Hypericum cumulicola Demography in Unoccupied and Occupied Florida Scrub Patches with Different Time-since-Fire

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Summary

1 Metapopulation models predict that unoccupied, but suitable, patches will exist for species subject to extinction and colonization dynamics. We compared the demographic responses of *Hypericum cumulicola*, a rare herbaceous species almost entirely restricted to Florida rosemary scrub, when transplanted to occupied or unoccupied patches.

2 Seedlings were transplanted and seeds buried into Florida rosemary scrub patches differing in time since last fire, and in the presence or absence of *H. cumulicola*. We used a replicated, factorial design to place the transplants and seeds in the field, and monitored their performance for 18 months.

3 Neither time-since-fire nor prior *H. cumulicola* site occupancy affected survival of transplants. Only time-since-fire affected growth. Time-since-fire, *H. cumulicola* occupancy, and their interaction affected reproductive effort, but these effects were not consistent between years.

4 Flowering and seed production led to subsequent seedling recruitment near transplants, mainly in recently burned sites. Genetic screening of transplants and seedlings showed that transplants in occupied sites could have crossed with nearby resident plants, but that offspring in sites previously unoccupied were likely to have been parented only by nearby transplants.

5 Seeds buried, and later exhumed, germinated after 1 or 2 years of burial, demonstrating a persistent soil seed bank from which populations could recover after fire. Neither time-since-fire nor *H. cumulicola* occupancy affected seed dormancy or germination.

6 Similar demography in unoccupied and occupied patches suggests that the patchy pattern of site occupancy by *H. cumulicola* is probably due to limited dispersal and periodic extinction, especially associated with long fire-free intervals. Conservation measures need to protect unoccupied patches to allow metapopulation dynamics and persistence.

Keywords: conservation, isozymes, Lake Wales Ridge, management, metapopulation, rare species

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Introduction

Current concern with the biological consequences of habitat destruction and alteration has increased interest in the effects of spatial structure, local extinction and recolonization on long-term species persistence (Harrison 1993; Hanski 1996). Habitat destruction may affect population persistence beyond the immediate consequences of habitat loss, by reducing patch sizes, increasing distances between patches, and modifying environmental heterogeneity (Lovejoy *et al.* 1986; Harrison 1993; Andrén 1994; Hanski 1996).

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In spatially fragmented populations, persistence will depend on the balance between extinction, a product of local forces, and colonization, a regional process (Harrison 1991, 1993; Fahrig & Merriam 1994; Andrén 1994; Husband & Barrett 1996; Harrison & Taylor 1997).

Metapopulation models describe the role of regional extinction–colonization dynamics of groups of populations on species persistence (Hanski 1989, 1991; Hanski & Gilpin 1991; Harrison 1991; Hanski & Thomas 1994). However, the relevance of habitat spatial structure and local extinction to regional persistence depends on amount of habitat available, environmental correlation, and species dispersal abilities (Harrison 1991, 1993). A review of empirical evidence (Harrison 1991, 1993) indicates that local extinction may be irrelevant to regional persistence when (i) co-ordinated local extinctions associated with catastrophes preclude metapopulation persistence; (ii) large and persistent patches provide most of the colonists; or (iii) high interpatch dispersal results in a continuous population over the patch system.

Although metapopulation theory is an important paradigm in conservation biology, direct evidence of the importance of regional habitat structure on species persistence is still largely lacking (Eriksson 1996; Husband & Barrett 1996; Hanski 1997). A critical prediction of metapopulation models is that some suitable habitat patches are vacant because of the ubiquitous risk of extinction and low rates of colonization (Harrison 1993; Hanski 1996).

An analysis of the distribution patterns of plant species in Florida scrub showed an association between species occurrence and both patch size and patch aggregation, for several species virtually restricted to this habitat (Quintana-Ascencio & Menges 1996). In this study, we tested the hypothesis that patches of Florida rosemary scrub unoccupied by the habitat specialist *Hypericum cumulicola* are, in fact, suitable habitat for this species. The performance of individuals transplanted to occupied and unoccupied patches was compared. We argue that an explanation for the absence of *H. cumulicola* in some patches is its limited dispersal ability, and suggest that this limited colonization, coupled with declining populations of this species with time since last fire in local rosemary scrub patches, may result in a dynamic process of colonization and extinction.

Materials and methods

STUDY COMMUNITY AND SPECIES

Florida scrub consists of communities dominated by evergreen shrubs on sandy, infertile and well-drained soils, and fire plays an important role in shaping the composition and dynamics of its plant populations (Abrahamson *et al.* 1984; Myers 1990; Menges &

Hawkes 1998). The rosemary phase of the sand pine scrub is an open and particularly xeric community that occurs on excessively drained white sands, often in small, discrete patches. Long fire intervals (20–80 years) and the occurrence of large open areas (thereafter gaps) between shrubs inside this community provide favourable habitats for several endemic plants (Christman & Judd 1990; Johnson & Abrahamson 1990; Hawkes & Menges 1996; Menges & Kimmich 1996). These gap-dependent species decline between fires, and are absent or rare in the more densely vegetated, more fire-prone, scrubby flatwoods and flatwoods that dominate the landscape which surrounds the rosemary scrub (Abrahamson *et al.* 1984; Johnson & Abrahamson 1990; Menges & Kohfeldt 1995).

Hypericum cumulicola (Small) P. Adams is one such rare species, endemic to the Lake Wales Ridge in central Florida, which is almost entirely restricted to open areas of well-drained white sand in rosemary scrub (Harper 1948; Quintana-Ascencio & Morales-Hernández 1997). The stems of this small, short-lived perennial herbaceous species are branched, many-flowered and indeterminate. Its flowers are bisexual and arranged in cymes. *Hypericum cumulicola* is self-compatible. Native solitary bees (*Dialictus* spp. and *Augochloropsis* spp.) appear to play an important role in pollen transfer in this species (M. Evans, personal communication). Most seeds are produced between June and September. Seeds do not show any obvious primary dispersal mechanism and are probably dispersed passively by gravity. Fire kills established *H. cumulicola* individuals and a proportion of its seeds in the soil. Postfire population recovery therefore depends on surviving seeds and/or dispersal from nearby populations. A number of characters, including seedling establishment, individual survival, plant growth rate and number of flowers and fruits produced, are highest during the first few years following burning and decrease with time-since-fire (Quintana-Ascencio & Morales-Hernández 1997).

EXPERIMENTAL TRANSPLANTS

We evaluated survival, growth and fecundity of transplanted *H. cumulicola* in patches of Florida rosemary scrub in the west section of Archbold Biological Station. This portion of the research station extends over 1070 ha and comprises a mosaic of scrub, flatwoods and seasonal ponds (Abrahamson *et al.* 1984). Scrub patches ranged between 0.03 and 3.6 ha, and collectively all patches accounted for approximately 4% of the total area of the study site (Quintana-Ascencio & Menges 1996). Plant species surveys made in 1988, 1989 and 1994 in each of 89 rosemary scrub patches were used to determine occupancy pattern of *H. cumulicola* (Quintana-Ascencio & Menges 1996). This showed that established individuals of *H. cumulicola* were present in 52 of them and that no population turnover of established *H. cumulicola* had

occurred between 1988 and 1994. Records of fire occurrence (1968–present) were used to determine fire history for each patch, which, in January of 1995, varied between recently burned and more than 30 years since the last fire. We used a factorial design with three levels of time-since-fire (< 3 years, 8–10 and > 20 years) combined with two levels of *H. cumulicola* occupancy (established individuals present or absent) to select 28 rosemary scrub patches for transplanting of *H. cumulicola* (Table 1).

We collected 40 mature fruits of *H. cumulicola* from each of seven rosemary scrub patches during the first week of September 1994. These samples represented populations along the north–south axes of Archbold. No more than two fruits were collected from the same plant. One day after their collection, the seeds were placed in Petri dishes with moist filter paper and allowed to germinate. One- to 4-day-old seedlings were transplanted individually to containers (250-ml disposable baby feeding bags) previously perforated to allow drainage and filled with soil obtained from each transplant site (17–24 bags per site, *n* = 607). Seedlings were watered every other day and maintained in a greenhouse to allow their establishment. The young plants were moved to an outdoor shade-house 22–29 days after being transplanted to the bags, and water-soluble fertilizer was applied once (3 ml of a solution of 1.25 ml in 3.78 l of water; Miracle-Gro 15-30-15).

Between 23 January and 10 February 1995 (103–137 days after germination) the young *H. cumulicola* were transplanted to the field. Patch of origin for

Table 1 Summary of rosemary scrub patches used in the transplant experiment. Patch identification number (ID), *H. cumulicola* occupancy (unoccupied or occupied), year of last fire (Fire), patch area (ha), soil type (Carter *et al.* 1989), seed source (multiple, M, or single, S), number of seedlings transplanted to pots (total *n* = 607), percentage survival in the pots at the time of transplant (S), number of cages (C), and number of juveniles transplanted to the field (T)

ID	Fire	Area	Soil	Source	*n*	S	C	T
Unoccupied and <3 years after fire								
51	July 1993	0.058	Satellite	M	20	75.0	4	15
49	July 1993	0.707	Archbold	M	23	52.2	3	12
Unoccupied and 8–10 years after fire								
86	June 1986	0.063	Satellite	M	19	73.7	4	14
43	May 1983	0.596	Archbold	M	20	30.0	2	6
79	June 1986	0.615	Archbold	S	20	95.0*	5	18
26	January 1985	0.790	Archbold-Satellite	S	20	30.0	2	6
Unoccupied and >20 years after fire								
35	<1967	0.048	Satellite	M	21	66.7	4	14
56	1968	0.051	Satellite	M	20	80.0	4	16
14	<1967	0.102	Satellite	S	20	40.0	2	8
Occupied and <3 years after fire								
57	July 1993	0.094	Satellite	M	20	45.0	3	9
48	July 1993	0.168	Archbold	S	19	78.9	5	15
50	July 1993	0.376	Archbold	S	20	55.0	3	11
28	July 1994	0.482	Satellite	M	21	66.7	5	14
41	July 1993	0.628	Archbold-Satellite	S	20	65.0	4	13
42	July 1993	1.693	Archbold	S	20	35.0	2	7
Occupied and 8–10 years after fire								
12	September 1984	0.075	Satellite	M	24	75.0*	5	17
10	September 1984	0.107	Satellite	S	21	66.7	4	14
30	January 1985	0.139	Satellite	S	20	75.0	4	15
89	July 1986	0.206	Archbold	M	17	35.3	2	6
67	July 1986	0.595	Archbold	S	20	35.0	2	7
91	July 1986	0.807	Archbold-Satellite	S	19	89.5	5	17
29	January 1985	1.259	Archbold	M	21	71.4	4	15
Occupied and >20 years after fire								
32	<1967	0.174	Satellite	S	20	40.0	3	8
38	<1967	0.291	Satellite	M	17	64.7	4	11
59	1968	0.366	Archbold	S	21	66.7	4	14
93	1972	0.697	Archbold	S	22	68.2	4	15
1	<1967	1.852	St Lucie	S	21	66.7	4	14
54	1968	3.578	St. Lucie	M	20	95.0*	5	18

* One plant was killed during transplanting.

transplants was not evenly distributed among sites because of a large variation in time to germination and in the proportion of seeds germinated among source populations. Seed source of transplants was from a single, but not always the same, rosemary scrub patch for 15 transplant sites and from multiple rosemary scrub patches for 13 transplant sites (Table 1). None of the individuals was reintroduced to its patch of origin. Between six and 18 individuals were transplanted within each chosen rosemary scrub patch (Table 1). Because previous research showed that *H. cumulicola* survival decreases with proximity to the dominant shrub, Florida rosemary (*Ceratiola ericoides*) and in the presence of ground lichens (Quintana-Ascencio & Morales-Hernández 1997), individuals were transplanted into gaps between the shrubs. Regardless of *H. cumulicola* patch occupancy, we placed the transplants into open microsites that were already occupied by at least one of the four most frequent herbaceous neighbours of this species in Archbold: *Lechea cernua* (27% of the transplant microsites), *Lechea deckertii* (25%), *Paronychia chartacea* (59%) and *Polygonella basiramia* (40%) (P. F. Quintana-Ascencio & M. Morales-Hernández, unpublished data; nomenclature follows Wunderlin 1982). Each transplant was at least 60 cm from the nearest Florida rosemary (321 cm ± 316 SD), and at least 25 cm from the nearest oak (156 cm ± 105 SD; mostly *Quercus inopina* but also *Q. geminata* and *Q. chapmanii*). Litter, ground lichens and all herbaceous plant species within a 30-cm radius were removed before transplanting.

Plants were transplanted in sets (four or fewer plants per group, 20 cm from each other plant, two to five groups per habitat patch, 5-m minimum distance between groups). We made holes with a soil auger (8-cm diameter). The bottom and one side of each bag was cut, then the opened bag together with an enclosing hard plastic cylinder (PVC) were buried in the sand. The bag was removed together with the plastic cylinder. Plants were watered once shortly after transplanting (*c.* 0.5 litre). Plant groups were covered with wire cages to protect them from large herbivores (46 × 46 × 30 cm, 0.5 cm mesh).

Seedling survival was evaluated from germination to transplanting, from transplanting to age 1 month, and thereafter every 2 months until July 1996. Height and total stem length were measured, and number of stems and of reproductive structures (flowers and fruits) were counted at the time of transplant, 1 month later, and thereafter every 2 months until December 1995, and again in July 1996. We also searched for *H. cumulicola* seedlings inside cages and in the immediate vicinity (50-cm radius), and throughout all unoccupied transplant patches. Distances from every seedling to the nearest cage were recorded. Transplants were removed after their last evaluation in June–July 1996, and screened using isozyme analysis to assign multilocus genotypes to each individual. We removed

any seedlings around transplanted plants in June–July and December 1996, and they were also screened to assess whether they could be the progeny of the transplants.

SEED BANK EXPERIMENT

We determined survival rates of seeds buried for 1 and 2 years in the soil of rosemary scrub patches with different time-since-fire and *H. cumulicola* occupancy. The contents of mature fruits collected from 54 plants in patch 86 during September 1994 (no more than three fruits per plant) were first examined under a microscope to eliminate damaged and deformed seeds. Twenty visually viable brown seeds were wrapped inside plastic mesh bags (2 × 2 cm; Delnet non-woven polyolefin plastic resin; Applied Extrusion Technologies; hole size 0.8 mm) together with dry sand from a patch not occupied by *H. cumulicola* (*c.* 2.5 cm³). We selected sites (three to six replicates) representing the studied combinations of time-since-fire and *H. cumulicola* occupancy. Five pairs of bags were buried at 10 cm depth every 5 m along a random transect in each site. In addition, five pairs of bags were kept indoors buried in sand within a container. One of the bags in each pair was unearthed after 1 year (October 1995), and the other after 2 years (October 1996). Seeds were recovered and examined under a microscope. Obviously damaged seeds were counted and eliminated. Undamaged seeds were placed on moist filter paper in Petri dishes, and monitored for germination during 4 months. Initial viability was estimated from another two groups of 100 seeds placed to germinate in Petri dishes immediately after their collection in October 1994, and monitored until no more seedlings germinated in 2 consecutive weeks. Seeds that failed to sprout were dissected under the microscope. Only seeds with white, full endosperm were considered sound.

ELECTROPHORETIC PROCEDURES

The genetic relationships of transplanted plants with their putative progeny were evaluated using electrophoresis. Flower buds were used from transplants. Most newly recruited plants were not reproductive, so leaf and/or stem tissue was used for analysis. The collected material was kept in a cooler, placed in plastic bags with moist paper towels, and shipped to the laboratory at Butler University within 24 h, where they were processed for horizontal starch gel electrophoresis. Tissue was ground in microfuge tubes with a modified Wendel's sorghum buffer (Morden *et al.* 1987), and centrifuged for 3 min at 3000 r.p.m. prior to application to filter paper wicks.

A previous survey of 35 populations from across the geographical range of *H. cumulicola* revealed five variable loci (R. W. Dolan *et al.*, unpublished data) and these were assayed to assign multilocus geno-

types: 6-phosphogluconic acid dehydrogenase (6-PGD) and mendadione reductase (MNR) were run on Tris-citrate, pH 7.2 (Kephart 1990), at 50 ma for 5 h; whereas malate dehydrogenase (MDH), isocitrate dehydrogenase (IDH) and glyceraldehyde-3-phosphate dehydrogenase (G-3-PDH; developed with NADP) were run on a morpholine–citrate system at pH 6.1 (Clayton & Tretiak 1972). All five enzymes were polymorphic and presented two alleles among the transplants, but only one enzyme system, MNR, could be resolved for seedlings.

DATA ANALYSIS

Failure time analysis (Wilcoxon test) was used to compare differences in survival distributions of transplanted *H. cumulicola* between treatments. This test of heterogeneity between groups compares observed with expected numbers of deaths in each interval (Fox 1993). We used Profile analysis (Multivariate Repeated-Measures Analysis; Pillai's test; von Ende 1993) to examine differences in height growth after transplanting to patches with different time-since-fire and *H. cumulicola* occupancy. The effect of these variables on final above-ground biomass (natural logarithm-transformed) was evaluated with an analysis of covariance using days to transplant as a control for differences in initial size. The effect of fire history and *H. cumulicola* occupancy on total number of reproductive structures in October 1995 and July 1996 (data natural logarithm-transformed) was assessed using analysis of covariance. Height at time of evaluation was included in these models as a covariate. We used analysis of variance to evaluate differences in the proportion of seed bags damaged (data arcsine transformed), and in survival of buried seeds inside intact bags (data arcsine transformed) among patches with contrasting fire and occupancy treatments.

Results

PLANT CHARACTERISTICS AT TRANSPLANT TIME

Survival and size at transplant time were not affected by whether the soil in the pots was from an occupied or an unoccupied site. Nor was survival in the pots due to soils from patches with different time-since-fire (occupancy: $F_{1,24} = 1.42$, $P = 0.24$; fire: $F_{2,24} = 0.59$, $P = 0.56$; occupancy × fire interaction: $F_{2,24} = 0.17$, $P = 0.84$, arcsine transformed data). Approximately two-thirds of the seedlings in the pots survived until transplant to the field. Height at transplant was slightly, but significantly, different among plants potted with soils from patches with contrasting time-since-fire (mean and SD 2.77 ± 1.53 cm in recently burned patches, 2.17 ± 1.33 cm a decade postfire, and 2.54 ± 1.34 cm in long unburned patches; $F_{2,343} = 4.42$, $P = 0.013$; using covariate days from ger-

mination to transplant, $F_{1,343} = 62.08$, $P < 0.001$), but there were no significant differences among plants in soil with contrasting *H. cumulicola* occupancy (2.50 ± 1.66 cm in unoccupied patches, and 2.44 ± 1.29 cm in occupied patches; $F_{1,343} = 0.07$, $P = 0.798$, same test as above).

SURVIVAL, GROWTH AND FECUNDITY OF TRANSPLANTED PLANTS

Patch occupancy did not affect transplant survival or growth. After 509–553 days (January 1995–July 1996), 86% of the *H. cumulicola* transplants remained alive. There were no significant differences in survival between plants in patches with contrasting *H. cumulicola* occupancy or time-since-fire (Wilcoxon statistic: fire, 1.626, $P = 0.44$; occupancy, 1.777, $P = 0.183$). Surviving plants reached between 14 and 78 cm height and 0.05–13.7 g above-ground biomass by July 1996. Trajectories for changes in height over time diverged for different fire regimes (time × fire in Table 2 and Fig. 1). Above-ground biomass in July 1996 was greater for transplants in recently burned patches (mean and SD, 2.93 ± 3.03 g) than for either those plants transplanted in patches a decade after fire (1.46 ± 0.97 g) or in long unburned patches (1.67 ± 1.18 g). Neither *H. cumulicola* occupancy nor its interaction with fire affected above-ground biomass (covariate days to transplant: $F = 64.81$, $P < 0.001$; fire: $F = 3.82$, $P = 0.023$; occupancy: $F = 0.02$, $P = 0.903$; fire × occupancy: $F = 0.20$; $P = 0.816$).

Most surviving *H. cumulicola* transplants produced flowers and fruits during the 2 years of the experiment (October 1995: 94% of transplants presented flowers or fruits, mean and SD of number of flowers and fruits 160.9 ± 162.6, range 2–1033; July 1996: 95%, 170.5 ± 222.4, range 2–1853). Height was a good predictor of number of reproductive structures, and the slope of their relationship can be considered as a crude estimate of reproductive effort (Table 3 and Fig. 2; see also Quintana-Ascencio & Morales-Hernández 1997). During both years, the highest number of reproductive structures was found in the tallest transplants in recently burned patches. Fire, patch occupancy and their interaction significantly affected the number of reproductive structures and reproductive effort. However, the significance of these effects was not consistent between years (Table 3).

RECRUITMENT AND DISPERSAL

Seedling recruitment was affected by fire history but not by patch occupancy. We found seedlings around the transplants in every recently burned patch (20–100% of the cages among patches), but in only one patch a decade after fire (20% of the cages). No recruitment was observed around the transplants in long unburned patches. There were no significant

Table 2 Results of profile analysis (Pillais trace, MANOVA) of changes in *H. cumulicola* height after transplanting in unoccupied and occupied patches with contrasting time-since-fire. The number of days from germination to transplant (natural logarithmic transformed) was used as a covariate to control for differences in initial size. Between-subject refers to the overall variation due to factors (fire, occupancy), and within-subject refers to variation of factors over time. Num, Numerator; Den, Denominator

Source of variation	Between-subject			
	MS	d.f.	F	P
Covariate: days to transplant	35816.33	1	113.62	<0.001
Fire	284.25	2	0.90	0.407
Occupancy	991.78	1	3.15	0.077
Fire × occupancy	1307.62	2	4.15	0.017
Error	315.59	295		

Source of variation	Within-subject			
	F	Num. d.f.	Den. d.f.	P
Time	8.78	6	290	<0.001
Time × days to transplant	15.92	6	290	<0.001
Time × fire	3.68	12	582	<0.001
Time × occupancy	1.51	6	290	0.301
Time × fire × occupancy	1.59	12	582	0.089

differences between recently burned occupied and unoccupied patches in the proportion of cages with seedlings (Kruskal–Wallis test corrected for ties, chi-square$_1$ = 0.42, P = 0.52) nor seedling number by cage (Mann–Whitney test, U = 54, P = 0.118). Seedling numbers within 0.5 m of cages, regardless of previous occupation, varied between 1 and 41. Between June and December 1996, we found a total of 44 and 138 seedlings in the two recently burned, initially unoccupied patches: numbers of seedlings decreased exponentially with distance from their putative parents (median 85 cm, range 8–485 cm), and their orientation was biased to the west.

SEED BANK

Hypericum cumulicola has a persistent seed bank. On average, 45.6% of the seeds inside intact bags exhumed after 1 year of burial germinated in the laboratory, and 43.5% after 2 years (Fig. 3). We considered these values to be an estimate of viability since fewer than 0.03% of the initial seeds remained sound but ungerminated by the end of the tests. There were no significant effects of interval since seed burial, post-fire interval or *H. cumulicola* occupancy on the proportion of seeds germinated (P > 0.20). About 69% of the undamaged seeds tested immediately after their collection in October 1994 germinated within 4 months (Fig. 3).

Seed predation contributed to *H. cumulicola* seed dynamics. We found 28% and 18% of the bags damaged in the first and second years, respectively. More than 80% of the seeds inside damaged bags disappeared or were dead. We did not find any significant effect of seed burial interval, fire history or *H. cumu-*

licola occupancy on the proportion of damaged bags per patch (P > 0.09). We found termites (*Reticulatermes* sp.) within damaged bags and small holes in the testa of empty seeds in both intact and damaged bags. The presence of mummified seedlings indicated the occurrence of fatal germination (Murdoch & Ellis 1992).

SEEDLING PARENTAGE

Genetic screening of transplants and seedlings surrounding the transplant cages revealed that newly recruited plants found in the proximity of four of 14 cages could not have been parented solely by the nearby transplants (Table 4). All these seedlings were found in already occupied habitat, indicating crossing between transplants and nearby non-experimental, previously established plants, or possibly emergence from a local seed bank. In other cases (including all seedlings produced in uninhabited sites), seedlings could have been parented by transplants in the closest cage.

Interestingly, our survey of 190 seedling MNR genotypes indicated 36 heterozygotes (18.9%), almost all from the two unoccupied, recently burned sites (Table 4). Previous survey work (R. W. Dolan *et al.,* unpublished data) on this species detected very few heterozygotes, (25 of 975, or 2.5% of all plants) and high differentiation among populations (FST = 0.73). The heterozygous individuals found indicate that plants from different sources had produced outcrossed seedlings.

Discussion

This study demonstrates the existence of suitable habitat, not currently occupied by *H. cumulicola,*
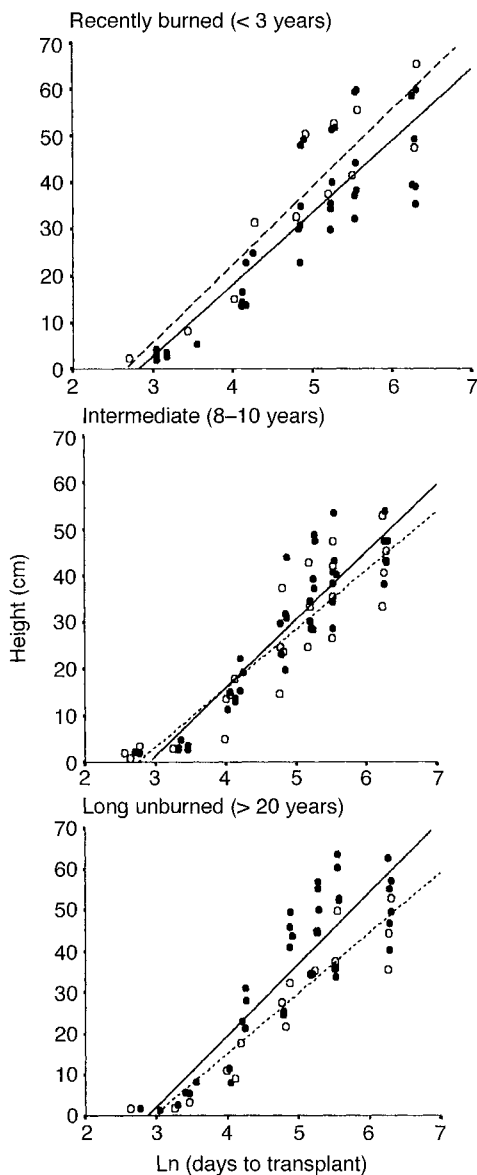
Recently burned (< 3 years)

Fig. 1 Mean height growth per site of transplanted *H. cumulicola* in Florida rosemary scrub patches with different time-since-fire and prior *H. cumulicola* occupancy; present – filled circles and continuous line; absent – open circles and broken line.

within its geographical range. The absence of this species from some Florida rosemary scrub patches cannot be attributed to reductions in germination, survival, growth and fecundity, compared with those of plants in occupied patches. These results, coupled with the significant association between *H. cumulicola* occurrence and scrub patch isolation and scrub patch size (Quintana-Ascencio & Menges 1996), indicate that unoccupied patches are ecologically suitable but probably remain vacant because of limited dispersal and periodic extinction.

Although we have not been able to document any local population extinction, our results corroborate prior evidence of the decline in *H. cumulicola* survival, growth, fecundity and establishment with time-since-fire (Quintana-Ascencio & Morales-Hernández 1997). Fire therefore results in increasing population abundances. There is general evidence that fire can stimulate germination and growth because it temporarily enriches soils by releasing nutrients, consumes organic matter in the surface layers, enhances water-retentive properties of the soil, and eliminates organic chemicals suppressing microbial symbionts (Zedler & Zammit 1989; Moore 1996). In rosemary scrub, fire also reduces above-ground biomass and can release herbaceous species from competition (Quintana-Ascencio & Morales-Hernández 1997). Recruitment, survival, growth and fecundity of *H. cumulicola* in the rosemary scrub decline with the recovery of shrubs and lichens and the reduction of open habitat. Simulations of *H. cumulicola* population dynamics based on census data from 15 populations representing the time-since-fire gradient and seed dormancy and seed viability estimates found in this study indicate that fire intervals shorter than 20 years are needed if local extinction of relatively large populations in under 300 years is to be avoided (Quintana-Ascencio 1997; P. F. Quintana-Ascencio & E. S. Menges, unpublished data). In these simulations lack of fire for longer periods extirpated local populations after seed bank depletion.

In central Florida, rosemary scrub often occurs as scattered patches within a matrix of less xeric com-

Table 3 Results of analysis of covariance of number of reproductive structures (natural logarithm transformed) in October 1995 and July 1996 among *H. cumulicola* transplanted to unoccupied and occupied patches with contrasting time-since-fire. Heights at time of evaluation were used as covariates

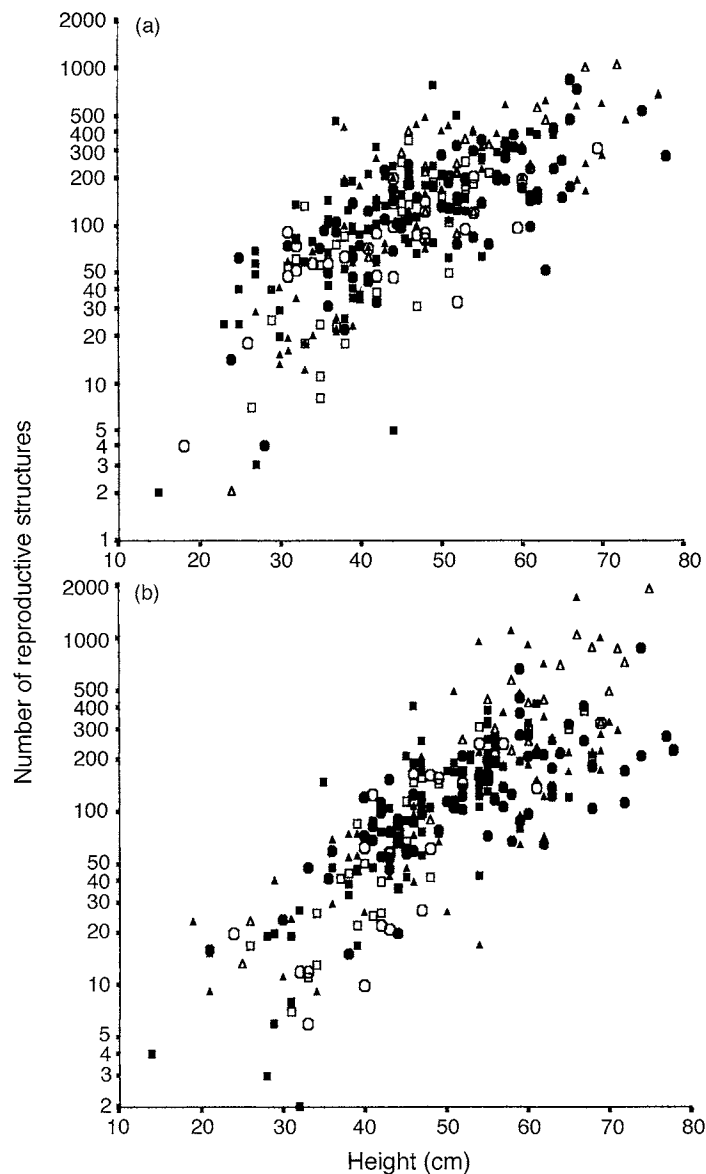| Source of variation	October 1995		July 1996	
	F	P	F	P
Fire	3.23	0.04	2.11	0.12
Occupancy	2.80	0.09	4.78	0.03
Fire × occupancy	0.63	0.53	4.04	0.02
Covariate: height	283.21	<0.001	433.49	<0.001
Occupancy × height	2.37	0.12	5.23	0.02
Fire × height	4.64	0.01	2.14	0.12
Fire × occupancy × height	0.85	0.43	4.09	0.02

Fig. 2 Plot of number of reproductive structures and height of transplanted *H. cumulicola* in Florida rosemary scrub patches during (a) October 1995 and (b) July 1996. Symbols represent patches with different time-since-fire: triangles, <3 years; squares, 8–10 years; circles, >20 years; and prior *H. cumulicola* occupancy: occupied patches, filled symbols; unoccupied patches, open symbols.

munities. For example, at Archbold Biological Station it accounts for only 4% of the vegetation (Abrahamson *et al.* 1984; Quintana-Ascencio & Menges 1996). This spatial pattern may provide conditions for independent colonization and extinction dynamics of patches in the region. Models based on percolation theory and computer simulations suggest that, as the proportion of suitable habitat decreases, the effects of habitat loss on population persistence are amplified by the consequences of patch area and isolation (Turner 1989; Andrén 1994). These predictions are supported by studies on large vertebrates that show a linear correlation between population density and patch area in landscapes with a large proportion of suitable habitat, but non-linear correlation between population densities and patch area

in landscapes with less than a third of suitable habitat (Andrén 1994).

Habitat arrangement may increase or decrease regional species persistence depending on the importance of demographic stochasticity, inbreeding depression and the correlation of environmental factors among sites (Nunney & Campbell 1993). Spatially structured models indicate that patch aggregation may enhance persistence of populations with uncorrelated extinction and limited dispersal (Fahrig & Paloheimo 1988; Adler & Nuernberger 1994). Large fires may aggregate optimal *H. cumulicola* habitats by making several adjacent patches available. However, even within large landscape fires, rosemary scrub tends to burn less evenly than other vegetation types, often leaving unburned patches (K. Main and E. S.
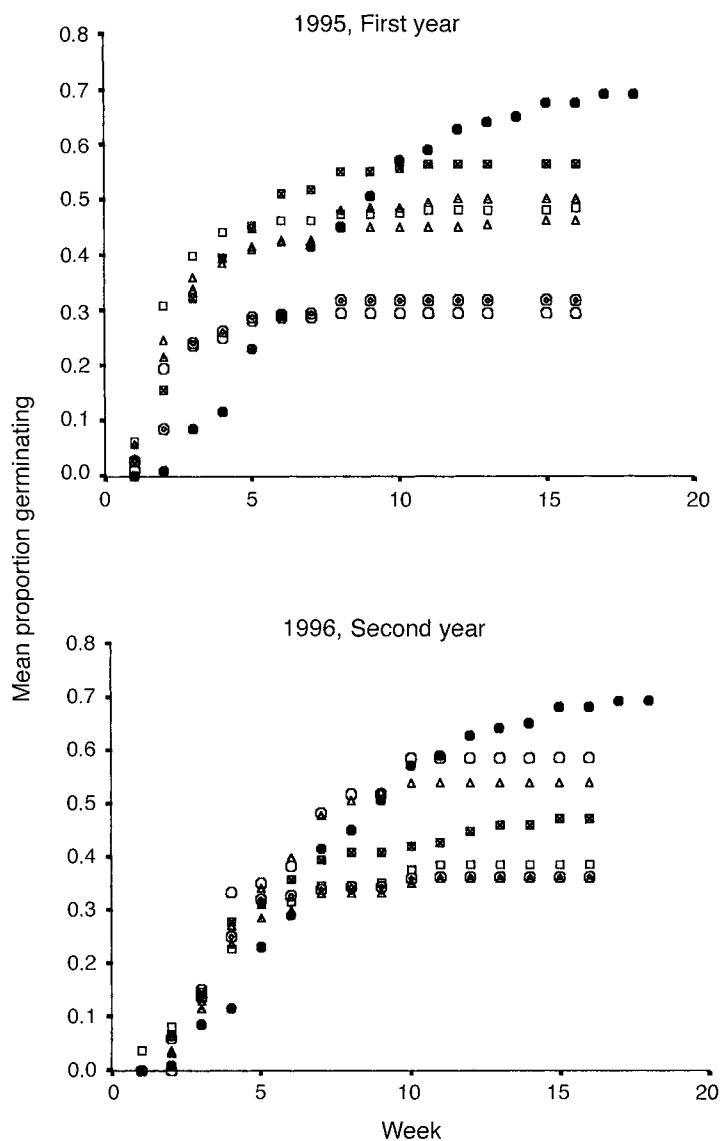
Fig. 3 Mean cumulative proportion of *H. cumulicola* seeds from intact bags germinating after 1 (1995) and 2 (1996) years of burial in rosemary scrub patches with different time-since-fire (recently burned: circles; 8–10 years after fire: squares; >20 years: triangles) and prior *H. cumulicola* occupancy (absent: empty symbols; present: filled symbols). Seed germination immediately after collection in October 1994 (black circles) is shown for comparison.

Menges, unpublished data). Lack of fire gradually makes many habitat patches less suitable. Therefore, fire frequency and magnitude together with heterogeneity within individual fires determine the rates of local extinction and the abundance and distribution of suitable patches for colonization. An optimum fire management regime for *H. cumulicola* should provide suitable habitat within dispersal distance, yet maintain a diverse array of communities with different time-since-fire.

Metapopulation dynamics and habitat fragmentation have the potential to alter species' genetic structure (Olivieri *et al.* 1990; McCauley 1991; Young *et al.* 1996; Harrison & Hastings 1996). Various models predict contrasting patterns of population genetic variation depending on sampling consequences associated with founder events (Wade & McCauley

1988; Hedrick & Gilpin 1997). In particular, during population turnover, decreasing numbers of founders coming from a few source populations may enhance genetic differentiation (Wade & McCauley 1988). A recent study of the genetic variation of *H. cumulicola* throughout its geographical range showed high values of genetic differentiation among populations and low levels of heterozygosity (R. W. Dolan *et al.*, unpublished data). Our observations show that unoccupied Florida rosemary scrub patches can be successfully colonized by a few individuals during the initial years following fire events. Although we do not know actual rates of dispersal and colonization, the occurrence of recruitment following transplantation in previously unoccupied patches indicates that metapopulation dynamics may maintain high levels of genetic differentiation among *H. cumulicola* populations. This

Table 4 Number of mendadione reductase genotypes (MNR) of transplanted *H. cumulicola* (including all plants that flowered during the experiment) and seedlings from transplanted areas (some seedlings had too little material to run). *Seedling genotypes could not be parented by transplants in the nearest cage; **seedlings could be produced by outcross between transplants

Site	Cage	Transplant genotypes			Seedling genotypes		
		BB	BC	CC	BB	BC	CC
Occupied							
28	579			3			9
28	590			2	1*		2
29	308	3			1	2*	5*
29	309	2					2*
41	611	2		1	2		
48	334				2*		
50	829	3		1	1		
57	736	3			3		
Unoccupied							
49	580	1		2	24	21**	18
49	581	2		1	28	8**	20
49	582	1	1		2		
51	345	1		1	2	1**	1
51	821	3	1		29	1	
51	864		1	2		1	4

phenomenon may be exacerbated by the short-distance movements of the primary pollinators of this species (M. Evans *et al.*, unpublished data).

Our results emphasize the danger of focusing species conservation measures on currently occupied sites (Hanski & Simberloff 1997). Populations of *H. cumulicola* tend to decline with time-since-fire (Quintana-Ascencio & Morales-Hernández 1997), and demographic simulations suggest large population turnover due to periodic local extirpations between fires even for relatively large populations (Quintana-Ascencio 1997). Models of metapopulation dynamics suggest that the number of suitable patches should exceed the number of extant populations to assure long-term persistence (Hanski *et al.* 1996). The fraction of empty suitable patches necessary to avoid extinction increases with population turnover rate, patch isolation and environmental correlation (Hanski *et al.* 1996). Rosemary scrub patches are often isolated, and large fires may provide positive environmental correlation. Many patches of suitable unoccupied scrub habitat may therefore be needed to complement the patches occupied at any time. Sporadic colonization of suitable uninhabited sites may have a critical role in the persistence of specialists like *H. cumulicola*, and assuring the persistence of metapopulations should be therefore a primary goal of conservation.

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