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Effects of Time-Since-Fire and Microhabitat on the Occurrence and Density of the Endemic Paronychia chartacea ssp. chartacea in Florida Scrub and Along Roadsides

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ABSTRACT.—Conservation of an imperiled plant species requires an understanding of its local occurrence and density in relation to habitat variation. *Paronychia chartacea* ssp. *chartacea* is a federally threatened species restricted to gaps in fire-maintained Florida rosemary scrub and to roadside sites that mimic scrub gaps. To assess the effects of time-since-fire and microhabitat on the occurrence and density of *Paronychia* populations, we conducted surveys of 119 scrub gaps and 16 roadside macroplots. In rosemary scrub, we found that the frequency of gap occupancy decreased with time-since-fire and that *Paronychia* occurrence and density were greater in the centers of large gaps than in small gaps or large gap edges. In roadside sites, the distance from adjacent rosemary scrub did not affect the presence of *Paronychia*, but density increased with distance from rosemary scrub vegetation. *Paronychia* densities in roadside sites were most similar to densities in recently burned rosemary scrub. Time-since-fire and microhabitat quality affect the occurrence and density of *Paronychia* and should be considered in management of *Paronychia* populations.

INTRODUCTION

The environmental conditions affecting the occurrence and density of plant species must be understood to promote successful conservation (Clubbe *et al.*, 2004; Jacquemyn *et al.*, 2009; Sankaran, 2009). In many habitats, natural disturbances such as fire, wind, flooding, drought and animal activity affect the local densities of plant species (White, 1979; Sousa, 1984). Fire, for instance, creates open spaces, which provide opportunities for colonization and persistence of many species (Menges and Hawkes, 1998). Anthropogenic disturbances such as roads create habitats that may mimic the effects of natural disturbances (Forman, 1995; Petrů and Menges, 2004), thereby creating artificial habitats that may be beneficial for some imperiled species. Therefore, assessment of the occurrence and density of an imperiled plant species in both natural and anthropogenic habitats is necessary to develop a conservation plan.

Fire is a natural disturbance in many shrubland ecosystems (Little, 1979; Abrahamson, 1984; Christensen, 1985; Keeley and Keeley, 1988; Moreno and Oechel, 1994; Bradstock *et al.*, 2001). Plant species in pyrogenic habitats have evolved a variety of mechanisms that allow them to persist and recover after fire (Sousa, 1984; Christensen, 1985; Whelan, 1995).

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Some species are resilient to fires and resprout after burning, some are killed by fire and recolonize via seedling recruitment, and others both resprout and recruit seedlings after fire (Keeley, 1977; Keeley and Zedler, 1978; Myers, 1990; Menges and Kohfeldt, 1995; Whelan, 1995; Weekley and Menges, 2003). Fire removes woody dominant species and creates open areas that are favorable for seedling recruitment (Sousa, 1984), which is important for obligate seeding species that cannot become established in densely vegetated areas (Connell and Slatyer, 1977).

Open patches within the dominant vegetation, often called gaps, occur in many ecosystems (Pickett and White, 1985). Gaps provide areas for seedling recruitment and growth of both woody and herbaceous species (Platt and Weis, 1977; Goldberg and Gross, 1988; Canham, 1989; Rebertus and Burns, 1997; Quintana-Ascencio and Menges, 2000; Kwit and Platt, 2003; Menges *et al.*, 2008). Plants in gaps appear to experience reduced competition (Morgan, 1997; McGuire *et al.*, 2001; Suding and Goldberg, 2001; Petrů and Menges, 2003). Within gaps, spatial variation (*e.g.*, center vs. edge) in resources can affect plant establishment, growth and survival (Brokaw and Busing, 2000). Furthermore, the amount of open space in a habitat affects the distribution and density of plant species (Went, 1942; Wu and Levin, 1994; Hawkes and Menges, 1995, Menges *et al.*, 2008).

Disturbances such as fire can create gaps by consuming vegetation, while other mechanisms likely contribute to gap persistence. For example, gaps may be maintained by allelopathic chemicals released by dominant shrubs (Hunter and Menges, 2002; Hewitt and Menges, 2008), particularly in ecosystems with areas of bare soil and low plant densities (Muller, 1966). Allelopathic chemicals can inhibit germination, limit growth of herbaceous species (Muller, 1966) and reduce the effective gap size for plants that require open space, which influences species occurrences and densities.

The occurrence and density of a particular plant species is affected by human disturbances such as roads. When roads and road edges are similar to natural areas, they may provide habitat for native plants (Petrů and Menges, 2004; Quintana-Ascencio *et al.*, 2007), and roadsides may act as refugia and connections between natural habitats (Andrews, 1990). Furthermore, seed dispersal can be facilitated by wind in roadside habitats (Forman *et al.*, 2003). On the other hand, roadsides can be detrimental to native plants due to alteration of water movement, erosion processes and invasion by exotic species (Forman *et al.*, 2003). Orientation of roadsides affects habitat quality, with south-facing edges having the highest light availability and temperature and lowest moisture (Matlack, 1993). Furthermore, the distance from the edge of vegetation patches into roadsides may affect species interactions. The ability of roads to provide adequate habitat may affect the occurrence and density of plant species.

Our study took place in Florida scrub habitats on the Lake Wales Ridge in central peninsular Florida, where fire maintains ecosystems including xeric upland habitats such as shrub-dominated Florida scrub (Abrahamson *et al.*, 1984; Myers, 1990; Menges, 1999). Gaps in the shrub matrix are created by fire, but also occur in long-unburned rosemary scrub, perhaps due to allelopathic properties of Florida rosemary (*Ceratiola ericoides*) (Hunter and Menges, 2002; Hewitt and Menges, 2008). Many species are gap specialists, occurring mainly in recently burned areas or in sites with larger gaps (Menges and Kohfeldt, 1995; Menges *et al.*, 2008). Previous studies of Lake Wales Ridge endemic species have shown the importance of fire, open space and microhabitat (*e.g.*, presence/absence of leaf litter) in determining population occurrences and densities (Hawkes and Menges, 1995; Menges and Kimmich, 1996; Hunter and Menges, 2002; Menges and Quintana-Ascencio, 2004) and that roadsides can support higher population densities than natural scrub habitats (Menges *et al.*, 2006;

Quintana-Ascencio *et al.*, 2007; E. Menges, pers. obs.). *Paronychia chartacea* ssp. *chartacea* (hereafter *Paronychia*) is a scrub endemic that is smaller in stature and shorter-lived than other rare scrub herbs. It is one of the most abundant species in the rosemary scrub seed bank (E. Menges and N. Kohfeldt, pers. obs.; J. Navarra, pers. comm.) and occurs along the sides of sand roads. *Paronychia* recruits from seed (Mengen and Kohfeldt, 1995) and increases in cover after fire (Johnson and Abrahamson, 1990).

In this study, we investigated the occurrence and density of *Paronychia* in Florida rosemary scrub and roadside populations in relation to time-since-fire and microhabitat. In rosemary scrub, we focused on gap size and location within a gap, whereas in roadsides, we evaluated distance from rosemary scrub and roadside aspect. Our study addressed three main questions: (1) How do time-since-fire and microhabitat affect the occurrence and density of *Paronychia* in rosemary scrub? (2) How do microhabitat and time-since-fire affect the occurrence and density of *Paronychia* in roadsides? (3) How does density of *Paronychia* plants in scrub populations compare to roadside populations? Based on previous studies of other rosemary scrub specialists (Menges and Kohfeldt, 1995; Menges and Kimmich 1996; Quintana-Ascencio *et al.*, 2007), we hypothesized that *Paronychia* gap occupancy and density in rosemary scrub would be greater in recently burned than in long unburned sites and greater in large gap centers than in large gap edges and small gaps. We hypothesized that *Paronychia* occurrence and density would be lowest in south facing roadsides and would increase with distance from rosemary scrub. Furthermore, we hypothesized that *Paronychia* density would be greater in roadsides than in rosemary scrub.

METHODS

STUDY SITE AND SPECIES

This study was conducted in rosemary scrub and roadsides at Archbold Biological Station (ABS) in Highlands County, Florida, USA (27°10′50″N, 81°21′0″W). ABS typically has warm wet summers and cool dry winters (Abrahamson *et al.*, 1984). Mean annual precipitation is 136.5 cm (ABS weather records, 1932–2004), and mean annual temperature is 22.3 C (ABS weather records, 1952–2004). ABS comprises a mosaic of plant communities including seasonal ponds, flatwoods, scrubby flatwoods, oak-hickory scrub and sand pine scrub. Rosemary scrub (also known as the rosemary phase of sand pine scrub) is characterized by xeric white sand and even-aged stands of Florida rosemary (*Ceratiola ericoides* Michx.), with areas of bare sand colonized by herbaceous and suffrutescent species and ground lichens (Abrahamson *et al.*, 1984). In addition, numerous unpaved sand roads, which serve as fire breaks, traverse ABS property, creating open habitats that are colonized by many scrub endemics (Quintana-Ascencio *et al.*, 2007).

Paronychia chartacea Fern. ssp. *chartacea* L.C. Anderson (Caryophyllaceae) is endemic to central peninsular Florida, state endangered (Coile and Garland, 2003) and federally threatened (USFWS, 1999). *Paronychia* is herbaceous and has been described as both an annual (Christman and Judd, 1990) and a short-lived perennial (Anderson, 1991; Menges and Kohfeldt, 1995). Plants above ground for at least 3 mo vary in length (0.1 to 33.7 cm), width (0.1 to 29.9 cm) and height (0.4 to 9.8 cm) (J. Schafer, pers. obs.). *Paronychia* is considered a gap specialist because it occurs at greater densities in areas of open bare sand (Hawkes and Menges, 1996). *Paronychia* recovers after fire through germination from seed (Menges and Kohfeldt, 1995), colonizes recently burned areas more quickly than other species endemic to the scrub (Christman and Judd, 1990) and appears in areas postfire where it was scarce or absent prefire (Johnson and Abrahamson, 1990). *Paronychia* occurs primarily in Florida rosemary scrub and along the edges of associated sand roads.

TABLE 1.—Summary of rosemary scrub sites. Small gaps were 1 to 4 m^2 in area and large gaps were greater than 4 m^2 in area

Years since fire (fire class)	# of gaps	% of gaps occupied by *Paronychia*	# of gaps with plots (small, large)	Mean gap area (SE) (m^2)
2 (2)	196	55.6	4,4	30.9 (15.2)
2 (2)	53	41.5	4,1	9.3 (5.8)
2 (2)	113	39.8	4,4	9.4 (3.0)
2 (2)	59	52.5	4,2	8.4 (3.6)
4 (5)	531	34.3	4,4	23.9 (8.4)
6 (5)	83	67.5	4,4	15.5 (3.8)
6 (5)	119	50.4	4,4	26.6 (12.0)
6 (5)	265	46.4	4,4	13.3 (4.6)
10 (10)	46	37.0	4,4	15.9 (3.2)
10 (10)	203	58.6	4,4	23.6 (8.2)
10 (10)	73	35.6	4,4	17.3 (6.2)
10 (10)	44	36.4	4,4	16.0 (6.4)
17 (>15)	46	23.9	2,4	26.0 (9.4)
17 (>15)	179	16.2	4,4	23.9 (8.8)
31 (>15)	119	43.7	4,4	37.3 (13.3)
39 (>15)	30	30.0	4,2	14.7 (6.3)

ROSEMARY SCRUB AND ROADSIDE SAMPLING

We studied *Paronychia* populations in 16 rosemary scrub sites and 16 roadside sites at ABS. In rosemary scrub, we randomly selected four sites from each of four time-since-fire classes (2, 4–6 (hereafter 5), 10 and >15 y since fire) (Table 1). Within each rosemary scrub site, we marked all gaps, defined as areas of open sand within the shrub matrix with two perpendicular axes ≥ 1 m in length (thus, a gap is ≥ 1 m^2 in area) (Menges *et al.*, 2008). Dominant shrubs include Florida rosemary, clonal oaks (*Quercus inopina* Ashe, *Quercus geminata* Small, *Quercus chapmanii* Sarg.), ericads (*Lyonia* spp.) and palmettos (*Serenoa repens* (W. Bartram) Small and *Sabal etonia* Swingle ex Nash); gap boundaries were defined by shrubs ≥ 50 cm tall. Gaps were grouped into large and small size classes; small gaps had their entire area within 1 m of the gap edge, and thus were 1 to 4 m^2 in area, whereas large gaps had some area greater than 1 m from the gap edge, and thus were greater than 4 m^2 in area. Open areas among dominant shrubs can include bare sand, litter, ground lichens, mosses and herbaceous and suffrutescent plants. In Nov. and Dec. 2002, each gap (n = 2159) was checked for the presence of *Paronychia*.

To assess the distribution and density of *Paronychia*, four small and four large gaps with *Paronychia* were randomly selected in each of the 16 rosemary scrub sites. We randomly placed three circular plots (50 cm diameter) in each small gap, in each large gap edge (within 1 m of the gap edge) and in each large gap center (≥ 1 m from the gap edge). In three rosemary scrub sites fewer than four small gaps or four large gaps were occupied by *Paronychia*, and in one rosemary scrub site several large gap centers were too small to fit three plots. Thus, the number of plots per rosemary scrub site varied between 30 and 36. Overall, we established 186 plots in small gaps, 189 plots in large gap edges and 185 plots in large gap centers. In Feb. 2003, we checked each plot for the presence of *Paronychia* and counted all *Paronychia* plants present. Although plots were established only in gaps with *Paronychia*, some gaps had, by chance, no plots with *Paronychia* present.

In Apr. 2003, we measured the area of all gaps where *Paronychia* occupancy and density were assessed (n = 119). To determine the area of large gaps, we mapped the edge of the gap using a Trimble Pro X-R Global Positioning System (GPS) with submeter accuracy. Because the GPS is less accurate for smaller areas, we measured eight distances from the gap center to the gap edge and calculated the area of the resulting triangles to determine the area of small gaps.

We located roadside sites adjacent to rosemary scrub vegetation (different sites than those described above) and randomly selected four sites for each of four roadside aspects (North, South, East and West). We established a macroplot in each of the 16 roadside sites, and we determined the width of a macroplot as the distance from the rosemary scrub vegetation to the road as indicated by the presence of tire tracks. Macroplots ranged from 0.5–3 m in width, from 4–12 m in length, and varied in area from 6–12 m^2. Rosemary scrub vegetation bordering roadside macroplots varied from 2 to 39 y since fire. Within each macroplot, 24 circular plots (50 cm diameter) were randomly established: 12 near Florida rosemary ($\leq$ 1 m away from the edge of Florida rosemary scrub) and 12 far from Florida rosemary (1–3 m away), if possible. When a roadside macroplot was $\leq$ 1 m wide, all plots were located near Florida rosemary. Overall, we established 240 plots near rosemary and 144 far from rosemary. In Feb. and Mar. 2003, we checked each plot for the presence of *Paronychia* and counted all *Paronychia* plants present.

STATISTICAL ANALYSES

We used Kruskal-Wallis tests to evaluate the effect of time-since-fire on the number and size of gaps in rosemary scrub sites. We used a one-way ANOVA to analyze the relationship between the percentage of gaps occupied by *Paronychia* and time-since-fire. The percentage of gaps occupied by *Paronychia* across rosemary scrub sites met the assumptions of normality and homogeneity of variances.

We evaluated logistic regression models of *Paronychia* occurrence in rosemary scrub with time-since-fire (as a continuous variable) and microhabitat (small gap, large gap center or large gap edge). For presence of plants in roadsides, we evaluated logistic regression models with distance from vegetation (near or far), time-since-fire (as a continuous variable) and roadside aspect (North, South, East, or West). We included site as a random factor to account for pseudoreplication due to multiple plots within rosemary scrub patches and within roadsides (Crawley, 2007). We used the Akaike Information Criterion corrected for small sample size (AIC_c) to determine the relative support for each model (Burnham and Anderson, 2002). Models were ranked based on their weights. The Akaike weights (w_i) give an estimate of the differences in relative information among the models (Burnham and Anderson, 2002). We analyzed logistic regression models of the odds of presence/absence of *Paronychia* as the dependent variable. Each model evaluated a set of contrasts for the categorical variables using a reference. Small gaps were the reference for the model of *Paronychia* in rosemary scrub. North aspect was the reference for the model of *Paronychia* in roadsides. To evaluate the alternative models, we used R (CRAN 2006, R Development Core Team).

We used linear regression to analyze the relationship between time-since-fire and *Paronychia* density in rosemary scrub patches. We calculated *Paronychi*a density per m^2 for each gap and then calculated the mean gap density for each rosemary scrub patch. Mean densities were log transformed to meet the assumptions of the analysis. Time-since-fire was considered as a continuous variable.

Considering that microhabitat can affect the occurrence of *Paronychia,* we also wanted to determine if there were differences in density among microhabitats with *Paronychia* present. Thus, for rosemary scrub and roadsides, only plots with *Paronychia* were included in the analysis (n = 49, 32, and 78 for small gaps, large gap edges and large gap centers in rosemary scrub, respectively; n = 145 and 81 for near and far from rosemary in roadsides,

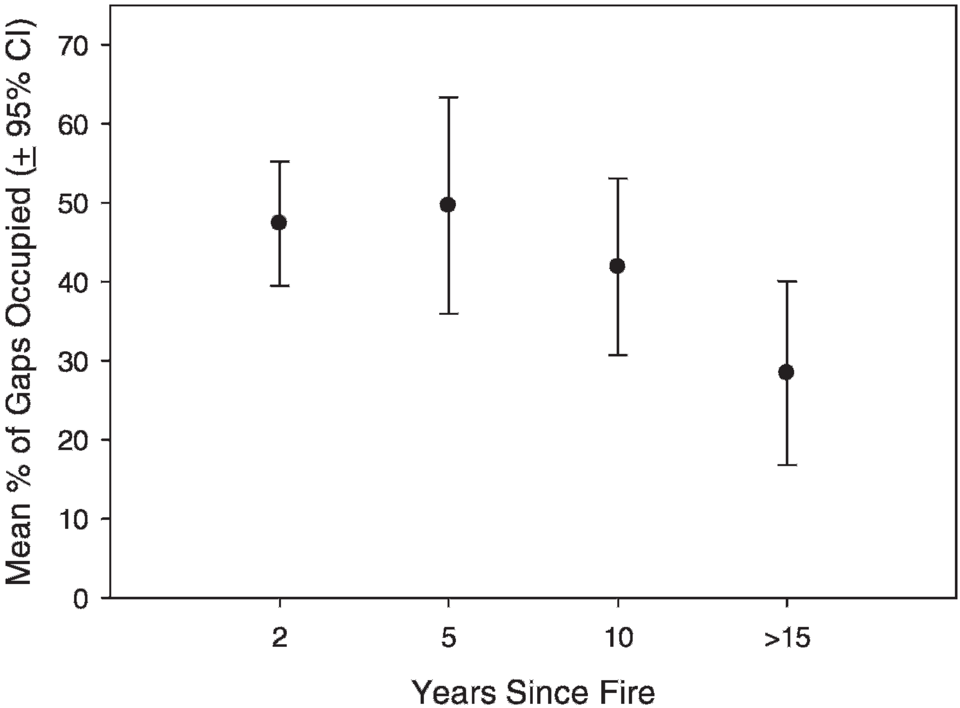

FIG. 1.—Mean percentage of rosemary scrub gaps occupied by *Paronychia* with time-since-fire (F = 2.83, df = 3,12, P = 0.083). Error bars represent 95% confidence intervals

respectively; n = 61, 57, 72, and 36, for North, South, East and West roadside aspects, respectively). Densities of *Paronychia* (per m^2) in rosemary scrub and roadsides could not be transformed to normality, so we used Kruskal-Wallis tests. Significant differences were determined using Bonferroni adjusted significance values (Sokal and Rohlf, 1995).

We used a Kruskal-Wallis test to assess the relationship between habitat (rosemary scrub vs. roadside) and *Paronychia* density. For this analysis, we included plots with and without *Paronychia* (n = 384, 134, 144, 144, and 138 for roadsides and sites 2, 5, 10 and >15 y since fire, respectively). Significant differences were determined using Bonferroni adjusted significance values (Sokal and Rohlf, 1995). All statistical analyses other than the logistic regressions were conducted in SPSS version 11.5 (SPSS, 2000).

RESULTS

The number of rosemary scrub gaps did not vary significantly with time-since-fire (Kruskal-Wallis $\chi^2 = 3.83$, df = 3, P = 0.280), but the size of rosemary scrub gaps tended to increase with time-since-fire (Kruskal-Wallis $\chi^2 = 6.27$, df = 3, P = 0.099). The percentage of rosemary scrub gaps occupied by *Paronychia* tended to decrease with time-since-fire, but the trend was only marginally significant (F = 2.83, df = 3,12, P = 0.083; Fig. 1). Gap occupancy was highest 2 y (mean ± SE = 47.4% ± 3.9%) and 5 y postfire (mean ± SE = 49.7% ± 6.9%) and lowest > 15 y postfire (mean ± SE = 28.5% ± 5.8%).

TABLE 2.—AIC_c results of logistic regression models of odds of presence/absence of *Paronychia* in plots in rosemary scrub patches as the dependent variable. MH = microhabitat; TSF = time-since-fire; B = rosemary scrub patch as a random effect; K = number of parameters in the model; −2 log likelihood = test parameter from the logistic regression model; AIC_c = corrected Akaike Information Criterion; Δ_i = difference between AIC_c and AIC_{min}, the minimum AIC_c of all models; w_i = Akaike weight indicating the degree of support for each model. n = 560 for all models

Model	K	−2 log *likelihood*	AIC_c	Δ_i	w_i
MH × TSF + B	7	599.1	585.2	0	0.907
MH + TSF + B	5	599.6	589.7	4.6	0.092
MH + B	4	608.0	600.0	14.9	0.0005
TSF + B	3	630.5	624.5	39.4	<0.001

There was a significant association between the presence of *Paronychia* in rosemary scrub and time-since-fire, microhabitat and their interaction (Tables 2 and 3). Overall, the percentage of plots occupied by *Paronychia* changed with time-since-fire (40.3%, 38.9%, 22.9% and 11.6% for 2, 5, 10 and >15 y since fire, respectively); however, this pattern varied among microhabitats (Fig. 2). The variation in plot occupancy with time-since-fire in small gaps was similar to large gap edges, but different from large gap centers (Table 3). Plot occupancy was highest in large gap centers in all sites except those > 15 y since fire, in which small gaps had the highest plot occupancy (Fig. 2).

In rosemary scrub, *Paronychia* density in gaps decreased with time-since-fire ($R^2 = 0.618$, $P < 0.001$; Fig. 3). For plots occupied by *Paronychia*, density (mean # of individuals per m^2 ± SE) differed among small gaps (8.4 ± 1.2; n = 49), large gap edges (17.2 ± 3.7; n = 32) and large gap centers (18.5 ± 2.4; n = 78) (Kruskal-Wallis $\chi^2 = 17.07$, df = 2, $P < 0.001$).

Presence of *Paronychia* in roadsides was best explained by a model including roadside aspect, distance from rosemary, time-since-fire and their interactions (Tables 4 and 5). Plot occupancy in roadsides with North aspects was similar to that in East and West aspects, but was significantly different from the South aspects (Table 5). Overall, there is weak evidence for an effect of distance from rosemary scrub on plot occupancy (Table 5). The effect of distance from rosemary scrub on plot occupancy varied among roadside aspects (Fig. 4). Plot occupancy was similar near and far from rosemary for the North, East and West aspects, but far from rosemary in the South aspect had lower plot occupancy (8.3%) than near to rosemary (68.5%). There was a significant interaction effect of time-since-fire and distance from rosemary scrub on *Paronychia* plot occupancy (Table 5). For plots near rosemary scrub, plot occupancy increased with time-since-fire, while for plots far from rosemary scrub, plot

TABLE 3.—Coefficients of the best logistic regression model of the odds of presence/absence of *Paronychia* in rosemary scrub patches as the dependent variable. TSF = time-since-fire. The reference model is small gap. n = 560. Random effect variance = 0.30147

Fixed effect	Estimate	SE	Z value	Pr(>|z|)
(Intercept)	−0.77	0.32	−2.43	0.02
Large gap edge	−0.08	0.40	−0.20	0.84
Large gap center	1.35	0.35	3.85	0.0001
TSF	−0.03	0.02	−1.45	0.15
Large gap edge * TSF	−0.07	0.04	−1.54	0.12
Large gap center * TSF	−0.05	0.03	−1.91	0.06

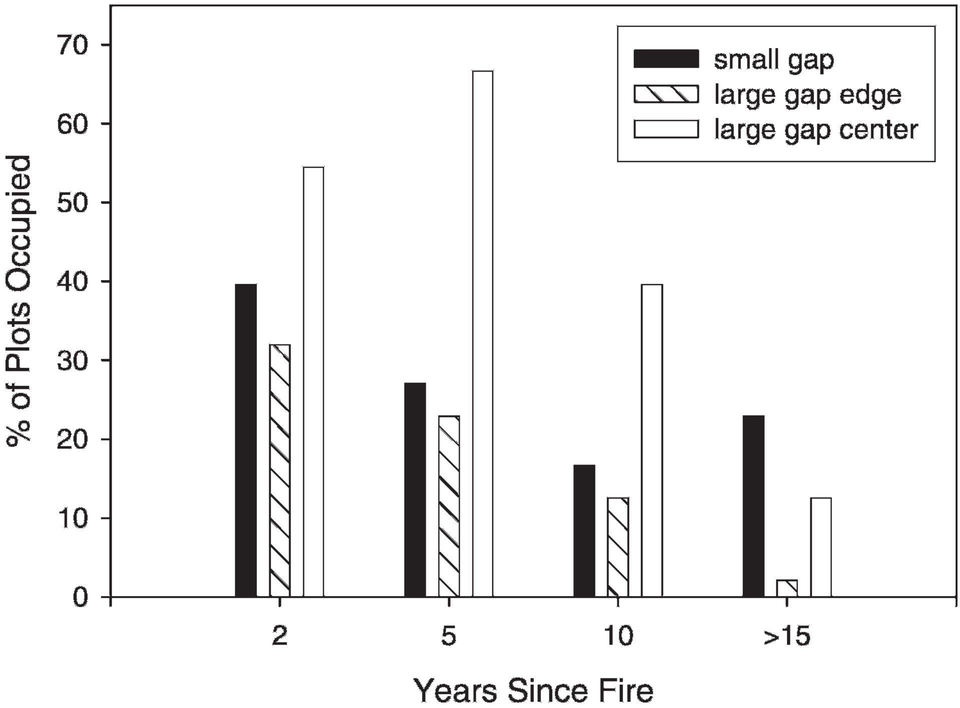

FIG. 2.—Percent of rosemary scrub plots occupied by *Paronychia* in relation to time-since-fire (2, 5, 10 and >15 y since fire; n = 134, 144, 144, and 138, respectively) and microhabitat (small gaps, large gap edges and large gap centers; n = 186, 189 and 185, respectively)

occupancy decreased with time-since-fire. Overall, 53.1% of roadside plots were occupied by *Paronychia*, which is greater than plot occupancy in rosemary scrub patches at any time-since-fire class.

Within roadsides, *Paronychia* density tended to differ with roadside aspect, though the trend was only marginally significant (Kruskal-Wallis $\chi^2 = 6.47$, df = 3, P = 0.091). *Paronychia* density (mean # of individuals per $m^2 \pm$ SE) was highest in roadsides with an East aspect (23.8 ± 2.3; n = 72) and lowest in roadsides with a West aspect (16.4 ± 3.4; n = 36). *Paronychia* density increased significantly with distance from rosemary shrubs (Kruskal-Wallis $\chi^2 = 8.78$, df = 1, P = 0.003). Mean density (± SE) was 17.7 ± 1.5 near rosemary (n = 145) and 28.3 ± 3.2 far from rosemary (n = 81). *Paronychia* density was higher in roadsides than in rosemary scrub sites regardless of time-since-fire of rosemary scrub sites (Kruskal-Wallis $\chi^2 = 135.83$, df = 4, P < 0.001; Fig. 5).

DISCUSSION

In rosemary scrub, *Paronychia* occurrence and density decreased with time-since-fire, and in both rosemary scrub and roadsides, *Paronychia* occurrence and density were higher in microhabitats associated with open space (*i.e.*, large gap centers and far from rosemary scrub). Thus, patterns of *Paronychia* occurrence and density are similar to herbaceous

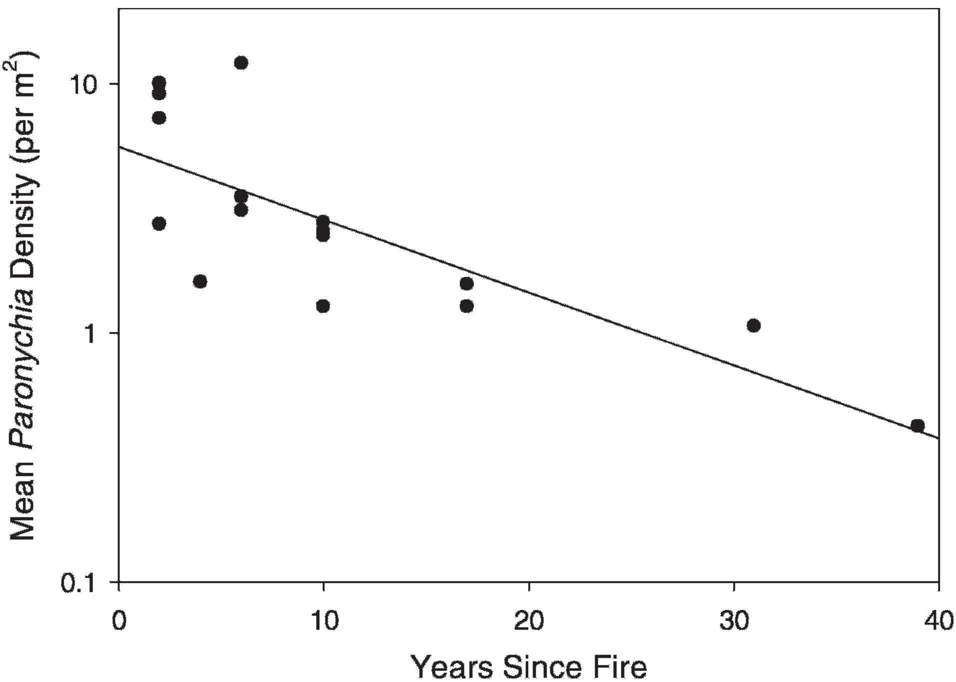

FIG. 3.—Relationship between time-since-fire and mean density of *Paronychia* in rosemary scrub sites ($R^2 = 0.638$, $P < 0.001$, log mean *Paronychia* density (m^2) = 0.731 − 0.029 * y since fire). Each point represents the mean of gap densities for one rosemary scrub site. The number of gaps sampled ranges from 5–8 per rosemary scrub site

species in other pyrogenic habitats, where fire removes litter, decreases shrub cover and creates open space. Although *Paronychia* density was higher in roadsides than in rosemary scrub, and roadsides may act as refugia among rosemary scrub patches, roadsides may alter demography (Menges *et al.*, 2006; Quintana-Ascencio *et al.*, 2007) or evolution (Schlaepfer *et al.*, 2002), providing inadequate habitat over the long-term.

In our study, *Paronychia* gap occupancy in rosemary scrub declined with time-since-fire, tending to be lower in long unburned sites. In contrast, Menges *et al.* (2008) found no effect of time-since-fire on *Paronychia* gap occupancy. We sampled 2159 gaps, every gap in the 16 rosemary scrub patches studied, whereas Menges *et al.* (2008) sampled 805 gaps, a subsample of gaps in 28 rosemary scrub patches. The apparent discrepancy between the two studies may reflect spatial variation in *Paronychia* gap occupancy within rosemary scrub patches or the ability of our larger data set to detect patterns not evident in the earlier study.

Within rosemary scrub gaps, *Paronychia* occurrence declined with time-since-fire. *Paronychia* requires open space, which is available in recently burned rosemary scrub. Ground lichens take 10–12 y to recover to preburn levels (Johnson and Abrahamson, 1990) and approach 100% cover in long unburned areas. Plant litter accumulates over time, which leads to a decrease in the amount of open space. Changes in plant and litter cover cause the quality of gap habitats to decrease over time, which could contribute to the decline in *Paronychia* occupancy with time-since-fire.

TABLE 4.—AIC_c results of logistic regression models of odds of presence/absence of *Paronychia* in roadside plots as the dependent variable. D = distance from rosemary; A = aspect; TSF = time-since-fire; R = roadside as a random effect. n = 384 for all models. Column headings are the same as in Table 2

Model	K	−2 log *likelihood*	AIC_c	Δ_i	w_i
D × A × TSF + R	17	450.3	452.0	0	0.999
D + A + TSF + R	7	472.8	473.1	21.1	<0.001
TSF + R	3	488.9	489.0	36.9	<0.001
A + R	6	507.0	507.3	55.2	<0.001
D + R	4	523.7	523.8	71.8	<0.001

As time-since-fire increased, density of *Paronychia* within rosemary scrub gaps also decreased. Similarly, Menges and Kohfeldt (1995) found that abundance of *Paronychia* significantly decreased with time-since-fire in rosemary scrub sites, and Johnson and Abrahamson (1990) found that *Paronychia* abundance was greater 2 y after fire than prefire. Fire has comparable effects on other species in fire-adapted habitats. For example, densities of annual and perennial herbs increased after fire in Mediterranean chaparral (Tyler, 1995), and densities of the perennial herb *Schwalbea americana* increased after fire in longleaf pine forests (Kirkman *et al.*, 1998). In Florida, densities of the endemic vine *Bonamia grandifloria* were greater in a burned scrub site compared to adjacent unburned habitat (Hartnett and Richardson, 1989), and mortality of the rare herb *Eryngium cuneifolium* was positively associated with time-since-fire (Menges and Kimmich, 1996; Menges and Quintana-Ascencio, 2004). Hawkes and Menges (1996) found no relationship between time-since-fire and density of *Paronychia*, but density of *Paronychia* was measured in randomly located plots across the upland landscape, including through the shrub matrix, so their measurements do not adequately represent density of *Paronychia* in gaps.

TABLE 5.—Coefficients of the best logistic regression model of the odds of presence/absence of *Paronychia* in roadside plots as the dependent variable. A = aspect; D = distance from rosemary; TSF = time-since-fire. The reference model is North aspect. n = 384. Random effect variance = 0.31396

Fixed effect	Estimate	SE	Z value	Pr(>|z|)
(Intercept)	−1.10	0.78	−1.41	0.16
A (South)	2.04	0.95	2.15	0.03
A (East)	18.46	9.70	1.90	0.06
A (West)	1.08	1.09	0.99	0.32
D	1.37	0.76	1.81	0.07
TSF	0.09	0.04	2.43	0.02
A(South) D	−3.27	1.21	−2.70	0.01
A(East) D	−7.16	5.24	−1.37	0.17
A(West) D	−1.48	0.85	−1.74	0.08
A(South) TSF	−0.09	0.06	−1.59	0.11
A(East) TSF	−2.05	1.12	−1.82	0.07
A(West) TSF	−0.08	0.06	−1.44	0.15
D * TSF	−0.06	0.03	−2.26	0.02
A(South) D * TSF	0.14	0.07	2.07	0.04
A(East) D * TSF	0.78	0.60	1.29	0.20
A(West) D * TSF	0.04	0.04	1.00	0.32

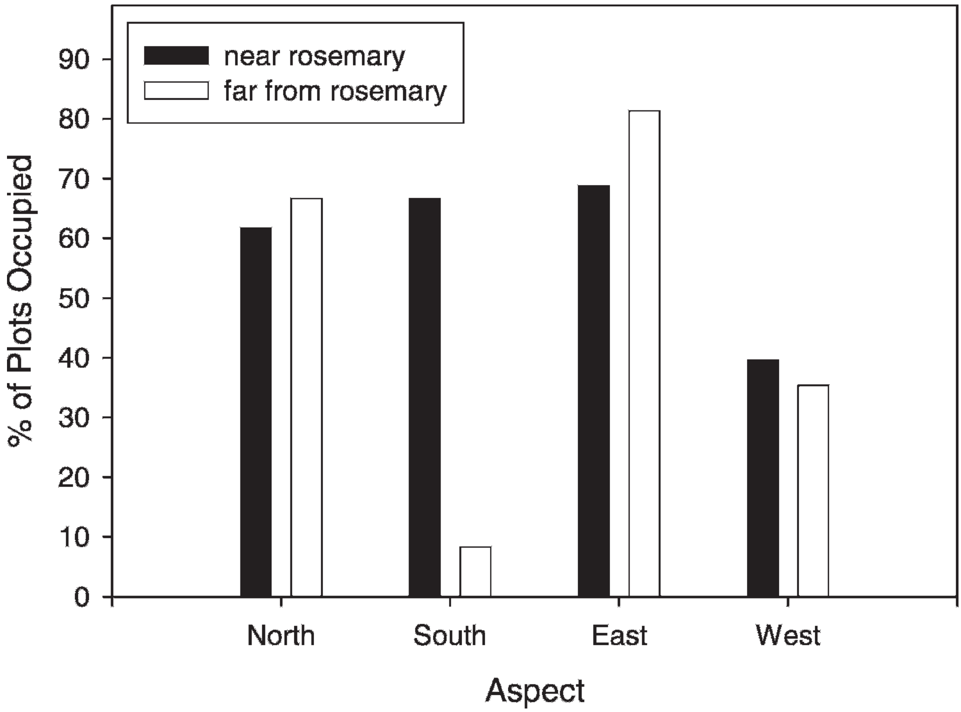

FIG. 4.—Percent of roadside plots occupied by *Paronychia* in relation to aspect (N, S, E, W; n = 96 for all aspects) and distance to rosemary individuals (near (<1 m away) or far (>1 m away); n = 240 and 144, respectively)

Within rosemary scrub gaps, the occurrence of *Paronychia* differed among microhabitats defined by gap size and location within the gap. Up to 10 y postfire, *Paronychia* was more likely to be found in the centers of large gaps, indicating *Paronychia*'s preference for bare sand microsites. Surprisingly, however, greater than 15 y postfire, *Paronychia* was more likely to be found in small gaps. Species richness of gap specialists increases as gap area increases (Menges *et al.*, 2008), suggesting that there are more species competing for resources in large gaps than in small gaps. Among gap specialists, *Paronychia* may be a weak competitor, but better able to recruit and persist in the limited open space in small gaps.

Regardless of time-since-fire, *Paronychia* occupancy was lower in the edges of large gaps than in either the centers of large gaps or small gaps (Fig. 2). In recently burned rosemary scrub, gap boundaries are defined by resprouting species such as oaks, ericads and palmettos because rosemary is killed by fire (Johnson and Abrahamson, 1990). Rosemary takes 10–12 y to recover to its preburn cover (Johnson and Abrahamson, 1990), so in longer unburned rosemary scrub, gap boundaries are more often defined by rosemary. Thus, our results suggest that shrubby hardwoods and palmettos as well as rosemary may limit *Paronychia* colonization. Other scrub endemics are similarly affected by shrubs. For example, the majority of *Hypericum cumulicola* individuals, another rosemary gap specialist, occur greater than 0.5 m away from rosemary and oak shrubs (Quintana-Ascencio and Morales-

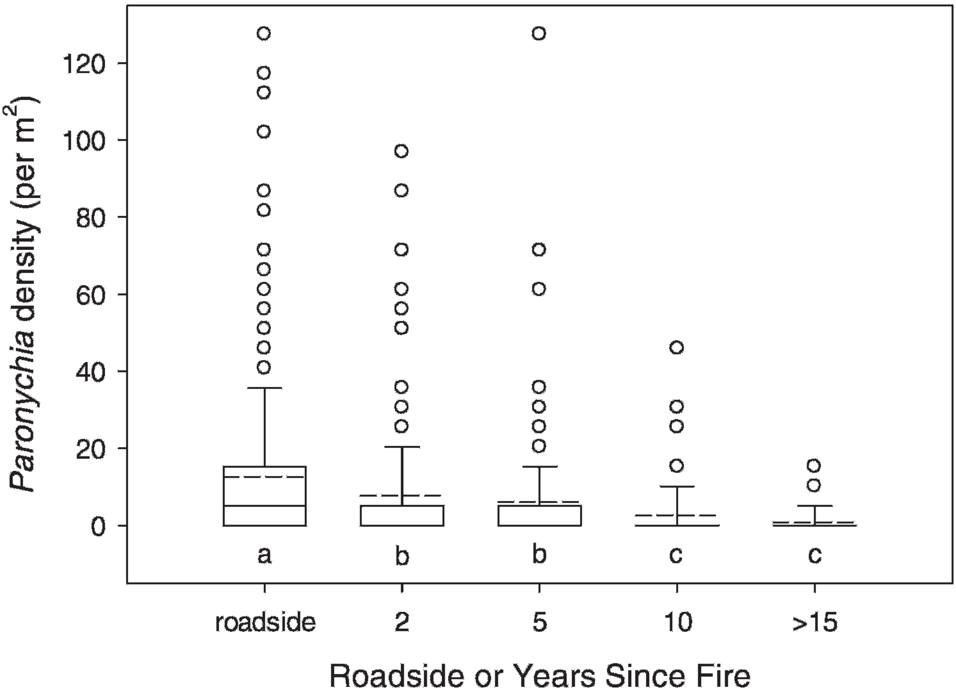

FIG. 5.—*Paronychia* density in rosemary scrub and roadside plots ($\chi^2 = 133.03$, df = 4, P < 0.001). The lower and upper bars of the boxplot represent the 25th and 75th percentiles, respectively; the solid middle bar represents the median; the dashed bar represents the mean. The lower and upper ''whiskers'' show the largest and smallest values that are not outliers. The circles are outliers (1.5 box lengths from 25th and 75th percentiles). Different letters represent significantly different values at α = 0.05 (determined with Kruskall-Wallis pairwise tests with Bonferroni adjustments). For roadsides, n = 96, and for rosemary scrub, n = 134, 144, 144, 138 for 2, 5, 10 and > 15 y since fire, respectively

Hernández, 1997), and *Eryngium cuneifolium* survival increased with distance from shrubs, and especially with distance from Florida rosemary shrubs (Menges and Kimmich, 1996).

Several factors may contribute to the decrease in *Paronychia* occupancy of large gap edges with time-since-fire (Fig. 2). First, litter depth is greater near gap edges in rosemary scrub (J. Schafer, pers. obs.), and litter depth has been shown to affect seedling recruitment in a fire-prone Mediterranean shrubland (Lloret, 1998). Second, density of rosemary roots is greater directly under rosemary individuals than 2 m away (Hunter and Menges, 2002; Hewitt and Menges, 2008). Petrů and Menges (2003) experimentally created complete (aboveground and belowground) gaps in rosemary scrub, and these complete gaps had higher colonization and seedling numbers than natural gaps, possibly due to decreased belowground competition. Finally, rosemary litter leachates have allelopathic effects on several herbaceous scrub species, including *Paronychia* (Hunter and Menges, 2002). Since cover of rosemary increases with time, rosemary litter also increases with time. Thus, the allelopathic effects of rosemary concomitant with increased litter depth and root density may contribute to the decline in *Paronychia* occupancy of large gap edges as time-since-fire increases.

Paronychia density was also influenced by gap size and location within a gap. *Paronychia* density was greatest in the centers of large gaps, which are the areas with the most open space and furthest from rosemary and shrub species. *Paronychia* density was intermediate in the edges of large gaps. Though these areas are near larger shrub species, they are also connected to a larger open area, unlike small gaps, which had the lowest density of *Paronychia.* Previous work in rosemary scrub has found that densities of both *Paronychia* and *Polygonella basiramia,* another gap specialist, increase with open space (Hawkes and Menges, 1995, 1996). Comparably, in old field habitats, seedling emergence and survival are greater in bare ground than in vegetated areas (Gross and Werner, 1982), and abundance of *Silene douglasii* var. *oraria* (Carophyllaceae), a grassland endemic, decreases with increasing vegetation height and cover, suggesting that competition may play a role in affecting its density (Kephart and Paladino, 1997). The centers of large gaps provide space for seedling recruitment and escape from shrub species, leading to greater densities of *Paronychia.*

Within roadside macroplots, the occurrence and density of *Paronychia* were influenced by distance from rosemary scrub. *Paronychia* occurrence near or far from rosemary scrub was not consistent among roads with different aspects, but across all roadsides, *Paronychia* density was greater further from the rosemary scrub edge. Although roadsides experience more vehicle disturbance further from rosemary scrub, allelopathic effects of rosemary (Hunter and Menges, 2002), above- and belowground competition for resources, and plant litter accumulation are greater near rosemary.

Roadside aspect also significantly affected *Paronychia* occupancy, but had minimal impact on density. Differences in *Paronychia* occurrence may be related to variation in sun intensity and soil temperature. In oak-chestnut forest patches, South-facing edges had the highest light levels, temperature, and the lowest litter moisture, while North-facing edges had low light levels and temperature, and high litter moisture (Matlack, 1993). Along roads through pastureland and forest in Germany, soil temperature was highest in West-facing roadsides and road shoulders (Ellenberg *et al.*, 1981; as cited in Forman *et al.*, 2003). We did not measure light levels, soil temperature or soil moisture in our study, but scrub roadsides with North, East and West aspects are shaded by vegetation at different times during the day. Although roadsides with a South aspect have sun present throughout the day, they had intermediate *Paronychia* occupancy and density.

Time-since-fire of the rosemary scrub vegetation bordering roads also contributed to variation in *Paronychia* occupancy of roadside habitats. Sand movement by wind can determine patterns of sand erosion and accretion, and vegetation along a roadside can protect the soil surface from wind erosion and act as a windbreak (Forman *et al.*, 2003). In rosemary scrub, the height and density of vegetation bordering roads increases with time-since-fire, which may lead to sand accumulation near rosemary scrub vegetation. Percent germination of *Paronychia* seeds has been found to decrease with burial depth (Petrů and Menges, 2004). Furthermore, taller and denser vegetation may cause increased shading of roadsides and increased competition. Nonetheless, *Paronychia* occurrence increased near rosemary scrub with time-since-fire, suggesting that the protective effects of vegetation outweigh negative interactions in roadsides.

Both *Paronychia* occupancy and density tended to be greater in roadsides than in rosemary scrub. The scrub endemic *Hypericum cumulicola* showed more variable temporal and spatial density in roadsides than in scrub, with some years and some roadsides having much higher densities than nearby scrub (Quintana-Ascencio *et al.*, 2007). Differences in microclimate and wind (Forman *et al.*, 2003) between roads and rosemary scrub habitats may explain differences in the density of *Paronychia.* First, during dry months, roadsides have higher soil moisture than rosemary scrub (Quintana-Ascencio *et al.*, pers. obs.). Thus, roads have greater water availability when water is most limiting. Second, sand movement is more variable along roads than in scrub gaps. Although sand accretion, which inhibits germination of *Paronychia*, is evident over short time intervals in roads, over longer intervals, sand erosion is greater (Petrů and Menges, 2004). The erosion of sand along roads may contribute to higher germination, and thus, higher densities of *Paronychia* in roadsides.

Roads may serve as connections between rosemary scrub patches and provide an important seed source for colonization of recently burned areas, but roadsides cannot replace rosemary scrub habitats. The scrub endemic *Dicerandra frutescens* had positive growth rates in oak-hickory scrub and negative growth rates in roadsides (Menges *et al.*, 2006), indicating that roadsides are not as stable as natural habitats. Sand roads and firelanes may provide refugia for *Paronychia* in fire suppressed habitats, but roads may act as an evolutionary trap (Schlaepfer *et al.*, 2002), providing open habitat that is of lower quality than open habitat in rosemary scrub. Effective fire management is preferable to the proliferation of roads for many reasons, including the danger of roads as conduits for exotic species in upland Florida ecosystems (Gordon *et al.*, 2005) and the possibility that environmental conditions of roads can alter extinction risks of threatened species (Quintana-Ascencio *et al.*, 2007).

This study did not investigate variation in the soil seed bank of *Paronychia*, though this could affect *Paronychia* occurrence and density because *Paronychia* recruits from seed after fire (Menges and Kohfeldt, 1995). *Paronychia* is one of the most abundant species in the seed bank of rosemary scrub (E.S. Menges and N. Kohfeldt, pers. obs.; J. Navarra, pers. comm.), and *Paronychia* recruits in areas where it was not present prefire (Johnson and Abrahamson, 1984). *Paronychia* seeds are primarily dispersed by gravity, but ants may move *Paronychia* seeds over short distances (L. Sullivan, pers. comm.), and wind and water may also be secondary dispersal agents. Postfire recruitment from seed dispersing from outside a burned area may occur on the edges of rosemary scrub patches, but it is unlikely that *Paronychia* seeds are dispersed over long distances. It is most likely that postfire recruitment occurs from a persistent belowground seed bank. *Paronychia* seeds have been found throughout rosemary scrub patches, both near and far from shrubs, but seeds are rare in disturbed scrub where introduced grasses are replacing scrub vegetation (J. Navarra, pers. comm.).

Paronychia has been characterized as both an annual (Christman and Judd, 1990) and a short-lived perennial (Anderson, 1991; Menges and Kohfeldt, 1995); many *Paronychia* individuals in rosemary scrub live for more than a year and some live for more than 2 y (J. Schafer, pers. obs.) In chaparral and sage scrub, many seeding herbaceous perennials have peak recruitment in the second and fifth years after fire (Keeley *et al.*, 2006). Annuals in these ecosystems exhibited a variety of postfire densities, and many species had the highest densities in the first 2 y after fire and remained present during the following years (Keeley *et al.*, 2006). Thus, patterns of *Paronychia* density with time-since-fire are comparable to densities of both perennials and annuals in other fire prone shrublands.

Patterns of *Paronychia* occurrence and density across gradients of time-since-fire and openness and among habitats suggest management strategies to protect this species. Both fire and open space are beneficial to *Paronychia* populations. Since fire and microhabitat quality (*i.e.*, open space) are not independent of one another, managing one component of rosemary scrub habitats will affect the other. The recommended fire return interval for rosemary scrub is 15–30 y (Menges, 2007), which should allow postfire recovery and maintain populations of *Paronychia chartacea* ssp. *chartacea*. Although roadsides supported the highest densities of *Paronychia*, individuals in roadsides appear to be shorter-lived than individuals in rosemary scrub (J. Schafer, pers. obs.), suggesting that roadsides may not provide adequate habitat for *Paronychia* over the long term.

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