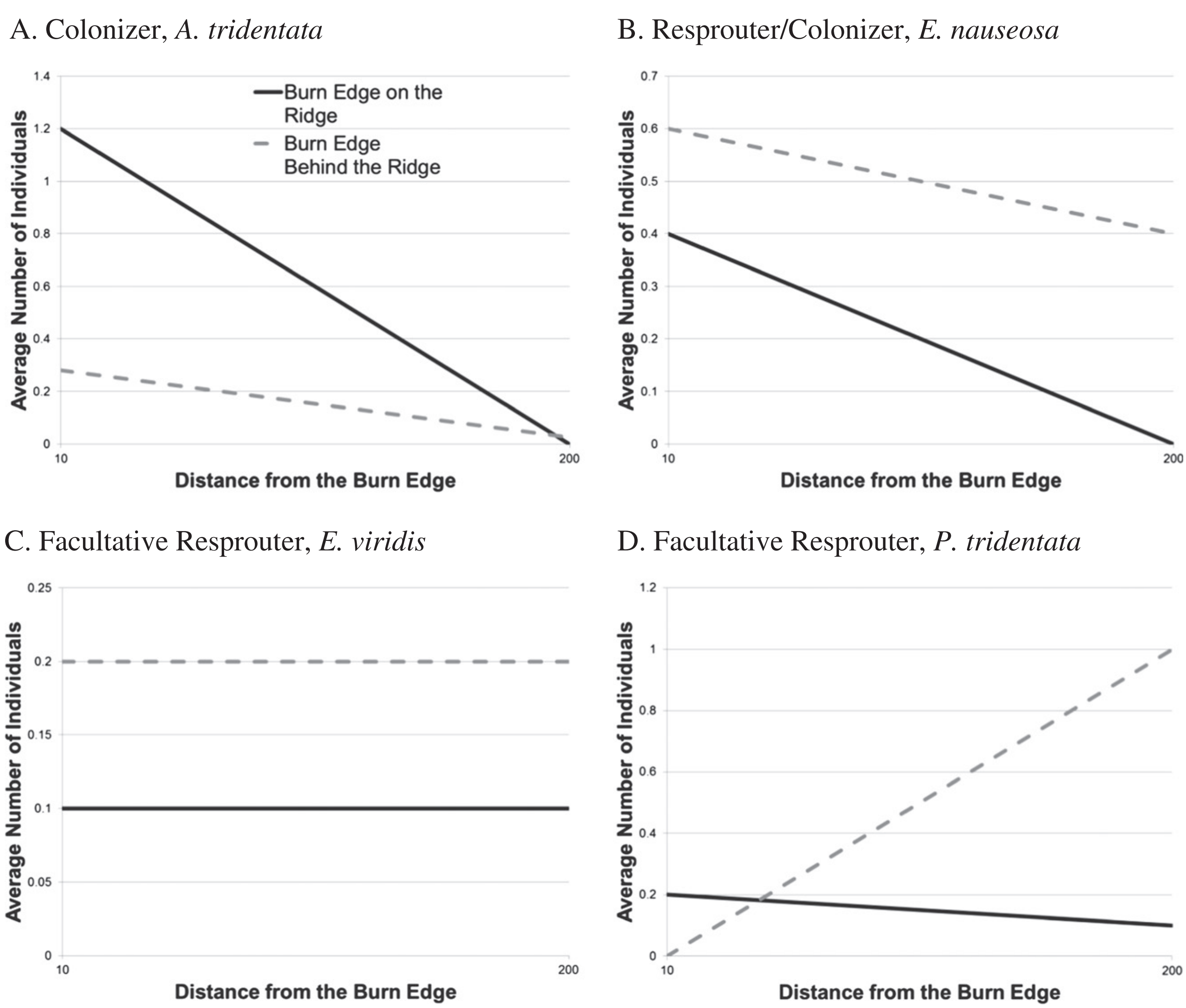


Fig. 2. Interaction plots showing the average number of individuals for each species as a function of distance from burn edge (x-axis) by plot type: —— OR, ---- BR. **A,** The colonizer, *A. tridentata* ssp. *vaseyana.* **B,** The resprouter/colonizer *E. nauseosa.* **C,** The facultative resprouter, *E. viridis.* **D,** The facultative resprouter *P. tridentata.*

(see Fig. 1) suggests strong limits on distribution due to distance-dependent seed dispersal. Most *A. tridentata* seeds move less than 3 m (Welch, 2005) with maximum observed dispersal distances of 33 m (Goodwin, 1956).

Although we could not unequivocally observe whether an individual shrub had resprouted or established from seed, the relative frequencies of individuals within life stages supported our interpretations concerning importance of seed dispersal limitation on shrub community structure. The lack of individuals in the seedling and juvenile life stages of *E. viridis* and *P. tridentata* suggests that postfire establishment of both species was mainly due to resprouting. Resprouting species did not show a negative relationship with distance from the burn edge because their recruitment is independent of proximity to unburned seed sources.

As we observed, the postfire recovery of seeding species is often less than that of surviving resprouting species, particularly in the absence of a persistent seed bank (Wambolt et al., 2001). *A. tridentata* seed shows persistence if buried (Wijayratne and Pyke, 2012). but if winter precipitation is not sufficient for establishment within 2–3 years following fire, *A. tridentata* reestablishment depends on not only proximity to seed sources (Ziegenhagen and Miller, 2009; Nelson et al., 2014) but also, as we have shown, the absence of topographic barriers to anemochorous dispersal. Practitioners can use this information to identify restoration priorities, and where possible, fire management should consider the importance of topographic position of the burn edge for influencing postfire establishment of colonizing species such as *A. tridentata* as this may reduce the need for expensive, and often unsuccessful, restoration efforts (Knutson et al., 2014). Although we only looked at a single fire within the Great Basin, our results imply that fire-related species traits may be a useful predictor for understanding the pattern of shrub recruitment following fire in other environments.

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