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# Inferring Metapopulation Dynamics from Patch-Level Incidence of Florida Scrub Plants

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**Abstract:** *Spatial structure and dynamics of multiple populations may explain species distribution patterns in patchy communities with heterogeneous disturbance regimes, especially when species have poor dispersal. The endemic-rich Florida (U.S.A.) rosemary scrub occupies about 4% of the west portion of Archbold Biological Station and occurs scattered within a matrix of less xeric vegetation. Longer fire-return times and higher frequency of open patches in rosemary scrub provide favorable habitat for many plant species. Occupancy of 123 species of vascular plants and ground lichens in 89 patches was determined by repeated site surveys. About two-thirds of the species occurring at more than 14 patches had a significant logistic regression of presence on time-since-fire, patch size, patch isolation, or their interactions. Species with presence related to the interaction between patch isolation and patch size were primarily herbs and small shrubs specializing in rosemary scrub. These results suggest the importance of spatial characteristics of the landscape for population turnover of these species. An incidence-based metapopulation model was used to predict extinction and colonization probabilities of those species with presence in rosemary scrub patches related to the studied spatial variables. This is the first attempt to apply incidence-based metapopulation models to plants. The results showed stronger effects of patch size and patch isolation on extinction probabilities of herbs than on those of woody species. Because of their effect on spatial heterogeneity and habitat availability, fire suppression and habitat destruction may decrease persistence probabilities for these rosemary scrub specialists, many of which are endangered species.*

Inferencia de dinámica de metapoblaciones a partir de la ocurrencia de especies de plantas en parches de matorral en Florida

**Resumen:** *La dinámica de metapoblaciones puede explicar la distribución de especies en comunidades que ocurren como parches y con disturbio impredecible, especialmente cuando las especies tienen dispersión limitada. El matorral dominado por *Ceratiola ericoides* es rico en especies endémicas de Florida, representa 4% de la porción oeste de la Estación Biológica Archbold y se distribuye de forma discontinua dentro de una matriz de vegetación menos xérica. Los ciclos de quema más prolongados y la mayor frecuencia de áreas abiertas entre los arbustos de éste matorral proveen hábitats para muchas especies de plantas. La presencia de 123 especies de plantas vasculares y líquenes se determinó durante muestreos repetidos. Dos tercios de las especies presentes en más de 14 parches mostraron una relación logística entre su presencia en la comunidad y el tiempo desde la última quema, el tamaño del parche, el aislamiento del parche o sus interacciones. Las especies con presencia asociada a la interacción entre el tamaño del parche y su aislamiento fueron principalmente hierbas y arbustos pequeños que ocurren casi exclusivamente en el matorral de *C. ericoides*. Los resultados sugieren la importancia de las características espaciales del paisaje para la persistencia de éstas especies. Se usó un modelo de metapoblaciones basado en la incidencia de las especies para predecir las probabilidades de extinción y colonización de aquellas especies con presencia asociada a las variables espaciales estudiadas. Este es el primer intento de la aplicación de este tipo de modelos a especies de plantas. Los resultados mostraron un mayor efecto del tamaño del parche y su aislamiento entre las hierbas en comparación con las especies leñosas. Debido a su efecto sobre la distribución y la disponibilidad de hábitat, la eliminación del fuego y la destrucción de los matorrales pueden disminuir la persistencia de especies de hábitat restringido, muchas de las cuales están en peligro de extinción.*

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## Introduction

Spatial structure and dynamics of multiple populations may be essential elements for the understanding of population turnover and management of many species in heterogeneous landscapes (Gilpin 1987; Menges 1990; Burgman et al. 1993; Fahrig & Merriam 1994). Although the omission of spatially explicit variables may result in more-tractable models of population dynamics (Burgman et al. 1993; Fahrig, unpublished data), spatial detail is indispensable for ecological theory when focal species have patchy distributions, limited colonization of favorable patches, and independent population extinction throughout the landscape (Gilpin 1987; Menges 1990; Burgman et al. 1993; Hanski 1994a; Fahrig & Merriam 1994).

Metapopulation models analyze the regional persistence dynamics of groups of populations by addressing the distribution of extinction risks and rates of migration among patches (Hanski 1991; Hanski & Gilpin 1991; Hanski 1994a; Harrison 1991; Alvarez-Buylla & García-Barrios 1993; Burgman et al. 1993). A recent approach, based on generalized incidence functions and equilibrium occupancy, allows the prediction of changes in occupancy patterns of spatially defined metapopulations (Hanski 1994b). This approach uses presence-absence data to estimate biologically significant metapopulation parameters that can be compared among species (Hanski 1991, 1994a, 1994b). These metapopulation parameters describe changes in colonization and extinction rates with patch size and patch isolation. The incidence approach to metapopulation dynamics has been successfully applied to insects (Hanski 1991, 1994a, 1994b), small mammals (Hanski 1991; Peltonen & Hanski 1991), and birds (Cook & Hanski 1995), but no such analyses of plant species have been made.

We analyzed the incidence of plant species across 89 patches of a distinct community in a shrub-dominated landscape. We examined the relationships of patch area, patch isolation and recent fire history to plant-species distribution in Florida rosemary scrub. We evaluated the statistical significance of incidence patterns among individual species, and we estimated specific extinction and colonization rates using Hanski's incidence metapopulation model (1991, 1994b).

### Study Site

Our study site was Archbold Biological Station (ABS), a 2000-ha preserve located on the Lake Wales Ridge in southcentral Florida. The preserve is located in part of the major paleo-dune system of the central ridge region at 36–67 m elevation. Soils are sandy, acidic, and poor in nutrients, ranging from excessively well-drained on the ridges to very poorly drained in the depressions (Brown et al. 1990). The regional climate has hot, wet summers

and mild, dry winters; the mean daily temperature in August is 27°C and in December is 12°C, based on a 43-year period, 1952–1994 (ABS unpublished data). Mean annual rainfall is 1349 mm, with about 60% of the total falling June through September. Fire and drainage play major roles in determining vegetation structure and composition (Komarek 1974; Abrahamson et al. 1984a; Myers 1985, 1990; Menges & Kohfeldt 1995). Lightning and prescribed fires maintain a mosaic of habitats with different fire histories. We studied patch occupancy in the western section of ABS, a 1075-ha area characterized by a mosaic of scrubby flatwoods, flatwoods, and seasonal ponds with scattered patches of rosemary scrub, our focal community (Abrahamson et al. 1984a).

### The Rosemary Scrub

Florida scrub consists of shrub-dominated, sporadically burned plant communities on well-drained soils (Abrahamson et al. 1984a; Myers 1990). Among types of Florida scrub, the rosemary phase of the sand pine scrub is particularly xeric, occurring on excessively drained white sands, often in small, discrete patches (Komarek 1974; Abrahamson et al. 1984a). The shrub layer of rosemary scrub in the southern Lake Wales Ridge of southcentral Florida is characterized by nearly pure stands of even-aged Florida rosemary (*Ceratiola ericoides*), interspersed with sparse clumps of sclerophyllous oaks (*Quercus* spp.) and palmettos (*Serenoa repens* and *Sabal etonia*; Abrahamson et al. 1984a; Gibson & Menges 1994). The occurrence of natural, bare-sand fire breaks makes this community less fire-prone than other more-densely-vegetated scrubs on less-well-drained soils (Abrahamson 1984). In contrast to the flatwoods and scrubby flatwoods that constitute the matrix surrounding the rosemary scrub, this community provides open-space microhabitats for a high concentration of endemic plants (Abrahamson et al. 1984a; Christman & Judd 1990; Hawkes & Menges 1996; Menges & Kimmich 1996), many of which are killed by fire and regenerate by seeding (Johnson & Abrahamson 1990; Menges & Kohfeldt 1995).

## Methods

### Occupancy Data and Analysis

Sites were identified using available vegetation maps of ABS (Abrahamson et al. 1984b). We slightly modified the maps to combine six pairs of previously independently mapped rosemary patches because of the continuous nature of the habitat between patches. Each of the 89 rosemary scrub patches within the west section of ABS was surveyed to record all plant and ground lichen species present in the patch. Species were identified follow-

ing Thomson (1967) for lichens and Wunderlin (1982) and Kartesz (1994) for vascular plants. Four visits were made in 1988, on 27 June-13 July and 4 October-10 November, and in 1989 on 4-26 April and 7-18 August. The same sites were revisited between 26 August 1994 and 2 February, 1995 to determine incidence changes in *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella basiramia*, three endemic perennial herbs virtually restricted to rosemary scrub.

Records of fire occurrence (1968-present) and field observations of the age of individual rosemary plants (Johnson 1982) were used to determine fire history of each rosemary scrub patch. Patch size and distance among rosemary scrubs (measured using polygon centers) were calculated with geographic information system (ARC/INFO) facilities. Patch isolation ( $S$ ) was estimated with the index (Hanski & Thomas 1994)

$$S_i = - \left( \sum_j^n \exp(-\alpha d_{ij}) * A_j \right), \quad (1)$$

where  $d_{ij}$  is distance in kilometers from focal patch  $i$  to patches  $j$  to  $n$ , and  $A_j$  is patch area in hectares. We do not have data to estimate  $\alpha$ , so we used  $\alpha = 1$  because it provided better estimates for the studied incidence-based metapopulation model than larger values did.

The influence of patch size, patch isolation, time since fire, and their two-way interactions on the presence of 62 species occurring in more than 14 sites were quantified by logistic stepwise regression (Fienberg 1987; Norusis 1994). Significant limits were set at  $p < 0.05$  to enter variables and at  $p > 0.10$  to remove them. Logistic regression results were related to habitat specialization (rosemary scrub versus scrubby flatwoods), life form, and main regeneration mechanism after fire (seeders or facultative resprouters versus obligate resprouters or clonal species) based on data collected by Menges and Kohfeldt (1995). Species with the ratio of relative frequency in scrubby flatwoods ( $n = 24$ ) to relative frequency in rosemary scrub ( $n = 24$ ) lower than 0.1 were considered rosemary scrub specialists.

### Metapopulation Model

We used the incidence functions of those species with significant logistic regressions of presence on patch size, patch isolation, or their interactions with each other or with fire to infer their metapopulation dynamics. We applied a linear, two-state (presence versus absence), first-order Markov chain model developed by Hanski (1991, 1994a, 1994b). The model assumes that occupancy of each species is determined by equilibrium colonization-extinction dynamics (Hanski 1991). The stationary probability of occurrence in patch  $i$  is given by the expression (Hanski 1991, 1994a)

$$J_i = C_i / (C_i + E_i), \quad (2)$$

where  $J_i$  is species incidence in patch  $i$ ,  $C_i$  is colonization probability as a function of patch isolation, and  $E_i$  is extinction probability as a function of patch size.

Patch-size-specific probabilities of extinction ( $E_i$ ) for each species were estimated as an exponentially decreasing relationship of this variable with patch size (Gilpin & Diamond 1976, 1981; Peltonen & Hanski 1991; Hanski 1991, 1994b)

$$E_i = e / A_i^x. \quad (3)$$

Equation 3 assumes that average population size increases with patch size ( $A_i$ ) and is based on evidence from studies of other species suggesting that larger populations have lower risks of extinction than smaller ones (Terborgh & Winter 1980; Diamond 1984; Lawton 1994). Parameter  $x$  describes how fast the probability of extinction decreases with increasing patch area (Hanski 1991; Peltonen & Hanski 1991). Parameter  $e$ , the extinction probability of a patch with unitary size, determines the critical patch size with extinction probability equal to one.

Patch-specific colonization probabilities may depend on levels of spatial isolation because immigration decreases with distance. Colonization can be modeled as dependent on the number of immigrants with the expression (Hanski 1994b)

$$C_i = M_i^2 / (M_i^2 + y^2). \quad (4)$$

Equation 4 gives a sigmoidal shape and assumes that lack of interaction among immigrants reduces population establishment at low densities. The parameter  $y$  determines the rate of approach of the probability of colonization ( $C_i$ ) to unity with an increasing number of immigrants ( $M_i$ ). The last variable is related to the pattern of patch isolation with the function (Hanski 1994b)

$$M_i = \beta S_i, \quad (5)$$

where

$$S_i = \sum_j p_j \exp(-\alpha d_{ij}) A_j. \quad (6)$$

In equation 6,  $p_j$  is equal to one for occupied patches and to zero for unoccupied patches;  $\alpha$  represents a constant that sets the survival rate of migrants over distance, with higher values in less-permeable environments;  $d_{ij}$  is

the distance in kilometers of patch  $j$  from focal patch  $i$  for patches  $j$  to  $n$ ; and  $A_j$  is the migrant-source patch area in hectares. The parameter  $\beta$  in equation 5 includes the effect of the density of individuals, the rate of emigration, and the fraction of emigrants of a particular patch moving to the focal patch.

Equations 1 through 6 can be rewritten and estimates of parameters  $x$ ,  $e$ , and  $y'$  obtained for the function (Hanski 1994b)

$$J_i = 1 / (1 + (1 + (y'/S_i)^2) e/A_i^x), \quad (7)$$

where  $y' = y/\beta$  describes colonization ability; species little-affected by isolation have smaller values of this parameter (Hanski 1994b).

Equation 7 does not account for the possibility of simultaneous extinctions and colonizations (Hanski 1991, 1994a,b). The substitution of the actual probability of extinction by  $(1 - C_i)E_i$ , where  $E_i$  is the probability of extinction in the absence of migration, allows for a rescue effect. Under this assumption equation 7 becomes

$$J_i = 1 / (1 + (e' / (S_i^2 A_i^x))), \quad (8)$$

where  $e' = ey'$ . Because of the composite nature of parameter  $e'$ , independent estimation of parameters  $e$  and  $y'$  requires additional field data on changes of patch occupancy with time.

Replacing the unknown probability of incidence ( $J_i$ ) by the occupancy state (presence versus absence) of the focal patch, we obtained for each species maximum likelihood estimates of the parameters  $e'$  and  $x$  (equation 8) with the quasi-Newton method of the nonlinear regression procedure of SYSTAT (Wilkinson et al. 1992). The values of the isolation index were calculated with algorithms written in Pascal.

## Results

### Landscape and Community Attributes

Rosemary scrub occupied 38.9 ha, approximately 4% of the total area of the west section of ABS. Patch size of these scrubs ranged from 0.03 to 3.6 ha and had an approximately lognormal frequency distribution (Fig. 1a). Fire-history variation of the rosemary scrub patches (in 1989) ranged from less than 3 to more than 25 years since the last fire (Fig. 1b). Spatial distribution of the rosemary balds within ABS is not homogeneous, but is scattered in the northern portion and clustered in the southern portion (Fig. 2). No significant correlation was found among the studied independent variables (time since fire, patch isolation, and patch size).

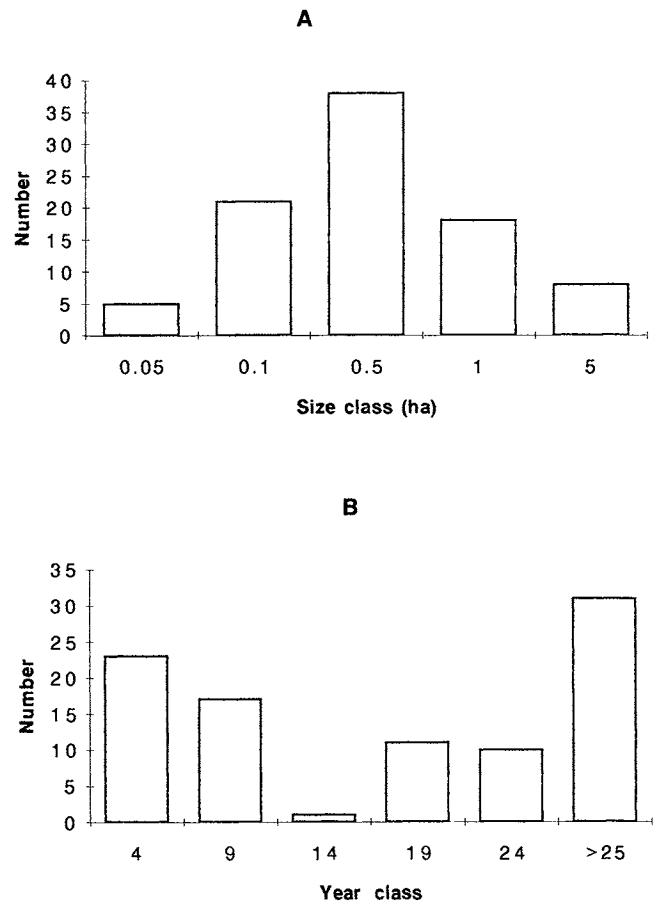


Figure 1. Frequency distribution of patch area (a) and time since last fire (years before 1989) (b) among rosemary scrub patches in the west section of Archbold Biological Station, Lake Placid, Florida.

A total of 123 species was found in the rosemary scrub patches, but only 80 species occurred in more than five patches and were included in the study (a table with the data matrix is available from the authors). Species richness by patch was positively correlated to  $\log_{10}$  of patch size and negatively related to the isolation index ( $r^2 = 0.44$ ,  $p < 0.001$ ; beta coefficients 0.57 for  $\log_{10}$  of patch size and  $-0.30$  for the isolation index), but it was not related to time since the last fire (beta = 0.04,  $T = 0.52$ ,  $p = 0.60$ ).

### Species Occupancy

Forty of 62 species occurring at more than 14 sites had significant logistic regression of presence on time since fire, patch size, the isolation index, or their interactions (Table 1). The probability of occurrence on rosemary scrub patches was positively related to time since fire in six species, half of them lichens, and negatively related to the same variable in three herbaceous species. The interactions of time since fire with patch size and/or the

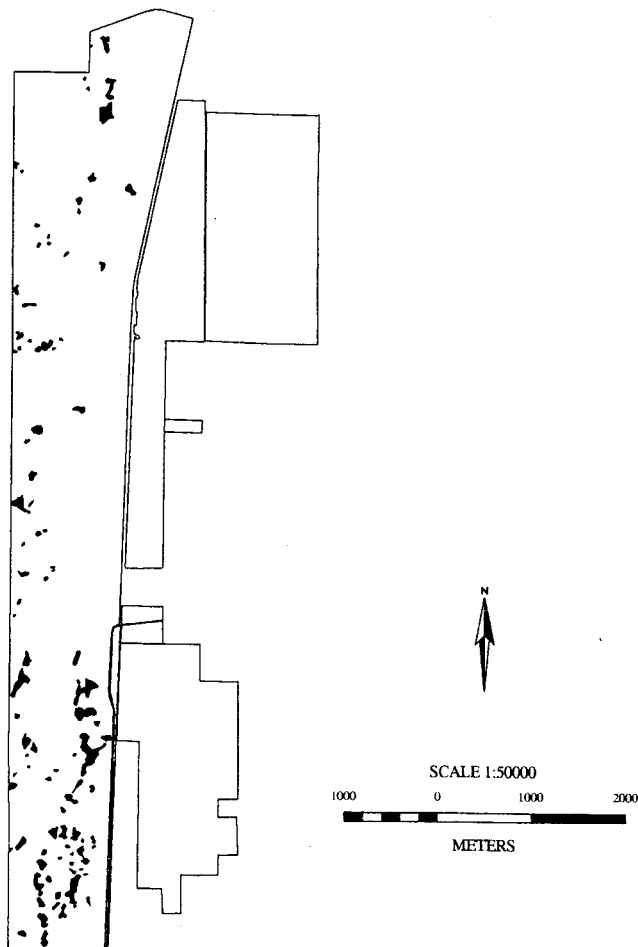


Figure 2. Map showing an outline of Archbold Biological Station. Filled areas indicate rosemary scrub patches in the study area. A few additional rosemary scrub patches in the southeastern portion of the station, not included in the study, are not shown. Based on vegetation map of Abrahamson et al. (1984b).

isolation index explained the presence of 15 other, primarily herbaceous species. Patch isolation was positively associated with the presence of the herbs *Baldwinia angustifolia*, *Galactia regularis*, and *Tradescantia roseolens* and negatively related to the occurrence of the woody species *Asimina obovata*, *Opuntia humifusa*, *Ilex opaca* var. *arenicola*, and *Pinus clausa*.

The rosemary specialists, most herbaceous plants or small shrubs, were not homogeneously distributed among these groups ( $G = 18.3$ , 4 d.f.,  $p < 0.001$ ; Table 1). Rosemary specialists represented only 18% of the species without response to the studied variables, and none of the species with presence associated with fire (9 species) or patch isolation (7). But rosemary specialists constituted 40% of the species with occurrence explained by the interaction of fire with patch size or patch isolation and 67% of the species with incidence simultaneously related to patch size and patch isolation or their interaction (Table 1).

There was no significant difference between the frequency distribution of herbaceous and woody species among the study responses ( $G = 6.24$ , 4 d.f.,  $p = 0.18$ ; Table 1), but fewer herbs and more woody species than expected did not have any significant response ( $G = 5.28$ , 1 d.f.,  $p = 0.02$ ; Table 1). The distribution of seeders and resprouters was not significantly different ( $G = 1.38$ , 4 d.f.,  $p = 0.85$ ; Table 1).

Six species largely or completely restricted to rosemary scrub had patch occupancy related both to the patch size and patch isolation or their interaction (Table 1; Fig. 3). The perennial herbs *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella robusta* are virtually restricted to open areas. The perennial herb *Liatris oblongerae* and the shrubs *Calamintha asbei* and *Bumelia tenax* are found in several microhabitats, including open sand (A. Herndon, personal communication). The other three species with incidence related to

Table 1. Number of species with presence related to several parameters of spatial structure and fire regime.<sup>a</sup>

|              | Total Species | Habitat    |               | Life form <sup>b</sup> |       | Regeneration <sup>c</sup> |          |
|--------------|---------------|------------|---------------|------------------------|-------|---------------------------|----------|
|              |               | Specialist | Nonspecialist | Herb                   | Woody | Seeder                    | Sprouter |
| S            | 7             | 0          | 7             | 4                      | 3     | 4                         | 3        |
| A + S, A × S | 9             | 6          | 3             | 6                      | 3     | 4                         | 5        |
| F × A, F × S | 15            | 6          | 9             | 9                      | 3     | 5                         | 4        |
| Fire         | 9             | 0          | 9             | 4                      | 1     | 3                         | 1        |
| None         | 22            | 4          | 18            | 8                      | 13    | 9                         | 10       |
| Total        | 62            | 16         | 46            | 31                     | 23    | 25                        | 23       |

<sup>a</sup>Only patch isolation (S); both patch size (A) and patch isolation concurrently (A + S) or their interaction (A × S); the interaction between fire and patch size or patch isolation (F × A, F × S); fire (Fire); and without significant response to the study variables (None). Species were sorted by habitat (rosemary specialists or nonspecialists), life form (herbs or woody species), and their main regeneration mechanism after fire (seeder or obligate resprouter). A complete table with the logistic regression model for each study species is available from the authors.

<sup>b</sup>Eight ground lichen species were not included.

<sup>c</sup>There is no information for regeneration after fire for 14 species.

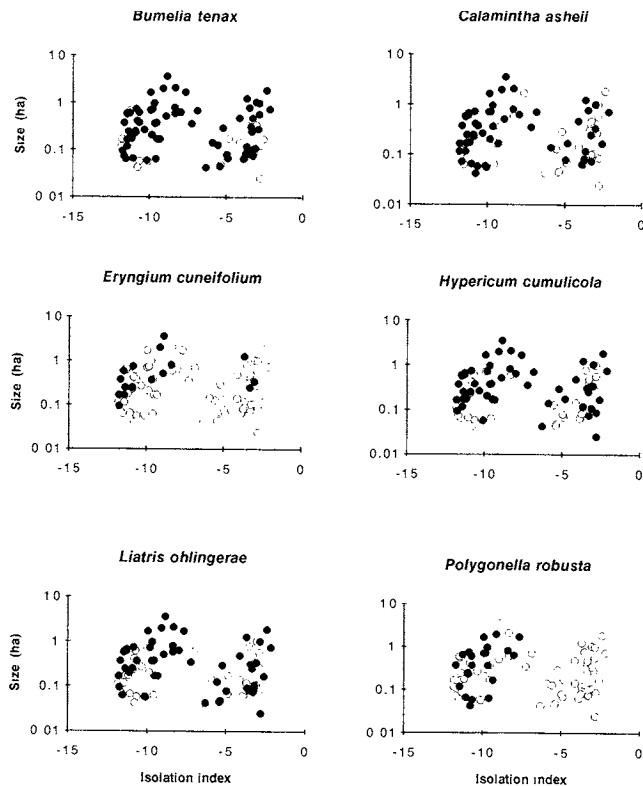


Figure 3. Patch presence (filled circles) or absence (open circles) of plant species almost or completely restricted to open areas, and with rosemary scrub occupancy related to patch size (ha) and patch isolation index or their interaction.

the interaction between patch size and patch isolation, the herbs *Asclepias pedicellata* and *Sisyrinchium solstitialis*, and the shrub *Lyonia fruticosa*, occur in both rosemary scrub and scrubby flatwoods.

No population turnover was observed among rosemary scrub patches for *Eryngium cuneifolium* and *Hypericum cumulicola* after 5 years (1989–1994). In 1994 no *Polygonella basiramia* plants were found in one long-unburned and previously occupied patch, subsequently burned in May 1989. In 1994 individuals of *P. basiramia* were present in six formerly unoccupied (aboveground) patches. Four of them had been burned within the 5 years prior to 1989. The other two had not burned for 17 and 25 years.

### Metapopulation Model

Estimated parameters of the incidence-based metapopulation models applied in this study may describe the spatial pattern of some Florida scrub plant species, particularly rosemary scrub specialists (Table 2). The range of positive values of parameter  $x$ , describing change of the probability of extinction with patch size, was 0.01 to 1.23 (equation 8 with  $\alpha = 1$ ; Table 2).

Higher  $x$  values indicate more rapidly decreasing extinction probabilities with increasing patch size. The  $x$  values were higher among shrub species than among perennial herbs (Mann-Whitney  $U$  test,  $z = -2.15$ , two-tailed  $p = 0.032$ , corrected for ties, 14 herbs, 6 shrubs; Fig. 4a; Sokal & Rohlf 1981). Nonsignificant differences in the value of this parameter were found between seeders and sprouters ( $z = -1.05$ , two-tailed  $p = 0.293$ ; corrected for ties, 13 seeders, 8 resprouters; Fig. 4b) and between rosemary specialists and species also occurring in other scrub vegetation ( $z = -1.776$ , two-tailed  $p = 0.076$ ; corrected for ties, 10 specialists, 15 nonspecialists; Fig. 4c). Negative  $x$  values for *Asimina obovata*, *Helianthemum nashii*, and *Schizachyrium niveum* suggest that these models do not describe their incidence in rosemary scrub patches. Although the values of the parameters  $e'$  and  $x$  depended on  $\alpha$  (a factor affecting the survival of migrant individuals),  $x$  was less sensitive, whereas  $e'$  had strong dependence on this factor's value (Table 2; see Hanski 1994b).

## Discussion

### Metapopulation Dynamics of Rosemary Scrub Specialists

Spatial structure and dynamics of subdivided populations may have an important role in determining the persistence of habitat specialists sporadically disturbed in heterogeneous landscapes. This study suggests that patch size and patch isolation affect the population turnover of rosemary scrub specialists.

Most of the rosemary scrub species also occurring in adjacent scrubby flatwoods and flatwoods did not have their presence in rosemary scrub related to the study variables. Some nonrosemary specialists, such as *Baldwinia angustifolia*, *Galactia regularis*, and *Tradescantia roseolens*, had a positive association of their presence in rosemary scrub with patch isolation, or, like *Asimina obovata*, *Helianthemum nashii*, and *Schizachyrium niveum*, had a negative value of  $x$ , meaning an increased probability of extinction with rosemary scrub patch size. All these species are common in more mesic habitats (Menges & Salzman 1992), and rosemary scrub may represent a secondary habitat for them. Areas with aggregated rosemary scrub or larger patches of this community may be excessively xeric for these species.

Several characteristics of the rosemary scrub may predispose some plant species to metapopulation dynamics. Many herbaceous species regenerating by seed increase in abundance when openings are created by fire. These seeders and most gap-dependent species decline between fires (Abrahamson et al. 1984a; Johnson & Abrahamson 1990; Menges & Kohfeldt 1995). For example, *Polygonella basiramia* can be found in large and small gaps between shrubs, but its density and fecundity

**Table 2.** Nonlinear regression-estimated parameters for the metapopulation model with rescue effect (equation 8).\*

| Species                          | $\alpha = 1$ |      |       | $\alpha = 3$ |      |      |
|----------------------------------|--------------|------|-------|--------------|------|------|
|                                  | ML           | x    | e'    | ML           | x    | e'   |
| Rosemary specialists             |              |      |       |              |      |      |
| <i>Eryngium cuneifolium</i>      | 38.9         | 0.66 | 18.00 | 36.5         | 0.94 | 1.24 |
| <i>Trichostema dichotomum</i>    | 50.0         | 0.01 | 11.53 | 51.7         | 0.14 | 0.51 |
| <i>Polygonella robusta</i>       | 37.8         | 0.59 | 19.65 | 45.1         | 0.70 | 1.38 |
| <i>Polanisia tenuifolia</i>      | 55.2         | 1.22 | 7.58  | 77.9         | 1.42 | 0.48 |
| <i>Calamintha asbei</i>          | 59.6         | 0.70 | 3.73  | 72.3         | 0.81 | 0.14 |
| <i>Cladonia prostrata</i>        | 53.9         | 0.81 | 2.83  | 66.3         | 0.92 | 0.10 |
| <i>Bumelia tenax</i>             | 42.7         | 0.83 | 1.32  | 48.4         | 0.89 | 0.05 |
| <i>Liatris oblongerae</i>        | 66.5         | 0.66 | 4.85  | 78.9         | 0.61 | 0.25 |
| <i>Hypericum cumulicola</i>      | 64.9         | 1.02 | 3.03  | 78.2         | 1.19 | 0.12 |
| <i>Polygonella basiramia</i>     | 35.0         | 0.62 | 1.21  | 44.7         | 0.84 | 0.03 |
| Nonspecialists                   |              |      |       |              |      |      |
| <i>Asclepias pedicellata</i>     | 52.6         | 0.64 | 12.93 | 64.3         | 0.76 | 0.97 |
| <i>Pinus elliottii var densa</i> | 62.4         | 0.27 | 14.23 | 72.4         | 0.18 | 0.74 |
| <i>Ilex opaca var arenicola</i>  | 55.2         | 0.49 | 10.40 | 70.4         | 0.47 | 0.81 |
| <i>Rhynchospora megalocarpa</i>  | 76.5         | 0.29 | 9.49  | 88.5         | 0.33 | 0.63 |
| <i>Commelina erecta</i>          | 56.5         | 0.59 | 9.21  | 73.2         | 0.78 | 0.68 |
| <i>Tillandsia recurvata</i>      | 63.6         | 0.57 | 9.24  | 79.3         | 0.56 | 0.58 |
| <i>Tradescantia roseolens</i>    | 69.8         | 0.10 | 7.70  | 79.7         | 0.12 | 0.37 |
| <i>Sisyrinchium solstitiale</i>  | 70.9         | 0.31 | 16.3  |              |      |      |
| <i>Balduina angustifolia</i>     | 81.7         | 0.28 | 7.41  | 96.0         | 0.20 | 0.41 |
| <i>Galactia regularis</i>        | 86.6         | 0.08 | 10.1  | 103.6        | 0.06 | 0.05 |
| <i>Lyonia fruticosa</i>          | 46.3         | 0.87 | 1.10  | 52.7         | 0.93 | 0.03 |
| <i>Persea humilis</i>            | 43.1         | 1.23 | 0.88  | 49.0         | 1.36 | 0.03 |
| <i>Pinus clausa</i>              | 50.6         | 0.70 | 2.21  | 57.3         | 0.79 | 0.07 |
| <i>Chapmannia floridana</i>      | 60.4         | 0.32 | 4.39  | 62.5         | 0.33 | 0.19 |
| <i>Opuntia humifusa</i>          | 22.6         | 0.75 | 0.59  | 23.3         | 0.77 | 0.02 |

\*We considered only those species with significant logistic regression, including patch size, patch isolation, or their interactions. Parameters listed are  $\alpha$ , survival index for migrant individuals; ML, value of the minimized maximum likelihood function; x, the rate of change of extinction probability with patch size; and e'. Species not included: *Asimina obovata*, *Helianthemum nashii*, and *Schizachyrium niveum* (negative x values), *Euphorbia floridana* (did not reach tolerance value), and *Quercus chapmanii* (e' = 0).

are highest in sites with the greatest area in gaps (Hawkes & Menges 1995).

Gaps are ephemeral in scrubby flatwoods and flatwoods, communities forming the matrix around rosemary scrub, limiting habitat availability for gap-specializing species (Menges & Kohfeldt 1995; Menges & Hawkes 1997). Flatwoods and scrubby flatwoods have a relatively short fire-return interval, burning every 5 to 20 years, with the dominant oaks and palmettos able to resprout vigorously after a fire (Abrahamson et al. 1984a). Bare ground cover in oak- or palmetto-dominated scrub peaks during the first year after fire (~ 30%) and decreases to low levels (~ 5%) during the following 2 years (Schmalzer & Hinkle 1992; Menges & Hawkes 1997). In contrast, rosemary scrub burns less frequently (20–60 years; Abrahamson et al. 1984a) and maintains more open space, declining from 40% cover in recently burned rosemary scrubs to about 28% cover during the first decade after fire, with large gaps remaining even in long-unburned rosemary scrubs (Hawkes & Menges 1996).

Many rosemary scrub-plant species do not survive burning, and population recovery requires the presence of buried seeds in the soil or their dispersal from nearby populations (Menges & Kohfeldt 1995). Most rosemary

scrub specialists appear primarily gravity-dispersed, without specialized dispersal mechanisms. The absence of seedlings in apparently favorable microhabitats and the aggregated distribution of individuals of *Eryngium cuneifolium*, *Calamintha asbei*, and *Hypericum cumulicola* suggest limited dispersal of these species. Post-fire distribution of *Calamintha asbei* seedlings was strongly related to pre-fire adult distribution in sand-pine scrub (Carrington 1996). Limited dispersal may also constrain colonization rates among the scattered patches of rosemary scrub.

Herbaceous plants, especially seeders, may be sensitive to local extinctions because of both short and long fire-return intervals. Species regenerating by seed may require many years between fires to build populations (Zedler et al. 1983; Malanson 1985), and short fire-return cycles may eliminate species unable to reach reproductive maturity between burns (Johnson 1982). Recruitment after fire may be followed by slow population declines due to habitat loss as dominant shrubs and ground lichens recover. Specific evidence for one rosemary scrub species supports this pattern. *Eryngium cuneifolium* requires large openings, and it has increasing mortality and decreasing growth and fecundity with time since fire (Menges & Kimmich 1996).



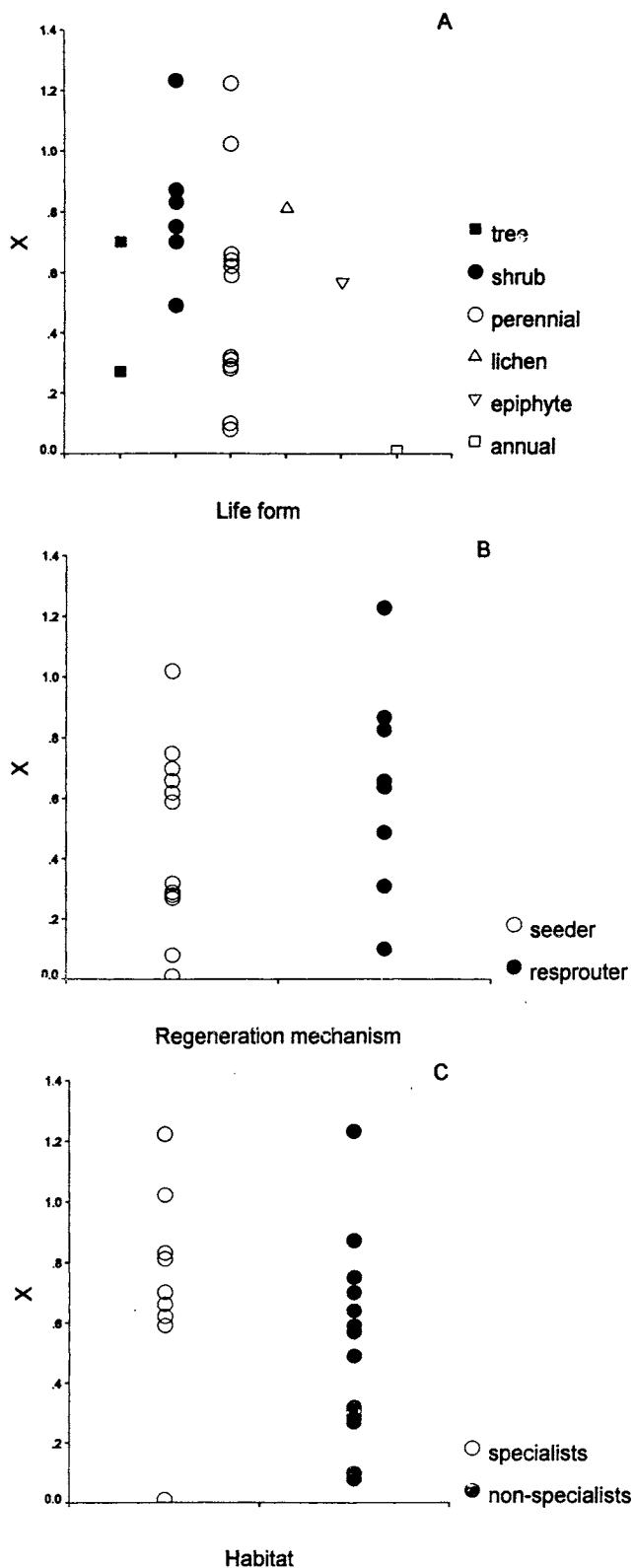


Figure 4. Plots of  $x$  ( $\alpha = 1$ ) parameter describing the rate of change of extinction probability with patch size against Florida scrub plant species sorted by life form (a), regeneration mechanism after fire (b), and habitat (c). Species modeled had rosemary scrub occu-

Although seed banks can buffer demographic fluctuations, local extinction may be frequent in species that are killed by fire and that regenerate from seed. Species presence may be ultimately determined by migration from other patches in rosemary scrub and other vegetation types dominated by seeders. The seeds of many species of the coastal sage scrub do not survive high temperatures, and recruitment after burning may depend on recently dispersed seeds (Malanson & O'Leary 1982; Keeley & Keeley 1984). The absence of *Polygonella bairamiae*, a rosemary scrub specialist, in recently burned patches and among germinants from soil seed-bank samples collected in the ABS study sites (N. Kohfeldt, unpublished data) suggests its dependence on newly dispersed seeds for post-fire colonization. In long-unburned communities, the contribution of migrants may increase in importance as seed banks are depleted. The post-burn recovery community of Florida scrub stands in which fire has long been suppressed did not include some herb species common in post-fire communities under shorter fire-return intervals (Abrahamson & Abrahamson 1996).

**Life Form and Local Extinction**

Among animals body size influences extinction risk because of its effect on geographic range, longevity, and population resistance and resilience to environmental changes (Pimm 1991; Cook & Hanski 1994; Lawton 1994). Lower extinction rates in long-lived animals suggest lower extinction rates for large-bodied species (Pimm 1991; Lawton 1994), but higher extinction rates in species with low densities and low resilience to disturbance suggest higher extinction risks for large-bodied species (Flessa et al. 1986).

For species in insular habitats, under the assumptions of the metapopulation models used in this study, the shape of the incidence function indicates the rate of change of expected population persistence with increasing population size (Cook & Hanski 1994). Analysis of birds and shrews in archipelagos showed larger  $x$  values in large-bodied species (Peltonen & Hanski 1991; Hanski 1991; Cook & Hanski 1994). A study of extinctions in remnants of chaparral in San Diego, California, also suggested longer persistence times for large-bodied rodents and birds (Soulé et al. 1988). No studies have examined these possibilities for plants.

Our incidence-based model for Florida rosemary scrub species showed higher values of  $x$  for shrubs versus herbs, suggesting that extinction rates are less dependent on patch size for shrubs. These results indicate a faster decline of extinction risk with population size for

pancy related to patch size, patch isolation, their interaction, or their interaction with fire. Three species with negative  $x$  values were excluded.

woody plant species. An analysis of extinction among plants in the chaparral indicated that deep-rooted plant species apparently persist longer than shallow-rooted plants (Soulé et al. 1992). The lower extinction risk of shrubs in Florida scrub and the better persistence of deep-rooted species in the chaparral may be related to their ability to cope with competitive interactions during periods without fire (Soulé et al. 1992). The greater sensitivity of herbs to extinction may also reflect their short lifetime and intrinsically more variable population fluctuations.

Although we believe that comparisons of metapopulation model parameters are useful, our quantitative estimates of colonization and extinction must be viewed with caution for several reasons. First, we do not know whether the data conform to the equilibrium between extinction and recolonization assumed in the model. Second, we have insufficient data to determine the precise length of the time step between presence and absence states.

### Spatial Structure, Fire, and Species Persistence

Our results suggest that patch distribution and patch size have important effects on the incidence patterns of some rosemary scrub species. Two main factors are currently modifying the spatial pattern of rosemary scrub in central Florida: changes in fire regimes and replacement of natural habitat by urbanization and agriculture. Fire is a major factor determining habitat availability and vegetation changes in rosemary scrub (Abrahamson et al. 1984a). Because most rosemary scrub species regenerate by seed, variable fire regimes and heterogeneous fire distributions may be required to provide opportunities for colonization and establishment of species with contrasting dispersal abilities, different growth rates, variable age of peak reproductive effort, and variable patch-size requirements (Ostertag & Menges 1994; Menges & Kohfeldt 1995; Menges & Hawkes 1997). Increases of species richness were associated with increasing variability in fire intervals in dry sclerophyll shrublands of Australia (Morrison et al. 1995). Long-term fire suppression may decrease gap sizes, increasing extinction probabilities for many herbs and small shrubs restricted to open habitats (Menges & Kimmich 1996). Extremely short fire cycles may eliminate species with slow recovery rates (Johnson 1982). Burn intensity, size, frequency, and spatial distribution may affect seed-bank density and the distance to sources of immigrants.

Current human activities are continuing to shrink the area of Florida scrub (Peroni & Abrahamson 1985; Christman & Judd 1990; Myers 1990). Decreasing size and increasing isolation of remnant scrub patches have potential negative effects on specialist species. Incorporation of spatial information in future management efforts may improve the chances of conserving many of the endemic species of central Florida.

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