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Annotating PDFs using Adobe Acrobat Reader DC

Version 1.7   June 27, 2016

1. Update to Adobe Acrobat Reader DC

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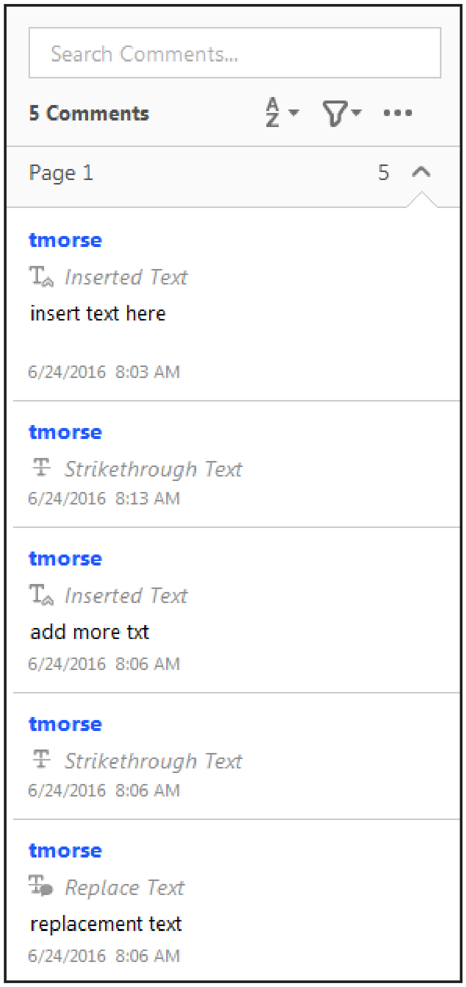

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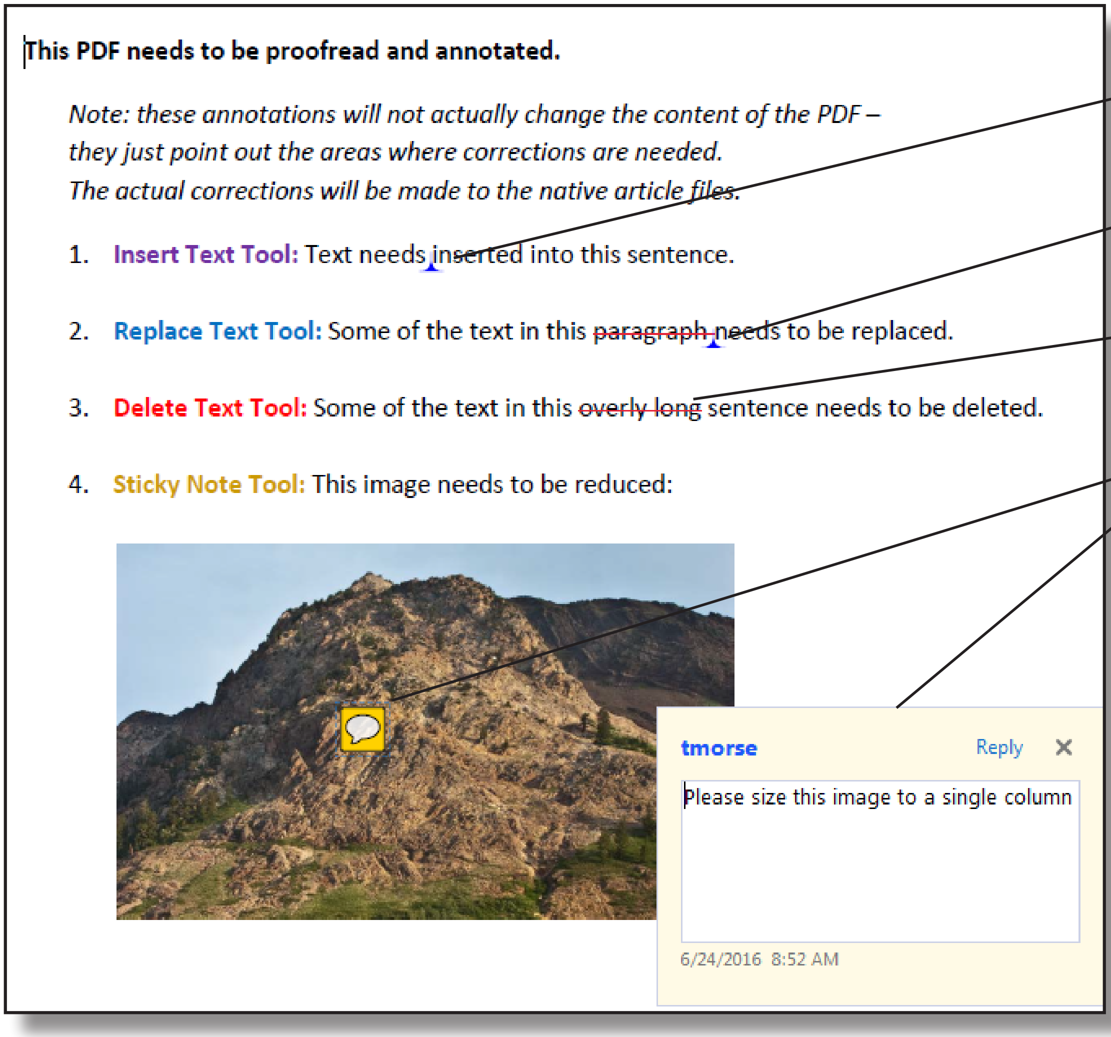

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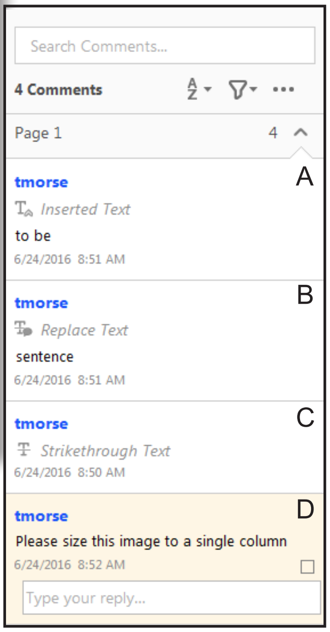

4 Comments

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RESEARCH ARTICLE

AMERICAN JOURNAL OF BOTANY

Dynamics of gaps, vegetation, and plant species with and without fire[1]

Eric S. Menges[2,5], Sarah J. H. Crate[3], and Pedro F. Quintana-Ascencio[4]

PREMISE OF THE STUDY: Areas lacking dominant plants, or gaps, can support high diversity and specialist species. Previous chronosequence research in Florida rosemary scrub showed indistinct gap area patterns with fire and the dependence of certain species on gaps. We hypothesized that fire and gap size would affect extinction, colonization, diversity, and vegetation composition.

METHODS: In 2011–12, we revisited gaps first sampled in 2003, recording vascular plant and ground lichen occurrence by species, gap area, and burn history. We analyzed gap, vegetation, and species dynamics using linear mixed models, with Florida rosemary scrub patch as a random factor.

KEY RESULTS: Gap areas declined quickly during the first 10 yr postfire and then stabilized. Between 2003 and 2011–12, unburned gaps usually remained extant or split, whereas burned gaps usually merged. Unburned gaps tended to shrink, whereas burned gaps became larger. Species richness was positively related to gap area, fire, and their interaction. Over time, richness declined in unburned gaps and increased in burned gaps. Local extinction and colonization of individual species were related to fire between 2003 and 2011–12. In burned gaps, ground lichens disappeared, but many herbaceous species, including those killed by fire, increased occupancy. Colonization of most species was favored by burning, large gaps, or both.

CONCLUSIONS: In Florida rosemary scrub, fire and increasing gap size increased species richness and many individual species occurrences, reduced local extinctions, and increased colonizations. Therefore, land management activities that encourage the creation and maintenance of large gaps will promote biodiversity in this system.

KEY WORDS colonization; extinction; Florida scrub; land management; species richness; time-since-fire

Gaps are relatively open areas within stands of dominant vegetation and are a key structural and functional attribute of many ecosystems (Pickett and White, 1985). Gaps may provide higher levels of resources such as light and moisture (Canham et al., 1990; Burton et al., 2014) and are essential microhabitats for subordinate (Petru and Menges, 2003; Delong and Gibson, 2012; Burton et al., 2014) and dominant plant species (Muscolo et al., 2014; Zhu et al., 2014).

Individual gaps display what is essentially a demographic process. Gaps are "born" as a result of the death or partial removal of dominant individuals (Schliemann and Bockheim, 2011; Richards and Hart, 2012; Karki and Hallgren, 2015), often from an ecological disturbance. Gaps "survive" for a time, and then they "die" (or become "dormant") as a result of closure of the vegetation from the sides or below (Belsky and Canham, 1994; Vepakomma et al., 2011). These dynamics can affect both community and population structure (Brokaw and Busing, 2000; Burton et al., 2014). Within individual species, subpopulations in gaps may have different life histories than subpopulations in the matrix (Abe et al., 2008).

Gap size is a fundamental property affecting community structure and population dynamics. Species richness is highest in larger (Hubbell et al., 1999; Schnitzer and Carson, 2001; Burton et al., 2014) or midsized (Kern et al., 2014) gaps. Larger gaps support different species assemblages than smaller gaps (Anderson and Leopold, 2002; Muscolo et al., 2014) and can support higher seedling survival (Pearson et al., 2003) and faster seedling growth (Huth and Wagner, 2006). The distribution of obligate seeding species (as compared to resprouters) in California chaparral was strongly predicted by the size of postdisturbance gaps (Keeley et al., 2016).

Despite the widespread occurrence and predominance of fire (Bond and Keeley, 2005), its effects on gap dynamics are little studied. While fire can cause gaps, large-scale fire disturbances are

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usually distinguished from local gap formation (e.g., Pham et al., 2004; McEwan et al., 2014). Although most work describing the effect of gaps on plants has been done in forests (recent examples include Sharma et al., 2016; Després et al., 2017; Nagel et al., 2017), gaps are also key features in habitats such as grasslands (Tozer et al., 2008; Franzese et al., 2009), shrublands (Dickinson et al., 1993; Lloret et al., 2005), woodlands (Pecot et al., 2007), and savannas (Rebertus and Burns, 1997). Few studies have explicitly looked at the effects of fire on gap dynamics in shrublands (but see Menges and Hawkes, 1998; Menges et al., 2008; Franzese et al., 2009).

Here, we explore gap dynamics in a fire-affected shrubland, Florida scrub, where gaps are important features in the landscape (Menges et al., 2008). Herbaceous species (e.g., *Eryngium cuneifolium*, *Hypericum cumulicola*) and woody subshrubs (e.g., *Dicerandra frutescens*) are among the species that are gap specialists and are most abundant in the first decade after fire (Hawkes and Menges, 1996; Quintana-Ascencio et al., 2003; Menges and Quintana-Ascencio, 2004; Menges et al., 2006). Gap area is potentially important in Florida scrub, because some species have greater occurrence, survival, and recruitment in larger than in smaller gaps (Menges and Kimmich, 1996; Menges et al., 2008; Schafer et al., 2010, 2013), and species richness is typically highest in larger gaps (Menges et al., 2008; Dee and Menges, 2014). Florida scrub is a hot spot for endemism (Christman and Judd, 1990; Dobson et al., 1997; Estill and Cruzan, 2001), with most endemics occurring in Florida rosemary scrub and many endemic species preferring gaps, so that understanding gap dynamics is important to conservation. Gap closure can be rapid in some types of Florida scrub, leading to declines in rare plants (P. A. Schmalzer and T. E. Foster, unpublished data).

Landscape and population dynamics of many species occurring in the Florida rosemary scrub can be conceptualized at two scales: open gaps, at the scale of meters (hereafter “gaps”); and larger rosemary scrub habitat patches, at the scale of 10 m to kilometers (hereafter “patches”), where metapopulation dynamics occur. At this larger scale, patch occupancy was higher for some species in larger, less isolated patches (Quintana-Ascencio and Menges, 1996), although observed extinctions and recolonizations at the patch level, while related to fire and life history, were not associated with patch size or isolation (Miller et al., 2012).

In a prior study (Menges et al., 2008), we considered a snapshot of gap properties based on 805 gaps in Florida rosemary scrub, sampled in 2003. We found that gap areas had a lognormal distribution and were smallest in long-unburned patches, but otherwise there was no evidence of gap area variation associated with time-since-fire. Species diversity and herbaceous plant diversity were highest in larger gaps, and herbaceous diversity decreased with time-since-fire. Larger gaps were refugia for several species, while long-unburned gaps were important for ground lichen species. The prior study (Menges et al., 2008) used a chronosequence approach (a space for time substitution) for inferences about time-since-fire; this assumes that spatial and temporal variation are equivalent (Pickett, 1989), and therefore it can lead to erroneous conclusions (e.g., Freestone et al., 2015). Here, by following changes over time with and without fire, we provide an approach that minimizes chronosequence issues.

In the present study, we resampled 480 of these gaps 7–8 yr later. We focus on the dynamics of gaps, species richness, species occurrence, and community composition between 2003 and 2011–12. Many gaps burned during this intervening period, allowing us to contrast gap and plant dynamics in gaps that were either burned or unburned. Our predictions were as follows:

(1) Gap area should decrease with time-since-fire and increase when fire occurs.
(2) Species richness should be highest in larger gaps and in recently burned areas, because of lower competition with dominant species and higher heterogeneity.
(3) Most individual species should show greater occupancy, less local extinction, and more local colonization into larger and more recently burned gaps. However, these patterns will be conditioned on species’ life histories, particularly their responses to fire.
(4) Plant community composition should be affected both by gap area and time-since-fire.

MATERIALS AND METHODS

Study system—The study was conducted in Florida rosemary scrub at Archbold Biological Station, in south-central Florida, USA (27°10′N, 81°21′W), during 2003 and 2011–12. Rosemary scrub (rosemary phase of sand pine scrub; Abrahamson et al., 1984) is a shrubland dominated by Florida rosemary (*Ceratiola ericoides*), resprouting scrub oaks (*Quercus* spp.), and palmettos (*Serenoa repens*, *Sabal etonia*). Rosemary scrub occurs on xeric white sands and is characterized by open gaps usually covering 10–40% of the ground area (Menges and Hawkes, 1998; Menges, 1999). These gaps are rich in endemic plant species (Menges et al., 2008). Rosemary scrub is often distributed as islands (patches) of habitat embedded within other vegetation (e.g., scrubby flatwoods) that are dominated by scrub oaks, palmettos, and other shrubs (Quintana-Ascencio and Menges, 1996; Miller et al., 2012) with canopy heights usually <2 m.

The fire regime is characterized by high-intensity crown fires moving through shrub canopies, historically ignited by lightning fires occurring during the growing season, especially in late spring (Menges et al., 2017). The fires are often patchy in rosemary scrub. Unlike co-occurring shrubs that are strong resprouters (Maguire and Menges, 2011; Schafer and Mack, 2014), Florida rosemary is killed by fire and recovers by recruiting from a soil seedbank (Johnson, 1982). Because Florida rosemary seedlings grow more slowly than the resprouting shrubs, gaps often persist in rosemary scrub for several years following fire. The fire return interval for rosemary scrub tends to be longer (15–25 yr) than fire return intervals for scrub dominated by resprouting shrubs (Menges, 2007; Menges et al., 2017). Florida rosemary produces allelochemicals (Williamson et al., 1992) that suppress seed germination of co-occurring plants (Hunter and Menges, 2002; Hewitt and Menges, 2008). However, after fires that remove Florida rosemary, many species will recruit seedlings (Menges and Quintana-Ascencio, 2004).

Data collection—Following Menges et al. (2008), we defined gaps as openings among canopies of dominant shrubs that were at least 1 m long and 1 m wide. Gaps are largely free of woody vegetation; the matrix is dominated by taller, more continuous woody vegetation. The gap boundaries were defined by dominant shrubs ≥50 cm tall. Subshrubs, herbaceous plants, and ground lichens can occur within gaps.

Initial sampling (2003) was detailed in Menges et al. (2008). In short, we chose 28 rosemary scrub patches initially stratified by seven time-since-fire classes (over time, with subsequent fires, time-since-fire changed for many patches). We characterized each gap's fire history using a combination of mapped fire-history data (Menges et al., 2017) and field observations made after each fire between 2003 and 2011–12. We calculated the time-since-fire for 2003 and 2011–12. From field observations of vegetation structure and fire severity, we characterized the burn status of each gap as unburned, partially burned (some unburned area within the gap), or completely burned between 2003 and 2011–12.

We selected the first gap randomly and then sampled adjacent gaps until we reached a sample size of ~28 gaps patch^{-1} (805 gaps in total). In 2011–12, we randomly resampled 480 of the original gaps and 691 gaps in total, including new gaps related to 2003 gaps by splitting or merging. For gaps >2 m on a side, we used a Trimble GeoXT GPS to define gap perimeters and measure gap areas, ensuring that we had ≥0.5 m accuracy. GPS data were downloaded into Pathfinder Office version 5.3 (Trimble Navigation Limited, Sunnyvale, California, USA) and exported to ArcView version 10.1 (Environmental Systems Research Institute, Redlands, California) for analysis. Each gap perimeter was edited to eliminate crossed lines and open polygons. For smaller, regularly shaped gaps, we measured lengths and widths of gaps in the field and calculated areas as ellipses. For irregularly shaped small gaps, we either divided gaps into multiple ellipses or measured eight radii from a center point and calculated the area by eight triangles defined by the radii. All measurements were made between shrub canopies rather than shrub bases. We subtracted areas of shrub islands within the gap from the gap's total area. In the summer or early fall of both 2003 and 2011–12, we identified every species of vascular plant (nomenclature follows the Atlas of Florida plants: http://www.florida.plantatlas.usf.edu/) and ground lichen (nomenclature follows Brodo et al., 2001) within each gap to determine species occurrences (presence). We included woody plants <50 cm tall if the individual was clearly within the gap and not bordering the edge. Because very small *Serenoa repens* and *Sabal etonia* are indistinguishable, their identity was assigned by reference to the nearest adult palmetto present. We characterized dominant vegetation along each gap boundary by dominant species combinations (oaks, palmettos, Florida rosemary, other woody plants) that made up at least one-third of each gap edge. For example, a gap surrounded by 50% oak cover and 40% palmetto cover would be characterized as having an oak/palmetto-dominated edge.

Gap dynamics—Using GPS data from both 2003 and 2011–12, we noted gap fate: gaps merged, split, remained extant, or became dormant. If gaps merged, we combined data into the resulting mega-gap. We noted which 2003 gaps contributed to the merged mega-gap. If gaps split into two or more smaller gaps, we defined the largest of these new gaps as the prior nonfragmented gap, and numbered new gaps, noting the linkage between the 2003 mother gap and the 2011–12 daughter gaps. If gaps fell below the minimum size for a gap (1 × 1 m), we considered them "dormant." We recorded the same data in all gaps with various fates except for dormant gaps, which were not sampled. A few gaps ($n = 11$) that both split off from the 2003 gap and merged with adjacent gaps were not included in most analyses. We considered composite species richness across premerge gaps in 2003 and postsplit gaps in 2011–12 to assess richness changes, and compared these to gaps that did not split or merge.

Analytical methods—We conducted statistical analyses using SPSS version 22 and R version 3.0.2 (R Core Team, 2013). Gap area was natural log-transformed for all analyses to normalize residuals and control heteroscedasticity. Gap fates were related to burn status and 2003 time-since-fire class (1–9, 10–19, 20+ years-since-fire) using chi-square tests; and to gap areas using one-way analyses of variance. We used linear mixed models (with normal errors and identity link) to analyze species richness in relation to burn status and gap area. Using Akaike's information criterion (AIC) corrected for small sample sizes (AIC_c), we evaluated the relative evidence for effects of each variable. We found no evidence that other variables (change in gap area, dominant shrub vegetation along gap edges, time-since-fire in 2003) had effects on species richness (AIC weights < 0.001; Appendix S1; see Supplemental Data with this article). We included random effects of patch because gaps were nested within patches. This approach accounts for common variation among gaps within a focal patch. We first evaluated the most informative configuration for either random effects on the intercept or both the intercept and the slope on the model with saturated fixed configuration and then assessed how likely the fixed effects (gap area, time-since-fire, and their interaction) were in predicting species richness (for code, see Appendix S2).

We also analyzed species occurrence patterns using generalized linear mixed models (with binomial errors, logit link, and random effects by patch) to predict both extinction and colonization, using all predictor variables initially, but later using burn status between 2003 and 2011–12, the natural log of gap area, and the time-since-fire in 2003 as predictors (fixed effects), because other variables were not important predictors of extinction or colonization. We considered the 54 most common species (i.e., those that had ≥10 occurrences in both 2003 and 2011–12). Data were adequate for models for extinction or colonization for 27 of these species. To estimate model fit, we used the lme4 R package (Bates et al., 2013) and r^2 for generalized linear mixed models (Nakagawa and Schielzeth, 2013).

We used nonmetric multidimensional scaling (NMDS; Vegan library; Oksanen et al., 2015) ordinations to interpret species occurrence patterns in relation to time-since-fire and gap area. Rarefaction curves (Vegan library; Oksanen et al., 2015) based on 2011–12 data showed clear asymptotes, indicating that our sampling well characterized the overall plant community. We used linear mixed models to assess the association of scores on major ordination axes to time-since-fire (2011–12) and gap area. Results are presented as means ± SE.

RESULTS

Gap dynamics—Gap areas in 2011–12 varied widely but generally decreased with time-since-fire during the first decade, before leveling off (Fig. 1). The most plausible model was logarithmic ($r^2 = 0.117$, df = 256, $P < 0.001$).

The fate of 2003 gaps from 2003 to 2011–12 included gaps that remained extant without merging or splitting (206, or 42.9%), gaps that merged (123, or 25.6%), gaps that split (89, or 18.5%), gaps that shrank to below minimal size (i.e., became dormant; 51, or 10.6%), and gaps that both split from old gaps and merged with other gaps (11, or 2.3%; not considered in further analyses). In addition, we noted 211 new gaps that split from older gaps.

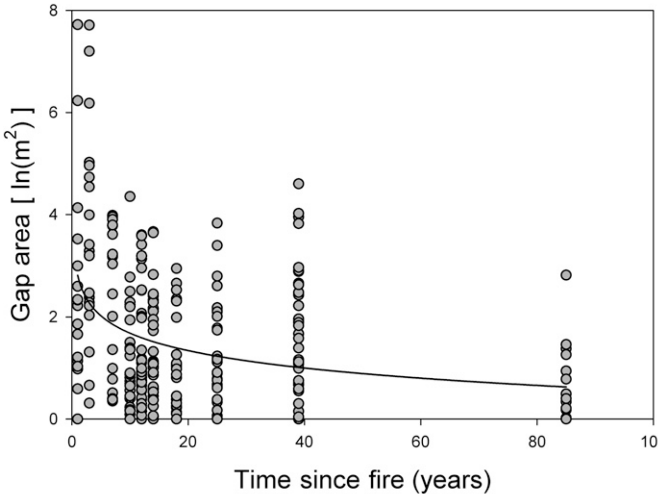

FIGURE 1 Gap area function of time-since-fire for gaps in 2011–12. Line is fit with ln (time-since-fire); $r^2 = 0.12$.

Whether gaps burned or not between samples had strong effects on gap dynamics (Fig. 2). Burned gaps usually merged (78.7%) while unburned gaps often remained extant (56.5%) or split (24.8%). Partially burned gaps were intermediate between burned and unburned gaps but most similar to burned gaps, with the most common fates merging (44.7%) or remaining extant (23.4%). Gap fate was strongly related to burn status ($\chi^2 = 282.6$, df = 6, $P < 0.001$). Time-since-fire in 2003 also affected gap fate ($\chi^2 = 155.2$, df = 18, $P < 0.001$), with recently burned gaps often remaining extant and most classes of long-unburned gaps having many splits. In fact, unburned gaps in all time-since-fire classes tended to remain extant or split (summing to 67–95% of gaps across 2003 TSF classes), whereas burned gaps in all time-since-fire classes tended to merge (76–82% across TSF classes). Gap splitting was uncommon (15%) for gaps <10 yr since fire but occurred at similar rates (30–40%) for longer time-since-fire.

Gap area in 2011–12 was influenced by prior gap area and intervening fire. Unburned gaps tended to shrink (slope <1), whereas burned gaps increased in size; partially burned gaps were intermediate and usually increased in size (Fig. 3). Burned gaps had greater increases in size between 2003 and 2011–12 than partially burned or unburned gaps (Fig. 3). A model that included prior gap area, fire, and their interaction explained 77% of the overall variance in 2011–12 gap area (Table 1).

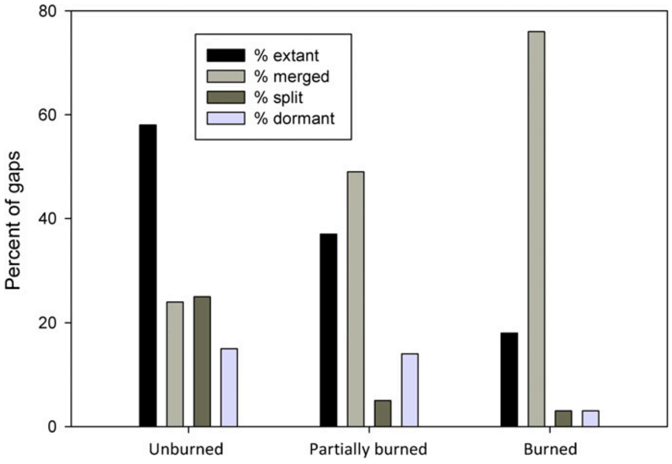

FIGURE 2 Fate of gaps that were either unburned, partially burned, or burned between 2003 and 2011–12, expressed as a percentage of gaps within each burn category.

As one would expect, the change in gap area reflected gap fates between 2003 and 2011–12. Merged gaps gained a mean of 429.9 ± 185.9 m^2; extant and split gaps both shrank in size (losses of 1.7 ± 0.5 m^2 and 17.8 ± 4.0 m^2, respectively). Gap fate affected the natural log of the change in gap area ($F_{2,\,164} = 78.9$, $P < 0.001$), with pairwise differences ($P < 0.05$) showing that gap area change was ordered as merged > extant > split.

Species richness in gaps—Gap dynamics, gap area, and fire affected species richness. Similar numbers of gaps gained richness (44%) as lost richness (41%); fewer maintained the same number of species (15%) between 2003 and 2011–12. Unburned gaps, especially large ones, tended to lose species richness (mean change in richness was −0.76 ± 0.25). Burned gaps (+6.14 ± 1.44) and partially burned gaps (+2.66 ± 1.1) tended to gain species richness (Table 2). Species richness also differed among gaps that merged, split, or did not change ($F_{2,\,312} = 78.2$, $P < 0.001$). Merged gaps had higher richness (27.6 ± 2.17) than split (13.6 ± 0.71) or extant (10.3 ± 0.36) gaps ($P < 0.05$ in post hoc tests).

Gap merging had strong positive effects on species richness. Gap merging created 24 mega-gaps in 2011–12 from 124 original gaps in 2003. Species richness in merged gaps was related to richness in the composite of gaps in 2003 that later merged ($r^2 = 0.774$, df = 23, $P < 0.001$). Two-thirds (16 of 24) of merged gaps increased

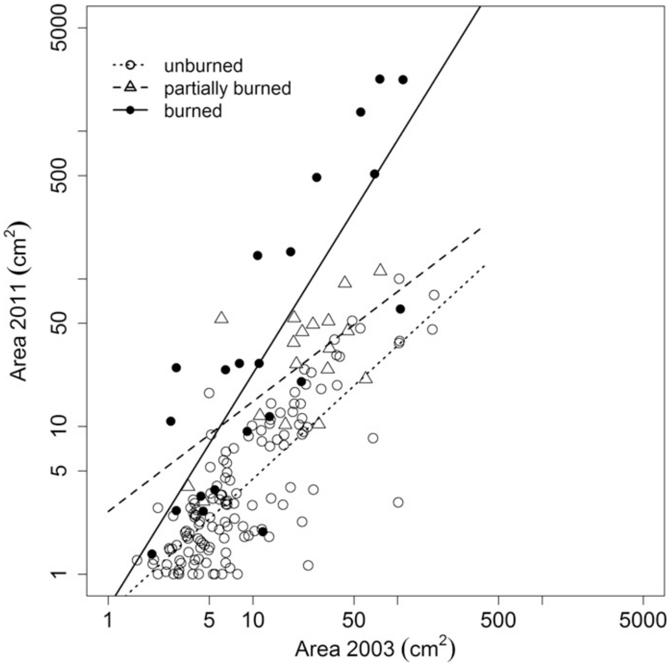

FIGURE 3 Gap area in 2011–12 as a function of gap area in 2003, divided by whether the gap was unburned, partially burned, or completely burned during the intervening years. See Table 1 for a summary of the analysis. R^2 for fixed effects was 0.75 and 0.77 for both fixed and random effects.

TABLE 1. Generalized linear mixed model results showing effects of initial gap area (log transformed), burn status, and their two-way interactions on final (2011–12) gap area. R^2 for fixed effects was 0.75 and 0.77 for both fixed and random effects. See also Fig. 3.

Predictor	df	Estimate	SE	*t*	*P*
Intercept	141	−0.589	0.172	−3.430	0.0008
Gap area (2003)	141	0.902	0.071	12.713	<0.001
Partial burn	141	1.567	0.727	2.156	0.033
All burned	141	0.075	0.438	0.172	0.864
Size*partial	141	−0.158	0.232	−0.681	0.497
Size*all Burned	141	−0.680	0.156	4.349	<0.001
Random effects of patch					
SD (intercept)			0.21		
Residual			0.76		

in richness, two gaps remained the same, and six became poorer. This net gain in richness for merged gaps was greater than for all gaps. Most (20 of 24) mergers happened when the gaps were partially or completely burned between 2003 and 2011–12. Among merged gaps, those that were burned gained a median of seven species; partially burned gaps gained three, and unburned megagaps lost 1.5.

Species richness patterns in split gaps were more nuanced. Gap splitting resulted in a total of 99 gaps splitting into 311 gaps by 2011–12. Species richness in the composite of split gaps in 2011–12 was related to richness in the mother gaps in 2003 ($r^2 = 0.829$, df = 86, $P < 0.001$). About one-quarter (24%) decreased in composite richness with splitting, 13% had the same number of species, and 63% gained in richness. Nearly all (86%) cases of splitting occurred without fire; only three occurred in gaps that were completely burned. Among split gaps, there was little difference in species richness change with burning (median + 2 for unburned, + 1 for partially or completely burned).

Species richness in 2011–12 increased with initial gap area (in 2003) and was affected by whether the gap had burned since 2003. Richness was generally higher in gaps burned between 2003 and 2011–12; in these burned areas, richness increased more rapidly with initial gap area (steeper slopes in Fig. 4A; Table 2). In analyses considering final gap area (2011–12), richness also increased with gap area, but whether gaps had burned since 2003 was associated with different richness patterns (Fig. 4B and Table 2). Differences among gaps burned and not burned were smaller (Fig. 4B). When considering final gap area, partially burned, large gaps had more species than large gaps with other burn histories.

Dynamics in gaps—Individual species occupancy varied widely by species in 2003 and 2011–12, at both the site and gap scales (Table 3). The most common species in rosemary scrub gaps included forbs (*Cnidoscolus stimulosus*, *Paronychia chartacea*, *Stipulicida setacea*, *Lechea deckertii*), ground lichens (*Cladonia leporina*, *C. prostrata*, *Cladina subtenuis*), a grass (*Aristida gyrans*), a clubmoss (*Selaginella arenicola*), a subshrub (*Licania michauxii*), and small palmettos (*Serenoa repens*). Typically, 10–30% of gaps showed changes in occupancy between sampling years (Table 3). Small sample sizes, lack of change in occupancy, or lack of diversity in burn histories meant that not all species could be modeled for effects of burn history between years, time-since-fire in 2003, and gap area on occupancy dynamics.

Extinction was affected primarily by whether gaps burned between 2003 and 2011–12, and secondarily by gap area (Table 4). For all ground lichen species that were successfully modeled, extinction was more likely if the gap was burned (positive coefficients for *Cladonia* and *Cladina* species in Table 4). For two forbs (*Lechea deckertii*, *Paronychia chartacea*), extinction was less likely if the gap was burned (negative coefficients in Table 4). Gap area had negative effects on extinction in four species, including the obligate seeder *P. chartacea* (Table 4). Time-since-fire in 2003 never had any significant effects on extinction (Table 4).

Colonization was affected by burning and by gap area in the majority of species for which models had enough data ($n = 25$). Burning increased colonization significantly for 13 species and never had significant negative effects on colonization (Table 4). The species whose colonization were favored by burning included five forbs but also included subshrubs (*Vaccinium myrsenites*, *Polygonella polygama*, *Opuntia humifusa*, *Palafoxia feayi*), small plants of dominant shrubs (*Ceratiola ericoides*, *Sabal etonia*), sedges (*Cyperus* spp.), and a vine (*Smilax auriculata*). Likewise, colonization was significantly more likely in larger gaps for 15 species (Table 4). Time-since-fire in 2003 had minor effects overall, increasing the likelihood of colonization for one ground lichen and decreasing this likelihood for two other species.

NMDS ordinations—For 2011–12 data, axis 1 of the NMDS ordination was strongly related to time-since-fire of 0–20 yr but showed little relationship to longer fire-free intervals ($\beta0 = 0.353 \pm 0.054$, $\beta1(\mathrm{tsf}) = -0.019 \pm 0.004$, $\beta2(\mathrm{tsf}^2) = 0.0001 \pm 0.00005$, $P < 0.001$; Fig. 5, upper left). In contrast, axis 2 (2011–12) was related to gap area ($\beta0 = 0.157 \pm 0.046$, $\beta02 = -0.099 \pm 0.009$, $P < 0.001$; Fig. 5, lower right) but not to time-since-fire ($\beta = 0.0001 \pm 0.002$, $P = 0.971$;

TABLE 2. Mixed model results showing fixed effects of initial and final (2011–12) gap areas (ln transformed), partial burn, unburned, and their two-way interactions on species richness in 2011–12. R^2 for fixed effects in the model with initial area was 0.58 and 0.70 for both fixed and random effects. R^2 for fixed effects in the model with final area was 0.81 and 0.87 for both fixed and random effects. See also Fig. 4.

	Area 2003					Area 2011–12				
Predictor	df	β	SE	*t*	*P*	df	β	SE	*t*	*P*
Intercept	292	3.42	0.85	4.03	<0.01	140	−1.02	2.69	−0.38	0.71
Gap area	292	3.60	0.28	12.54	<0.01	140	6.82	0.76	8.96	<0.01
Partial burn	292	0.84	2.75	0.30	0.76	140	7.55	2.75	2.75	0.01
All burned	292	−3.88	1.86	−2.08	0.04	140	5.11	2.80	1.82	0.07
Size*partial	292	1.39	0.91	1.54	0.12	140	−3.03	0.80	−3.77	<0.01
Size*all burned	292	4.67	0.68	6.86	<0.01	140	−1.91	0.79	−2.41	0.02
Random effects of patch										
SD (intercept)			2.58					1.87		
Residual			4.01					2.85		

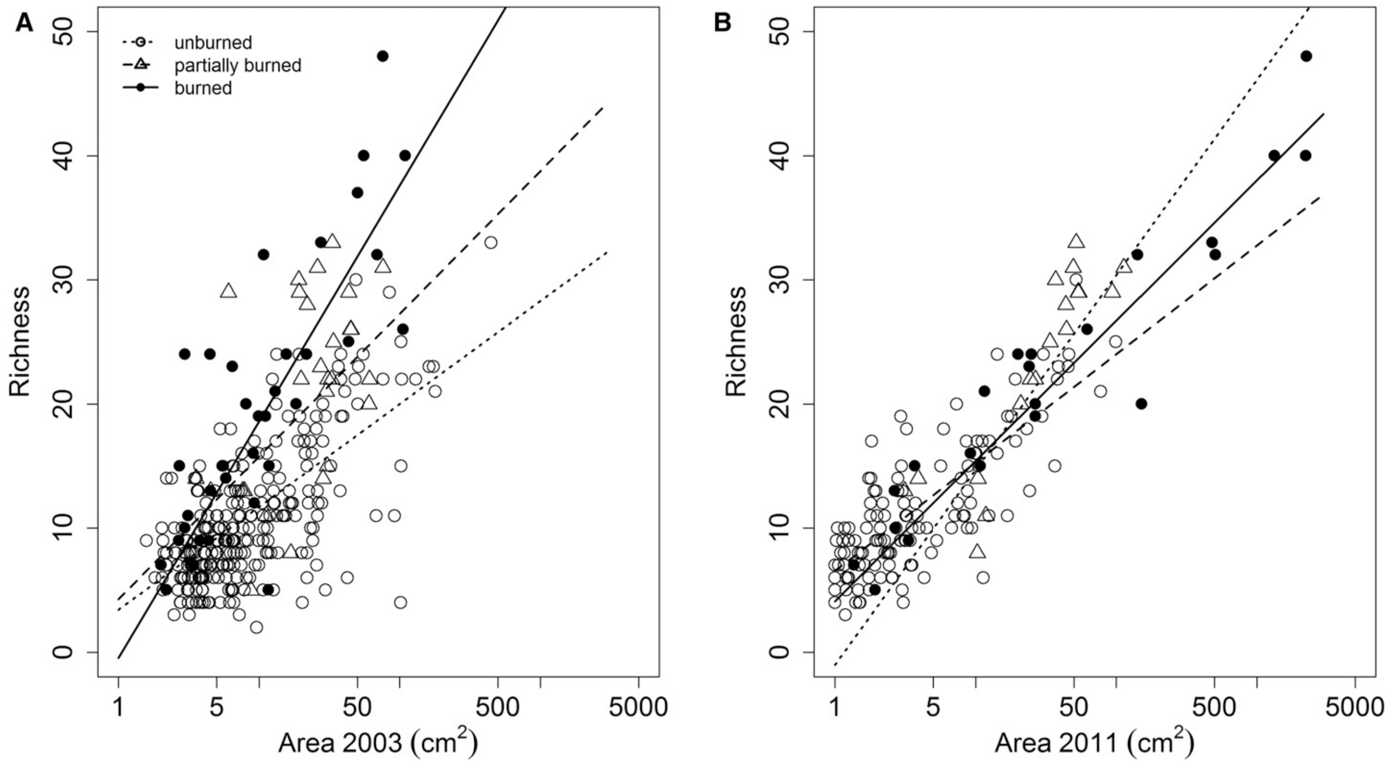

FIGURE 4 Number of species per gap in 2011–12 as a function of gap area grouped by burn status of gap between (A) 2003 and (B) 2011.

Fig. 5, upper right). An ordination of 2003 data showed that axis 1 of the NMDS ordination was related as a quadratic response to time-since-fire and gap area ($\beta 0 = -0.366 \pm 0.043$, $\beta 1(\text{tsf}) = 0.041 \pm 0.004$, $\beta 2(\text{tsf}^2) = -0.0004 \pm 0.00005$, $\beta 3(\log \text{area}) = -0.042 \pm 0.009$, $P < 0.001$). In contrast, axis 2 was not related to time-since-fire ($\beta = -0.002 \pm 0.003$, $P < 0.359$) but was related to gap area ($\beta = 0.124 \pm 0.009$, $P < 0.001$). Individual species correlations to ordination axes were consistent with the individual species analyses reported above. For example, ground lichens had significant negative correlations with axis 1, being favored in gaps with longer time-since-fire. Herbaceous species whose colonization was increased and extinction was decreased by fire (e.g., *Lechea cernua*) showed strong correlations with axis 1, being favored in patches that were recently burned.

DISCUSSION

In Florida rosemary scrub, fire affected landscape structure (as measured by gap areas and dynamics) and the responses of plants were affected by both the gap dynamics and recent fire history. Species richness, species composition, and individual species occurrence patterns responded to gap area and fire. In general, richness and most species' occurrences were favored by larger gaps and recent fires. In addition, local extinction and colonization of plants and lichens over 8 yr were strongly affected by fire and gap area, with extinction tending to occur in unburned and smaller gaps, and colonization more likely in larger and burned gaps.

Gap dynamics—Gap area distributions commonly include many small gaps and fewer large gaps (Denslow, 1980). In this study of gaps in Florida scrub, we found that gap area distributions were lognormal, with many small gaps and fewer large gaps. A lognormal (or similar) pattern has been found in prior studies in temperate, boreal, and tropical forests (Runkle, 1982; Kneeshaw and Bergeron, 1998; Myers et al., 2000). In one spruce–fir forest, a negative exponential gap-size distribution was fit (Foster and Reiners, 1986). The present study and Menges et al. (2008) are among the first papers to report a gap-size distribution for a nonforested ecosystem.

Gap areas in 2011–12 decreased logarithmically with time-since-fire in the present study, with most of the change in area occurring during the first decade postfire. This pattern contrasts with results from the chronosequence in 2003 (Menges et al., 2008), which suggested little change in gap area with time-since-fire except for a patch not burned in >40 yr. This inconsistency highlights weaknesses of the chronosequence approach, which makes inferences on long-term ecological trends by contemporaneous comparisons among sites differing in age or time-since-disturbance (Pickett, 1989; Freestone et al., 2015). The present study, by emphasizing gap dynamics over time within the same locations, was not subject to this weakness.

Gap dynamics were strongly affected by fire. Unburned gaps got smaller over time, and gaps unburned for >10 yr often split into smaller gaps. Gap closure ("dormancy") also occurred when areas were unburned. In contrast, burned gaps often merged together into larger gaps. These gap dynamics had profound impacts on species and vegetation dynamics.

Individual species responses—Fire had large effects on the dynamics of individual species in Florida rosemary scrub gaps. In the present study, observed extinctions were lowest with recent fire for two herbaceous perennials, and colonization was higher with

TABLE 3. Sample sizes for each of the 54 most common vascular plant and ground lichen species in this study: number of patches present in 2003 (of 28), number of patches present in 2011–12 (of 28), number of gaps present in 2003 (of 805) and 2011–12 (of 691), and percentage of gaps with changes in occupancy for that species. For taxa aggregated to the genus level, we also list the predominant species in our samples.

Species	Number of patches present, 2003	Number of patches present, 2011–12	Number gaps present, 2003	Number of gaps present, 2011–12	Percentage of gaps with changes in occupancy
Andropogon spp. (*A. floridanus*)	16	13	52	28	7.1
Aristida gyrans	28	28	555	367	33.6
Asclepias spp. (*A. curtissii*)	23	23	103	76	15.7
Balduina angustifolia	15	14	130	45	10.4
Bulbostylis spp. (*B. ciliatifolia*)	19	20	84	50	11.3
Calamintha ashei	13	14	110	99	11.3
Callisia (*Tradescantia*) *rosea*	17	10	73	20	7.8
Ceratiola ericoides	23	23	184	52	18.6
Chapmannia floridana	20	20	133	87	12.4
Cladina evansii	17	20	223	169	20.6
Cladina subtenuius	16	23	306	237	26.3
Cladonia leporina	22	28	483	416	40.3
Cladonia pachycladodes	17	19	106	122	20.0
Cladonia perforata	1	1	29	50	2.8
Cladonia prostrata	21	21	308	265	22.5
Cladonia subsetacea	15	15	145	131	16.2
Cnidoscolus stimulosus	28	28	342	254	32.2
Commelina erecta	21	17	58	27	8.7
Crocanthemum (*Helianthemum*) *nashii*	14	13	58	31	3.9
Cyperus spp. (*C. ovatus*)	28	23	197	82	20.9
Eryngium cuneifolium	3	3	10	12	2.1
Euphorbia rosescens	5	6	35	29	3.1
Galactia regularis	24	18	80	47	13.1
Gaylussacia dumosa	9	7	75	27	4.9
Hypericum cumulicola	13	11	37	27	3.3
Lechea cernua	15	13	119	91	10.8
Lechea deckertii	28	27	353	251	31.7
Liatris ohlingerae	14	12	49	23	7.3
Licania michauxii	28	28	463	316	21.6
Opuntia humifusa	20	17	194	123	14.6
Palafoxia feayi	27	26	198	121	25.5
Paronychia chartacea	28	28	492	338	35.0
Pinus clausa	4	10	14	22	5.2
Polanisia tenuifolia	13	8	64	23	7.3
Polygonella basiramia	21	15	131	97	11.7
Polygonella polygama	24	26	126	110	20.6
Polygonella robusta	8	7	28	29	3.8
Quercus chapmanii	26	26	127	88	16.9
Quercus geminata	27	28	252	159	18.7
Quercus inopina	28	27	175	85	20.0
Rhynchospora megalocarpa	18	15	54	26	4.2
Sabal etonia	27	25	114	69	12.4
Schizachyrium niveum	6	6	24	16	1.9
Selaginella arenicola	28	28	714	483	31.7
Serenoa repens	28	27	446	108	33.1
Sideroxylon tenax	20	18	103	56	10.3
Sisyrinchium xerophyllum	8	12	23	23	4.9
Smilax auriculata	25	24	103	76	18.5
Stipulicida setacea	27	27	350	221	24.4
Stylisma abdita	25	19	101	102	12.0
Trichostemum dichotomum	12	9	28	23	4.5
Vaccinium darrowii	9	6	33	17	4.2
Vaccinium myrsenites	27	26	216	129	14.5
Ximenia americana	22	15	63	34	9.9

burning for 13 species, including six herbaceous perennials. Two species with lower extinction and higher colonization with burning were the short-lived herbaceous perennials *Lechea deckertii* and *Paronychia chartacea*. Their distributions were also correlated with fire along the major axis of an NMDS ordination. These species' patterns are consistent with past research showing increases in these two species in the decade after fire (Johnson and Abrahamson, 1990) and that they are gap specialists (Maliakal-Witt et al., 2005; Menges et al., 2008; Schafer et al., 2010), so that their postfire dynamics are probably mediated by gap dynamics. More generally, many herbaceous perennials in Florida scrub show decreasing occurrences with time-since-fire (Menges and Kohfeldt, 1995). Fire

TABLE 4. Results of mixed model analysis for the subset of species for which we could evaluate the effects of patch identity ln gap area in 2003 (A), time-since-fire in 2003 (T), and burn status during 2003–11 (B), affecting loss of presence (“extinction”) or gain of presence (“colonization”) in a gap. ID = insufficient data to form a model with these variables. Variables significant at $P < 0.05$ are in bold; those with $P < 0.1$ are italicized. Obligate seeding species (after Menges and Kohfeldt, 1995) are in bold.

Species	Variables affecting extinction	SD patch	Variables affecting colonization	SD patch
Aristida gyrans	−**1.3** – *(0.9*B)* + (0.01*T) – (0.1*A)	0.31	−1.5 + (0.7*B) – (0.01*T) + (0.4*A)	0.63
***Asclepias* spp.**	ID		**−4.2** + *(1.1*B)* – (0.01*T) **+ (0.7*A)**	0.98
Calamintha ashei	−0.8 – (0.2*B) + (0.06*T) + (0.04*A)	0.69	ID	
Ceratiola ericoides	**+5.4** – *(4.0*B)* – (−0.07*B) – *(0.5*A)*	2.08	**−6.3 + (2.2*B)** + (0.02*T) + **(1.2*A)**	1.18
Cladina evansii	−0.0 + **(3.2*B)** – (0.02*T) – *(0.7*A)*	2.23	**−3.8** + *(0.9*B)* – *(0.03*T)* + **(0.5*A)**	0.59
Cladina subtenuius	−1.4 + **(2.1*B)** + (0.01*T) – (0.4*A)	0.16	**−3.1 –** (0.8*B) + **(0.04*T)** + **(0.7*A)**	1.05
Cladonia leporina	−1.1 + **(2.3*B)** – (0.01*T) – **(1.0*A)**	1.41	**−1.3** + (0.1*B) – (0.00*T) + **(0.9*A)**	0.55
C. pachycladoides	ID		**−5.2** – (0.9*B) + (0.04*T) + **(1.0*A)**	1.66
Cladonia prostrata	−1.7 + **(2.6*B)** – (0.00*T) – *(0.9*A)*	1.94	**−3.6** + (0.5*B) – (0.00*T) + (0.5*A)	2.24
Cladonia subsetacea	**+3.4 + (2.7*B)** – **(0.13*T)** – **(1.0*A)**	0.59	**−3.4 –** (0.6*B) + (0.02*T) + (0.2*A)	1.08
Cnidoscolus stimulosus	ID		**−2.4** + **(2.2*B)** – (0.02*T) + **(0.7*A)**	0.93
***Cyperus* spp.**	ID		**−2.6 + (2.3*B)** – (0.00*T) + (0.0*A)	0.56
Gaylussasia dumosa	ID		**−4.9** + (1.0*B) + (0.01*T) – (0.0*A)	0.87
Lechea cernua	+0.2 – (0.3*B) – (0.06*T) – *(0.6*A)*	0.23	**−5.2** + (1.2*B) – (0.02*T) + *(0.6*A)*	2.04
Lechea deckertii	−1.4 – **(3.0*B)** – (0.00*T) + (0.1*A)	1.18	**−2.5 + (1.5*B)** – (0.01*T) **+ (0.7*A)**	1.22
Opuntia humifusa	+0.1 + (0.0*B) – (0.01*T) – (0.4*A)	1.29	**−5.5 + (2.1*B)** + (0.01*T) + (0.5*A)	1.83
Palafoxia feayi	ID		**−5.1 + (2.1*B**) + (0.00*T) **+ (1.3*A)**	1.45
Paronychia chartacea	+0.1 – **(2.3*B)** + (0.00*T) – **(0.8*A)**	1.41	*−1.6* **+ (3.3*B) – (0.03*T)** + (0.6*A)	0.36
Polygonella basiramia	ID	0.49	**−3.0** – (0.5*B) – (0.05*T) + (0.3*A)	1.52
Polygonella polygama	+0.5 – (0.7*B) – (0.00*T) – (0.2*A)	0.41	**−2.9 + (2.1*B)** – *(0.05*T)* **+ (0.5*A)**	0.61
Sabal etonia	ID		**−3.7 + (1.6*B) – (0.02*T) + (0.5*A)**	0.47
Serenoa repens	**+1.7** – (0.2*B) + (0.00*T) – **(0.4*A)**	0.51	ID	
Smilax auriculata	ID		**−4.4 + (1.9*B)** – (0.01*T) **+ (0.8*A)**	0.43
Stipulicida setacea	−0.7 – (0.7*B) + (0.01*T) – (0.3*A)	0.71	**−1.7** + (1.0*B) – *(0.04*T)* + (0.4*A)	1.36
Stylisma abdita	−2.1 + (1.7*B) – (0.07*T) + (0.2*A)	2.08	**−5.6 + (1.5*B)** – (0.01*T) **+ (1.1*A)**	0.56
Trichostemum dichotomum	ID		**−7.8 + (2.5*B) + (0.03*T) + (0.8*A)**	1.89
Vaccinium myrsenites	**+2.3** – (0.8*B) + (0.03*T) + (0.4*A)	0.30	**−5.3 + (2.9*B)** + (0.01*T) **+ (0.7*A)**	0.67

reduced extinction rates of rosemary scrub specialists at a larger spatial scale, the rosemary scrub patch (Miller et al., 2012). In many other pyrogenic systems, abundances of herbaceous species increase strongly after fire (e.g., Barney and Frischknecht, 1974; Moreno and Oechel, 1991; Glitzenstein et al., 2003; Turner et al., 2003).

In contrast, all ground lichen species showed higher extinction, but no change in colonization, with fire. Fire in Florida scrub kills ground lichens (Yahr, 2000) and they are slow to recolonize, so many were not present when burned areas were resampled in 2011–12. Over longer chronosequences, ground lichen occurrences increase with time-since-fire (Menges and Kohfeldt, 1995).

Nearly all of the 27 modeled species responded positively to gap area. Four species had lower extinction and 15 species had higher colonization with larger gap areas. These dynamics are consistent with occupancy patterns at the gap scale reported by Menges et al. (2008; 14 species had positive effects of gap area on occupancy). The tendency of many species to do well in gap area is consistent with increasing densities of many species (especially obligate seeding herbaceous plants) with the amount of open space at the patch level (Hawkes and Menges, 1996; Menges and Hawkes, 1998). This consistency suggests that, to a great extent, patterns of species changes with fire or fire suppression are mediated by their responses to gaps, which are affected by fire.

Vegetation responses to fire and gap area—Gap dynamics had strong effects on species richness and composition patterns in Florida scrub, and these dynamics were largely controlled by fire. Fire expanded gaps and merged adjacent gaps. This was probably due to fire killing the dominant shrub, Florida rosemary, and temporarily reducing competition with resprouting shrubs. Recruitment of a new generation of Florida rosemary from seeds is a slow process. First, emergence of seedlings generally happens beginning the second winter after fire (Johnson, 1982; E. S. Menges, unpublished data) and seedling growth is quite slow (E. S. Menges, unpublished data). As seedlings grow, eventually gaps begin to shrink and merge. Other dominant shrubs such as oaks and palmettos resprout more or less in place (Menges and Kohfeldt, 1995) and therefore contribute less to gap dynamics, although their growth between fires will contribute to gap shrinkage. In Florida scrub dominated by oaks (e.g., scrubby flatwoods), gaps are small, less spatially dynamic, and more ephemeral than in rosemary scrub (Menges and Hawkes, 1998; Young and Menges, 1999).

Our finding that species richness is positively associated with gap area is consistent with ecological literature based mainly on forests. Species richness either peaks in larger gaps (Hubbell et al., 1999; Schnitzer and Carson, 2001; Burton et al., 2014) or is greatest in intermediate-sized gaps (Kern et al., 2014). Larger gaps support different species assemblages than smaller gaps (Anderson and Leopold, 2002; Muscolo et al., 2014), consistent with our finding that certain species are found mainly in larger gaps.

Fire also had strong effects on species richness, increasing richness patterns with gap area in 2003. Data from 2011–12 showed a weaker effect of fire on richness. This may be due to the fact that gap areas in 2011–12 reflect the strong effects of fire between 2003 and 2011–12 on gap area, with areas increasing and gaps merging in burned areas. This is evidence that the effects of fire on richness are due in part to the effects of fire on gap size. Interestingly, partially

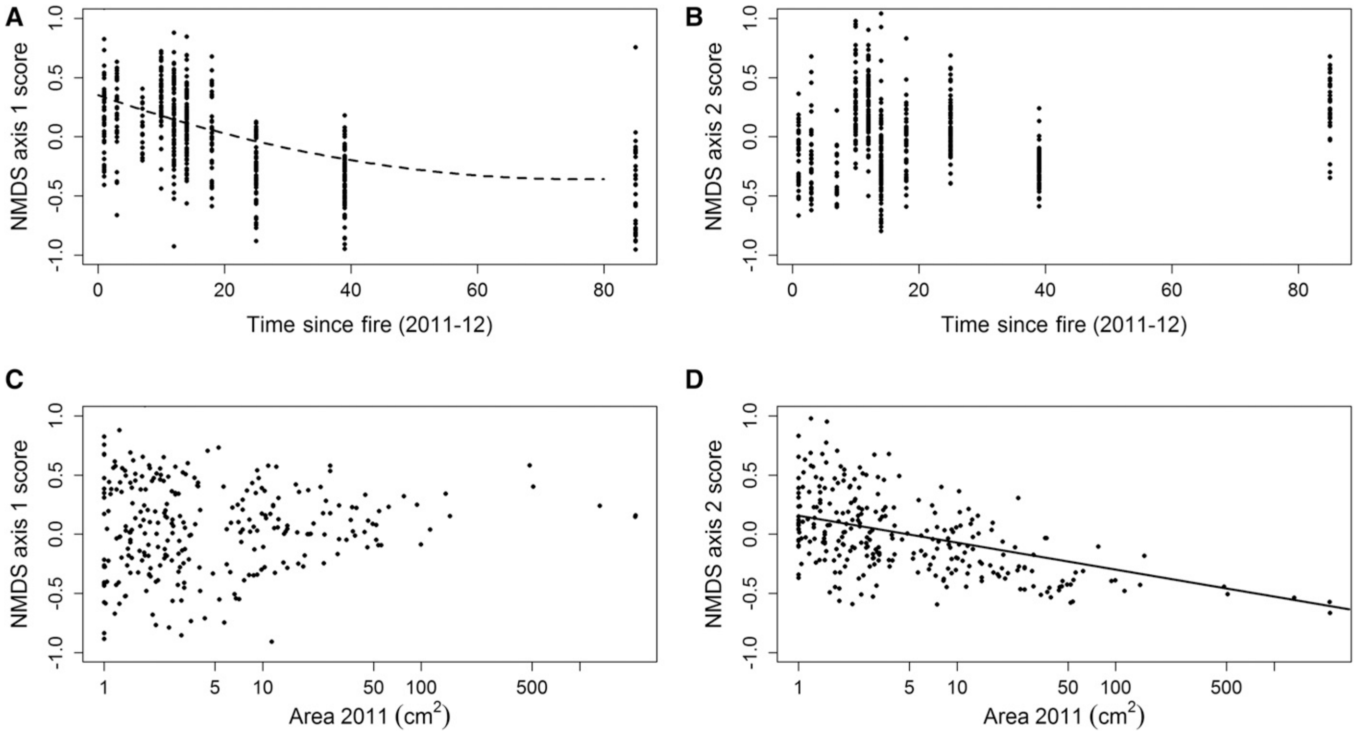

FIGURE 5 Relationships of time-since-fire (2011–12) and gap area (ln scale) to axis 1 and axis 2 scores in NMDS ordination. The lines represent the models using the coefficients of the fixed effects. (A) Axis 1 with time-since-fire. (B) Axis 2 with time-since-fire. (C) Axis 1 with ln (area). (D) Axis 2 with ln (area).

burned large gaps supported high species richness in 2011–12. This may reflect the fact that such gaps can support species that prefer postfire conditions (in burned parts) and ground lichens that are more abundant in unburned microsites.

Fire and gap area both affected species composition patterns, as revealed by NMDS ordinations. In the case of 2011–12 data, the ordination emphasized some independent effects of these two variables, as each were correlated with different ordination axes. Fire was the predominant driver, being strongly tied to the dominant ordination axis, especially over a time-since-fire range of 0–20 yr, when strong compositional changes occur. The 2003 analysis, on the other hand, showed that gap size had stronger effects (being correlated with each of the first two axes) and that time-since-fire and gap size were both correlated with one of the same axes. The stronger fire effects on vegetation composition in 2011–12 (compared to 2003) parallels the stronger pattern of gap size with time-since fire in 2011–12 than in 2003 (the latter discussed in Menges et al., 2008). Between these 2 yr, many gaps were burned and created a better distribution of time-since-fire values, possibly giving a stronger signal in 2011–12. One interpretation is that fire is a primary driver of vegetation composition in Florida rosemary scrub, but that fire acts mainly through an intermediary variable, gap size.

Scattered gaps in a landscape can be conceptualized as islands in a “sea” of more dominant vegetation, although these islands may have a temporary existence. They can also be considered as suitable habitats for species that cannot compete with more dominant vegetation. The fields of island biogeography and metapopulation theory make predictions of how scattered islands or populations may affect community and population properties. Island biogeography and metapopulation theory both predict greater species richness on larger patches (Kohn and Walsh, 1994; Hanski, 2004). However, patch quality also plays an important role. In Florida scrub, both gap area and time-since-fire (which may indicate patch quality for many species) had effects on diversity and on individual species occupancy. This is consistent with previous findings (Menges and Hawkes, 1998; Menges et al., 2008; Dee and Menges, 2014). In other ecosystems, richness generally increases with patch size, but patterns in relation to fire frequency or time-since-fire vary. In Wisconsin remnant prairies, diversity was also greater in larger and more recently burned sites (Alstad and Damschen, 2016). However, large and more severely burned patches tended to have lower diversity following the 1988 Yellowstone fires (Turner et al., 1997). In South African fynbos, species richness was highest at frequently and infrequently burned sites, compared to intermediate fire frequencies (Schwilk et al., 1997).

Although our results have focused on the interaction of fire with gap dynamics, most ecological literature linking disturbances with gaps is related to disturbances other than fire. In other ecosystems, disturbances may create gaps that allow for gap-specialist species to colonize and may increase diversity. Gaps caused by animals such as prairie dogs (Archer et al., 1987), badgers (Platt and Weis, 1977), and gopher tortoises (Kaczor and Hartnett, 1990) create openings in perennial-dominated vegetation (gaps) that can change plant species composition, favor certain life-history traits, and provide niches for fugitive species. Windfalls also create small gaps that may support specialist species and increase diversity (Denslow, 1995). In forest gaps created by wind and ice, trees on the edge of gaps may be at greater risks of dying and of gradually increasing gap size (Sprugel, 1976).

Because gaps may close laterally (from branch growth) or vertically (from growth of understory individuals), gap closure in forests is a complex process (Ogden et al., 1991).

Although it is perhaps the predominant disturbance worldwide (Bond and Keeley, 2005), fire is not usually credited with creating gaps, and gap closure between fires is little studied. This may be because many fires occur over larger areas and create a coarser-grained spatial pattern of burned and unburned areas than is typical of other gap-producing disturbances. Alternatively, in areas with low-intensity fires, disturbances other than fire may be responsible for most gap-creating events (King and Muzika, 2014; McEwan et al., 2014). Nonetheless, fires can be patchy and create complex mosaics of unburned, lightly burned, and intensely burned patches that affect plant regeneration (Turner et al., 1994).

Management implications—Because fire can be managed by humans, through prescribed burning or fire suppression, the possibility exists that land managers can control gap structure and thereby richness and species occupancy. In Florida scrub, land managers and scientists are using innovative techniques to create and maintain gaps providing habitat for certain plant species (P. A. Schmalzer and T. E. Foster, unpublished data). Large gaps promote richness and provide opportunities for species that are particularly poor competitors with dominant shrubs. In Florida rosemary scrub, these include many species listed as endangered or threatened by the U.S. Fish and Wildlife Service or the state of Florida. Managing for larger gaps will be a challenge but may involve attempting fires during drier periods when more complete and hotter fires are possible (Slocum et al., 2003; Platt et al., 2015). Because gap dynamics may ultimately drive species and vegetation dynamics with fire, understanding how fire affects gap dynamics is a useful link between fire and biotic responses.

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