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Source-sink dynamics within a plant population: the impact of substrate and herbivory on palm demography

Eric J. Berry · David L. Gorchov · Bryan A. Endress ·
Martin Henry H. Stevens

Abstract Site factors have frequently been shown to affect survival, growth, and reproduction in plant populations. The source-sink concept proposed by Pulliam is one way of integrating this spatial demographic variation into population models. Source-sink models describe a population where propagules from "source" habitats sustain less productive "sink" areas. We adapted this concept to model the population dynamics of the understory palm *Chamaedorea radicalis* on two substrates, rock outcrops and forest floor. In our model, sources and sinks correspond to fine-scale demographic structure within the population, rather than spatially discrete subpopulations as described in the Pulliam model. We constructed a stage-structured population matrix model that integrates the site-specific demography of individuals across two habitats types that are linked by migration. We then parameterized this model with field data from *C. radicalis*. To address whether observed differences in palm demography between rock outcrops and the forest floor were due to natural variation between microsites or due to differences in browsing intensity from free range livestock, we parameterized separate models based on the substrate-specific demography of protected, non-browsed palms and of palms exposed to burro browse. Results showed that herbivory reduced survival and fecundity on the forest floor, which in the absence of seed migration resulted in a projected decline of forest floor palms (sinks). However with seed dispersal, palms persisted and total population growth (both substrates) was projected to be positive, indicating that seed dispersal from non-browsed palms on rock outcrops (sources) was sufficient to sustain *C. radicalis* on the forest floor.

Keywords Arecaceae · *Chamaedorea radicalis* · Herbivory · Mexico · Population dynamics · Seed dispersal

Introduction

Plants occupy a variety of local habitats within a heterogeneous environment, with effects on growth, fecundity and mortality. Spatial heterogeneity, even at relatively small scales, can produce demographic variation within plant populations that is as large as the demographic variation between populations (Fowler and Antonovics 1981; Marshall et al. 1986). Such fine-scale variation in demography has been documented within populations for numerous plant species (e.g., Sarukhán and Harper 1973; Sarukhán 1974; Venable and Levin 1985; Moloney 1988; Kadmon 1993; Miller and Fowler 1994; Vavrek et al. 1997; Guàrdia et al. 2000; Vega and Montaña 2004). One result of this spatial variation in demography is that individuals occurring in the same habitat type may form local subpopulations that share demographic rates that are different from those in other habitat types (Kadmon 1993; Valverde and Silvertown 1998). A challenge for population biologists is to understand how each subpopulation contributes to overall population dynamics. Although demographic studies have been published for hundreds of plant species (Franco and Silverton

E. J. Berry (✉)
Biology Department, Saint Anselm College,
100 Saint Anselm Drive, Manchester, NH 03102, USA
e-mail: eberry@anselm.edu

D. L. Gorchov · M. H. H. Stevens
Department of Botany, Miami University, Oxford,
OH 45056, USA

B. A. Endress
Conservation and Research for Endangered Species,
San Diego Zoo, Escondido, CA 92027, USA

1990), relatively few studies have examined how spatial variation in demography affects plant population growth (e.g., Kadmon 1993; Cipollini et al. 1994; Horvitz and Schemske 1995; Valverde and Silvertown 1998; Vavrek et al. 1997; Guàrdia et al. 2000).

In addition to site-specific demography of individuals within a heterogeneous landscape, a species' distribution and abundance is also influenced by seed dispersal and dormancy (Kadmon and Shmida 1990; Valverde and Silvertown 1995). Seed dispersal in particular links different habitat types, with their respective demographic rates, to the broader plant population (Valverde and Silvertown 1997). This dispersal creates an overall population dynamic that is a function of both the specific demography of local subpopulations and the migration pattern of seeds among the entire population. The source-sink concept (Pulliam 1988; Pulliam and Danielson 1991) is one way of integrating seed dispersal and spatial variation in demography into population models. Source-sink models describe a population with a proportion of individuals occurring in "sink" habitats, where finite rates of population growth (λ) fall below the replacement rate of 1. However, these subpopulations persist due to continued immigration from more productive "source" habitats, where $\lambda > 1$.

Source-sink models have been mostly applied to animals (e.g., Carl 1971; Henderson et al. 1985; Dunbar 1987; Watkinson and Sutherland 1995; Figueira and Crowder 2006) and there is much less direct evidence for source-sink dynamics in plants (Eriksson 1996). Indeed, much of the evidence from plants is inconclusive because most of the applicable studies were not designed to specifically test the concept (Pulliam 1996). Some plant studies of habitat-specific demography and population growth rates suggest source-sink dynamics (Werner and Caswell 1977; Keddy 1981; Menges 1990; Charron and Gagnon 1991; Eriksson and Bremer 1993; Kadmon 1993), but only a few studies have examined seed dispersal between habitats (Keddy 1982; Watkinson 1985; Watkinson et al. 1989; Kadmon and Shmida 1990; Valverde and Silvertown 1997; Kadmon and Tielbörger 1999). These seed migration data are necessary to demonstrate the dependence of sinks on the continued migration of individuals from more productive source habitats, an essential feature of source-sink models (Dias 1996; Eriksson 1996).

The purpose of our study was to investigate how habitat-specific demography and inter-habitat seed migration shape population dynamics in the tropical understory palm *Chamaedorea radicalis* (Mart.). Specifically, we applied the source-sink concept to model palm population dynamics on two substrates, rock outcrop and the forest floor. Within our study area, *C. radicalis* abundance is associated with substrate (Jones and Gorchov 2000), and previous research suggests that palms on rock outcrops have different demographic rates than those on the forest floor (Berry and

Gorchov 2004, 2006; Endress et al. 2004a). However, palms on rock outcrops are also less frequently browsed (Endress 2002), confounding interpretation of whether observed differences in palm abundance and population structure are due to natural microsite differences between substrate types or due to differences in browsing intensity. If rock outcrops do represent higher quality microsites, either due to preferred microsite conditions or refuge from browse, seed dispersal from rock outcrops (putative sources) may sustain the rest of the population where λ is otherwise below the replacement rate of 1 (putative sinks).

Although the focus of our study was to investigate source-sink dynamics in *C. radicalis*, we present a generalized matrix model that is applicable to any population that is divided across two habitat types which are linked by seed dispersal. As a test for source-sink dynamics, this model allows us to calculate population growth for each habitat, providing a quantitative test for sources (λ, the finite rate of increase, above the replacement rate of 1) and sinks ($\lambda < 1$). This model also explicitly incorporates values for seed migration, providing a test for whether sources maintain sinks in this population.

Materials and methods

Study site

This study was conducted in the forests near the communities of San José and Alta Cima within the El Cielo Biosphere Reserve (hereafter El Cielo), Tamaulipas, Mexico (22°55′–23°30′N, 99°02′–99°30′W). El Cielo is located within the Sierra de Guatemala mountain range on the eastern slope of the Sierra Madre Oriental in northeast Mexico. Although El Cielo contains many vegetation types (Perrine and Gorchov 1994; Davis et al. 1997; Sánchez-Ramos et al. 2005), the primary sites for this study were in a montane mesophyll forest near Alta Cima, and in a transition zone between montane mesophyll forest and pine-oak forest near San José (Puig and Bracho 1987; Sánchez-Ramos et al. 2005). Temperature and precipitation within El Cielo depend on elevation. Nearby Rancho del Cielo is at a similar elevation to our study sites (1,100 m) and averages 2,500 mm year^{-1} of precipitation and has an average temperature of 13.8°C (Davis et al. 1997).

Study species

Chamaedorea radicalis Mart. (Arecaceae) is one of approximately 100 *Chamaedorea* species, many of which are economically valuable as either small, shade-tolerant potting plants or as harvested leaves in floral arrangements

(CEC 2002). Adult *C. radicalis* have approximately 4–8 pinnately compound leaves, while seedlings have bifid leaves (Hodel 1992). Most adult individuals appear stemless, because their stem typically forms a "heel" that grows into the substrate. Individuals with an erect, above ground stem can reach 2–4 m in height (Gorchov and Endress 2005). Villagers within El Cielo harvest leaves of adult *C. radicalis* for sale to international cut-foliage markets. Harvested leaves are usually ≥40 cm in length, and have minimal damage from insects or pathogens (Endress et al. 2004b). These palm leaves are the only natural resource that these villagers are authorized to harvest, and provide the main source of income for most families (Peterson 2001).

Within El Cielo, *C. radicalis* abundance and population structure are correlated with substrate, with rock outcrops having higher palm density than the surrounding substrates of rock or soil (Jones and Gorchov 2000) and having the highest proportion of large adult palms (Endress et al. 2004a). *Chamaedorea radicalis* is dioecious and when adult females on rock outcrops flower they have higher fruit production than flowering females on other substrates (Berry and Gorchov 2006).

Population model form

In order for the source-sink model (Pulliam 1988, 1996) to apply to a population, the following criteria must be met: (1) in the absence of migration, $\lambda > 1$ in source areas, (2) in the absence of migration, $\lambda < 1$ in sink areas, and (3) there is net positive migration from sources to sinks. To model source-sink dynamics in populations of *C. radicalis* on two substrates we modified a simple metapopulation model suggested in Caswell (2001), which describes a population in two geographic locations. Based on the two-substrate life cycle diagram of *C. radicalis* (Fig. 1), the stage-structured (Lefkovitch) projection matrix for this population can be written as
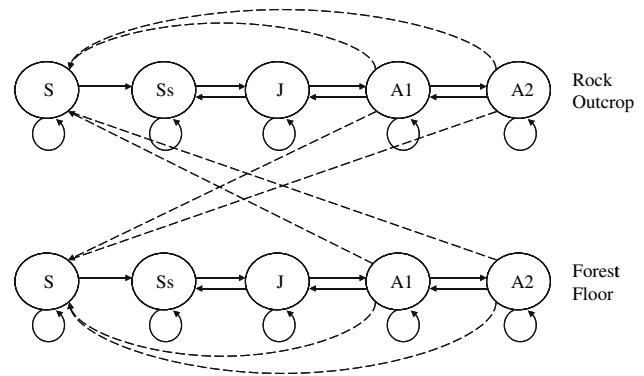

Fig. 1 Life cycle graph for *Chamaedorea radicalis* based on two substrates linked via seed dispersal. Classification criteria are based on the number of leaflets on the youngest fully-expanded leaf (Endress et al. 2004a). Life-history stage transitions are indicated by *arrows* with *solid lines* and reproduction is indicated by *dashed lines*. *S* Seed, *Ss* seedling (bifid leaves), *J* juvenile (3–9 leaflets), *A1* small adult (10–24 leaflets), *A2* large adult (>24 leaflets)

P_{ij}. For individuals on substrate j, G_{ij} is the probability of surviving and growing from stage i to stage $i + 1$, R_{ij} is the probability of surviving but regressing from stage i to stage $i - 1$, and F_{ij} is the fertility of stage i on substrate j. Migration between substrates depends on: a = proportion of outcrop seeds that disperse to forest floor and b = proportion of forest floor seeds that disperse to outcrops.

This projection matrix can be simplified and expressed in a more general form as submatrices (Caswell 2001),

$$\mathbf{A} = \left(\begin{array}{c|c} \mathbf{B_r} & \mathbf{M_{f \to r}} \\ \hline \mathbf{M_{r \to f}} & \mathbf{B_f} \end{array} \right),$$

where submatrix $\mathbf{B_r}$ is the population projection matrix for palms on rock outcrops (putative source), and $\mathbf{B_f}$ contains the transition probabilities for palms on the forest floor (putative sink). $\mathbf{M_{f \to r}}$ represents the probability of seeds that were produced on the forest floor but dispersed to rock outcrops. Likewise, $\mathbf{M_{r \to f}}$ is the submatrix for seed dispersal from rock outcrops to the forest floor. In this

$$\mathbf{A} = \left(\begin{array}{ccccc|ccccc} P_{1r} & 0 & 0 & F_{4r}(1-a) & F_{5r}(1-a) & 0 & 0 & 0 & F_{4f}(b) & F_{5f}(b) \\ G_{1r} & P_{2r} & R_{3r} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{2r} & P_{3r} & R_{4r} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{3r} & P_{4r} & R_{5r} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_{4r} & P_{5r} & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & F_{4r}(a) & F_{5r}(a) & P_{1f} & 0 & 0 & F_{4f}(1-b) & F_{5f}(1-b) \\ 0 & 0 & 0 & 0 & 0 & G_{1f} & P_{2f} & R_{3f} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & G_{2f} & P_{3f} & R_{4f} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_{3f} & P_{4f} & R_{5f} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & G_{4f} & P_{5f} \end{array} \right),$$

where r (rock) and f (forest floor) are the two substrates; individuals in stage i on substrate j survive and remain at the same stage (i) over 1 year's time with the probability of

simplified form, projection matrix A provides clear, testable hypotheses for each of the criteria of a source-sink population described above: (1) in the absence of seed

migration $\lambda_{Br} > 1$, (2) in the absence of seed migration $\lambda_{Bf} < 1$, and (3) seed migration is asymmetric, where $M_{r \rightarrow f} > M_{f \rightarrow r}$.

Population models for this study followed the linear population projection matrix model $\mathbf{n}(t + 1) = A \times n(t)$ (Caswell 2001). In this model, $\mathbf{n}(t)$ represents a column vector whose elements are the population's stage structure $\mathbf{n}$ at time t with the form

$$\mathbf{n}(t) = \left(\frac{\text{rock outcrops}}{\text{forest floor}} \right) = \begin{pmatrix} n_{1r} \\ n_{2r} \\ n_{3r} \\ n_{4r} \\ n_{5r} \\ n_{1f} \\ n_{2f} \\ n_{3f} \\ n_{4f} \\ n_{5f} \end{pmatrix}$$

and $\mathbf{n}(t + 1)$ is the stage structure at the next time interval (next year). For this study, $\mathbf{n}(t)$ was parameterized from the observed stage distribution of *C. radicalis* in El Cielo reported in Endress et al. (2004a). These data were collected from 15 belt transects along five hillsides within the valley Cañón del Diablo near Alta Cima during July and August of 2000 ($n = 922$ palms). As described above, transition matrix A represents the transition probabilities of each of the five life history stages for *C. radicalis* on two substrates. Based on the reproductive phenology of *C. radicalis* (Endress et al. 2004b), we used a birth-pulse model with a post-breeding census.

Although *C. radicalis* is dioecious, we used a one-sex, female-dominant model (Caswell 2001). One-sex models have been used in nearly all models for dioecious plants (e.g., Cipollini et al. 1994; Negrón-Ortiz et al. 1996; Bernal 1998), and are based on certain assumptions which have been supported for *C. radicalis*. Specifically, there is no apparent sexual dimorphism in vital demographic rates (Endress 2002), and female fecundity (flower number, fruit number, and fruit set) was shown to be independent of male density, nearest male distance, and sex ratio at both the individual neighborhood (Berry and Gorchov 2004) and at the population level (Berry and Gorchov 2006). For *C. radicalis* seedlings and juveniles, which are not possible to sex, we used demographic estimates based on pooled data for all individuals of a given life-history stage. Since adults of both sexes have similar growth and mortality rates (Endress 2002), transitions for these parameters were also calculated based on pooled data. Adult fecundity values were based on per capita fruit production of females, which were calculated as the total number of fruits divided by the total number of females. Since adults do not flower every year, and the sexes are indistinguishable when not

flowering, the total number of females was estimated as half the number of adults ($n/2$), based on the assumption that there is no sex-ratio bias in the population, which has been supported for *C. radicalis* (Endress 2002; Berry and Gorchov 2006). Similarly, half the seeds were assumed to be female.

Matrix model analysis

Population projections and eigenanalysis were conducted using Matlab version 7.0.1 (MathWorks 1989). We used eigenanalysis to estimate two population parameters, finite rate of increase (λ) and stable stage distribution (Caswell 2001). λ is the dominant eigenvalue (largest real root) of the matrix and is a measure of population fitness, as populations with $\lambda > 1$ grow, $\lambda < 1$ decline, and $\lambda = 1$ remain at size n. The 95% confidence intervals for λ were obtained by bootstrap analysis and resampling the original data set in the same manner that the data were collected (Scheiner and Gurevitch 1993). This analysis involved creating 1,000 resampled matrices for each treatment and calculating λ for each matrix. We then calculated 95% confidence intervals using the "Percentile Method," a nonparametric approach (Scheiner and Gurevitch 1993).

The population's stable stage distribution was obtained from the right eigenvector associated with λ, and is the percentage of individuals in each stage when the population is growing at λ. Chi-square (χ^2) goodness-of-fit tests were performed to test whether observed *C. radicalis* stage structure and observed proportions of plants on rock outcrops versus forest floor were different than the expected stable stage distributions from the projection matrices. Contingency tests (G^2) were performed to test whether fates of specific stages depended on substrate, or on the presence of livestock browse.

Matrix parameterization: substrate-specific demography

Stage-structured (Lefkovitch) transition matrices (Fig. 2, Appendix 2) were parameterized from demographic data collected over two consecutive years (2003–2005) on tagged palms in permanent plots, as well as data from seed germination and livestock browse experiments. For this study, rock outcrops were defined as rock substrate that protruded ≥1 m above the surrounding forest floor. Although these outcrops varied in size, most were a few square meters in area, based on the segment length for outcrops on line transects (range = 0.4–2.8 m, mean = 1.05, $n = 86$). Transition matrices included substrate-specific estimates of the following parameters for each stage: (1) the probability of

Fig. 2 Projection matrices for browsed and non-browsed *C. radicalis* on two substrates. Submatrices B_r and B_f are based on the five life-history stages defined in Fig. 1. B_r Rock outcrops, B_f forest floor, $M_{f \to r}$ migration from forest floor to rock outcrop, $M_{r \to f}$ migration from rock outcrops to forest floor

2003-04

$$
A_{control} = \begin{pmatrix}
0.00 & 0 & 0 & 0.01 & 0.55 & 0 & 0 & 0 & 0.00 & 0.05 \\
0.13 & 0.79 & 0.08 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.17 & 0.39 & 0.05 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.47 & 0.70 & 0.10 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.24 & 0.89 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.09 & 6.12 & 0.06 & 0 & 0 & 0.34 & 8.06 \\
0 & 0 & 0 & 0 & 0 & 0.16 & 0.62 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.29 & 0.50 & 0.03 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.45 & 0.66 & 0.05 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.26 & 0.90
\end{pmatrix}
$$

2004-05

$$
\begin{pmatrix}
0.01 & 0 & 0 & 0.05 & 1.70 & 0 & 0 & 0 & 0.03 & 0.33 \\
0.23 & 0.73 & 0.04 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.19 & 0.48 & 0.03 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.44 & 0.77 & 0.05 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.18 & 0.93 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.5 & 0.24 & 8.26 & 0.02 & 0 & 0 & 0.59 & 7.37 \\
0 & 0 & 0 & 0 & 0 & 0.25 & 0.67 & 0.04 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.24 & 0.43 & 0.04 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.43 & 0.65 & 0.06 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.24 & 0.92
\end{pmatrix}
$$

$$
A_{browse} = \begin{pmatrix}
0.00 & 0 & 0 & 0.01 & 0.55 & 0 & 0 & 0 & 0.00 & 0.01 \\
0.13 & 0.79 & 0.08 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.17 & 0.39 & 0.05 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.47 & 0.70 & 0.10 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.24 & 0.89 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.09 & 6.12 & 0.06 & 0 & 0 & 0.02 & 1.23 \\
0 & 0 & 0 & 0 & 0 & 0.16 & 0.58 & 0.08 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.20 & 0.44 & 0.04 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.20 & 0.53 & 0.09 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.27 & 0.86
\end{pmatrix}
$$

$$
\begin{pmatrix}
0.01 & 0 & 0 & 0.05 & 1.70 & 0 & 0 & 0 & 0.01 & 0.14 \\
0.23 & 0.73 & 0.04 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.19 & 0.48 & 0.03 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.44 & 0.77 & 0.05 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.18 & 0.93 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.24 & 8.26 & 0.02 & 0 & 0 & 0.22 & 3.07 \\
0 & 0 & 0 & 0 & 0 & 0.25 & 0.75 & 0.13 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.15 & 0.36 & 0.10 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.30 & 0.54 & 0.06 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.27 & 0.91
\end{pmatrix}
$$

survival and no growth (e.g., seedling to seedling), (2) the probability of survival and growth, (3) the probability of regression to a "smaller" stage, and (4) the fecundity of females (adult stages only).

Annual demographic rates were based on census of tagged palms ($n = 429$) from ten permanent plots near Alta Cima in Cañón del Diablo, beginning August 2003. These plots were established January 1999 (Endress 2002) and had been free from leaf harvest and livestock browse for 4 years. Plot size was variable and ranged from 53 to 290 m² (Endress 2002). In addition to the annual census, these sites were also examined quarterly (February, May, August, and November) to quantify flowering and fruiting. For each palm, the following parameters were recorded: substrate type (rock outcrop or forest floor), number of leaves, number of leaflets on the youngest fully-expanded leaf, leaf length, and when present, the phenological stage and sex of each inflorescence and fruit number. The demography of seedlings and juveniles was measured in 3×3 m nested subplots within five of the ten plots. Within each subplot all juvenile palms and emerging seedlings (recruits) were tagged and measured according to the same parameters listed above for the adults. As with the adults, these smaller palms were measured each August to calculate per capita annual demographic rates.

Seed germination rates were calculated from two 0.25 m² seed plots placed near each of the ten permanent plots. One seed plot was positioned on a rock outcrop and the other on the forest floor. Within each seed plot, 20 *C. radicalis* seeds were planted for a total of 200 on outcrops and 200 on the forest floor. Seed plots were placed away from large females to minimize "volunteer" seedlings that result from seeds that are naturally dispersed into the seed plots. Plots were inspected quarterly and emerging seedlings counted and tagged. Germinations rates for dormant seeds were not quantified, and so for the model, rates for dormant seeds were assumed to be equal to rates from current year seeds.

Matrix parameterization: seed dispersal

Fruit traps were used to estimate seed migration from one substrate to the other (e.g., rock outcrop to forest floor). Each *C. radicalis* fruit contains only one seed (mean = 0.8 cm in diameter; Agil et al. 2000), and therefore for this study, fruit migration reflects seed migration. Seed migration from rock outcrops to the forest floor was quantified as the difference between total mature fruit production of females on rock outcrops minus the number of fruits remaining on the rock outcrop after dispersal. Dispersed fruit remaining on rock outcrops was estimated by sampling ten outcrops with fruit traps composed of fiberglass mesh placed just above the ground under fruiting females. Traps

were constructed to be large enough ($\sim 1\,m^2$) to capture all fruits from an individual fruiting female. To minimize seed migration onto these sites that would confound calculations, only fruiting palms >15 m from other fruiting palms were selected. Seed migration in the opposite direction (i.e., from females on the forest floor to rock outcrops) was quantified as the number of fruits captured in fruit traps on rock outcrops where there were currently no fruiting palms ($n = 10$ outcrops). To minimize seed migration from other rock outcrops, these sites were within 1–3 m of fruiting palms on the forest floor, but >15 m from other rock outcrops with fruiting palms. Per capita values for female adults were calculated from these data as the product of the average seed production on a given substrate and the proportion of seeds dispersed to each substrate type.

The 15 m buffer around seed traps was sufficient to minimize seed migration from females other than those targeted based on seedling recruitment data showing that the vast majority of *C. radicalis* fruits disperse only a very limited distance ($\sim 95\%$ of seedlings recruit within 5.5 m of fruiting female). Although the vector of seed dispersal for *C. radicalis* is unknown, the general pattern of seedling recruitment is one of seedlings being down slope and near fruiting females (E.J. Berry, personal observation), which is consistent with primary seed dispersal by gravity and possible secondary dispersal a short distance by water from heavy rains. Such seed dispersal by gravity has been reported in at least two other species of *Chamaedorea* (Luna et al. 2005). Although *C. radicalis* seeds may be primarily gravity-dispersed, secondary dispersal must occasionally produce seed movements against the vector of gravity, which is evident in the fact that the population does infrequently recruit individuals onto rock outcrops. The vector responsible for such dispersal is not known for *C. radicalis*, but, among other *Chamaedoreas*, birds, mice, agouti, and other mammals have been documented as seed dispersers (Zona and Henderson 1989). Fruits of *C. radicalis* are small (~ 1 cm in diameter) and turn an orange to red color when ripe; colors which may promote occasional dispersal by birds.

Matrix parameterization: demography of browsed plants

In our study area, free-range burros, mules, and cattle browse *C. radicalis* at a rate far in excess of herbivory by native animals. To quantify demographic rates in *C. radicalis* exposed to free-range livestock, we monitored palms in an area subjected to an experimental browsing episode. Because the permanent plots used to parameterize the control matrices (non-browsed palms) are part of an ongoing experiment, a separate study area was established

to conduct the browse experiment. This area was located near the village of San José in a montane mesophyll forest similar to the forest type and substrate found in Cañon del Diablo where the control palms were located. At this site, three permanent browse plots were established during August 2003 in a 600-m^2 fenced-in location (Endress 2002) that was free of livestock for the previous 4 years. Within the study area, all palms were tagged, measured, and categorized according to the size and demographic parameters previously described ($n = 323$).

After all palms were measured, a burro was allowed to forage throughout the study plots. Although no time restrictions were imposed, the burro was removed from each plot only after it apparently finished browsing and had stopped eating for several minutes (approximate total time per plot 15–30 min.). Burros were chosen for this experiment because they are one of the most abundant livestock animals in Alta Cima and San José (Peterson 2001), and because they are able to browse more of the rugged terrain within El Cielo than horses or cattle (E.J. Berry, personal observation). Immediately after the browse event, each palm was re-censused and scored as either browsed or non-browsed. From these data we calculated, for each stage and each substrate, the proportion of palms browsed. To determine the demography of browsed palms and recovery after browse, demographic rates of browsed palms (outcrop and forest floor analyzed separately) were based on annual transitions during the year following browse (August 2003–2004). To incorporate these data into transition matrices, the overall demography for each life-history stage was a function of both browsed and non-browsed palms, weighted according to the proportion of palms browsed on a given substrate. Using juvenile growth as an example, if on a given substrate half of juveniles were browsed then the growth rate for this stage would be calculated as: overall juvenile growth = (browsed growth rate $\times$ 0.5) + (non-browsed growth rate $\times$ 0.5).

Results

The effect of substrate and livestock browse on demography

In the absence of livestock browse (control), there was little difference in *C. radicalis* mortality, growth, or fecundity between individuals on rock outcrops and those on the forest floor (Fig. 3). Mortality was highest among the smaller life-history stages, but other than seeds, overall mortality was relatively low (<10%). Growth and regression to an earlier life-history stage were similar between the substrates and there were no apparent trends among the stages. Female fecundity was also not dependent on
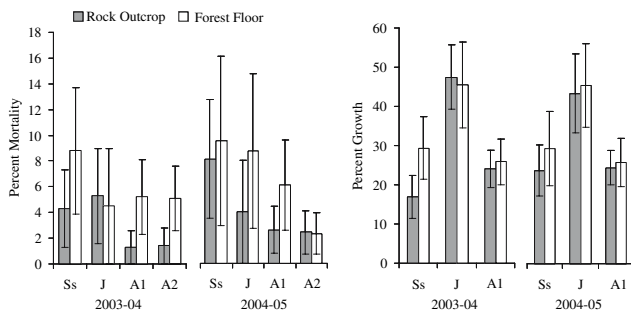
Fig. 3 Comparison of *C. radicalis* demography between rock outcrops and forest floor in the absence of browsing by free-range livestock. Reported are mean annual mortality and growth (stage transition) rates (±SE) for each of two consecutive years among ten control plots in Cañon del Diablo that were protected from livestock browse. Likelihood-ratio G^2 tests revealed no statistically significant differences ($P \geq 0.05$) between the two substrates. Abbreviations represent life-history stages as described in Fig. 1. Sample size for 2003–2004 (rock outcrops, forest floor): $Ss = 47, 34$; $J = 38, 22$; $A1 = 79, 58$; $A2 = 72, 79$. Sample size for 2004–2005: $Ss = 37, 21$; $J = 25, 23$; $A1 = 77, 49$; $A2 = 82, 89$
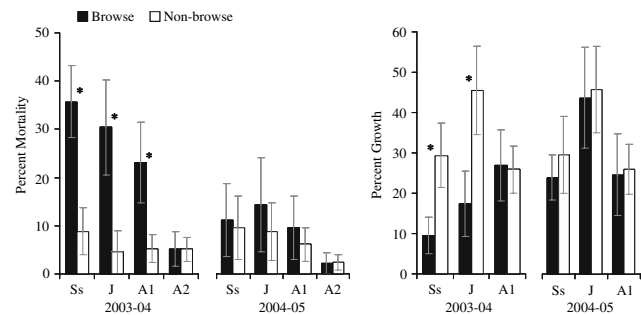
Fig. 4 Impact of burro browse on *C. radicalis* mortality and growth. Because no palms on rock outcrops were browsed during this experiment, reported are mean annual rates (±SE) among ten plots for browsed and non-browsed palms on the forest floor. The browse treatment occurred in August 2003, and therefore values for 2003–2004 reveal the immediate impact of burro browse, and values for 2004–2005 reflect palm growth and mortality after 1 year of recovery from browse. *Asterisks* indicate significant differences ($P < 0.05$) based on likelihood-ratio G^2 tests. Abbreviations for life history stages are as described in Fig. 1. Sample sizes for 2003–2004 (browsed, non-browsed): $Ss = 42, 34$; $J = 23, 22$; $A1 = 26, 58$; $A2 = 39, 79$. Sample sizes for 2004–2005: $Ss = 18, 21$; $J = 14, 23$; $A1 = 21, 49$; $A2 = 45, 89$

substrate, as there was no statistically significant difference in either female fruit production or the proportion of palms that fruited (Appendix 1).

We found no difference in the rate of seed germination between the two substrates ($P > 0.05$) for either year of this study. Mean seed germination for 2003–2004 on rock outcrops of 13.0% (±SE 2.6) was not statistically different from the forest floor rate of 15.5% (±3.1). In 2004–2005, seed germination on rock outcrops (22.5 ± 4.1%) and on the forest floor (24.5 ± 5.5%) was also similar, but both were higher than the previous year. Among seeds that did not germinate within the first year of planting, rates of seed dormancy, as indicated by a positive Tetrazoleum stain, were very low on both substrates for 2003–2004 (rock outcrop = 0.0%, forest floor 5.5%) and 2004–2005 (rock outcrop = 1.0%, forest floor 2.0%).

During the browse experiment, the burro had access to palms on both substrates. However, no palms on rock outcrops were eaten, and therefore all comparisons were between browsed and non-browsed individuals on the forest floor. The experiment revealed that the burro preferred juveniles, which were the least abundant stage but were the most frequently browsed, with the burro eating leaves from 92% of the individuals. Seedlings were the least frequently browsed (49%), while small adults (62%) and large adults (81%) sustained an intermediate level of herbivory. Unlike substrate alone, livestock browse had a large impact on vital demographic rates of *C. radicalis* (Fig. 4). The mortality rate for each stage except large adults was >4 times greater for palms that were browsed compared to those not browsed. Browsed palms were also

less likely to grow to a larger stage than individuals in the control plots. Female fecundity was also greatly reduced by burro browse, as no browsed adult produced flowers or fruits during the year following browse (August 2003–2004).
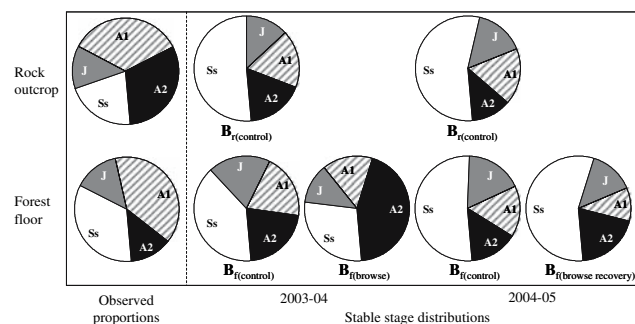
Substrate-specific population growth

Assuming no seed migration between the substrates, both rock outcrop ($\mathbf{B}_r$) and forest floor ($\mathbf{B}_f$) submatrices in the control plots were projected to increase (Table 1). Based on bootstrap analysis, the finite rates of population growth were not significantly different between the two substrates during or between 2003–2004 or 2004–2005. The stable stage distributions projected from matrix models of control populations were similar across both substrates and both years (Fig. 5). However, these model projections were different from the observed proportions calculated from population sampling. More specifically, in each year rock outcrops were projected to have a greater proportion of seedlings and smaller proportion of both adult stages than was observed. For the forest floor, model projections underestimated the proportion of small adults for both years and overestimated the proportion of seedlings during 2004–2005.

Forest floor palms exposed to burro browse ($\mathbf{B}_{f\ (browse)}$) were projected to have significantly lower population growth rates than non-browsed palms on either substrate (Table 1). Although demographic rates for the submatrix of browsed palms were weighted based on the demography of
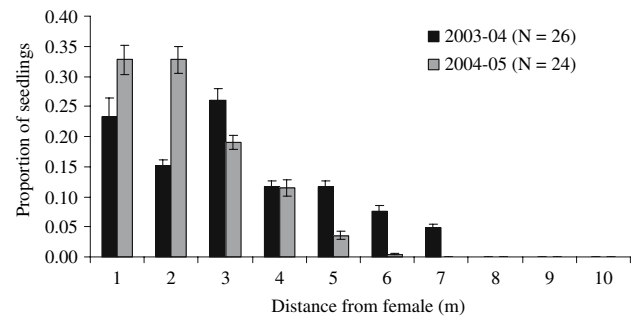
Table 1 *Chamaedorea radicalis* finite rates of population growth and 95% confidence limits

Treatment	λ	95% confidence interval
2003–2004		
Rock outcrops ($\mathbf{B_r}$), control	1.14	1.09–1.19
Forest floor ($\mathbf{B_f}$), control	1.14	1.08–1.21
Forest floor ($\mathbf{B_f}$), browse experiment	0.95	0.91–0.99
Two-substrate model (A), control	1.12	1.06–1.18
Two-substrate model (A), browse experiment	1.02	0.99–1.05
2004–2005		
Rock outcrops ($\mathbf{B_r}$), control	1.18	1.10–1.24
Forest floor ($\mathbf{B_f}$), control	1.17	1.08–1.26
Forest floor ($\mathbf{B_f}$), browse recovery	0.99	0.94–1.06
Two-substrate model (A), control	1.18	1.12–1.23
Two-substrate model (A), browse recovery	1.07	1.04–1.11

While model projections for submatrices $\mathbf{B_r}$ and $\mathbf{B_f}$ assume no seed migration, the two-substrate models incorporate subpopulations that are linked via seed migration between substrates. Models for populations exposed to livestock browse incorporated the demography of both browsed and non-browsed palms weighted according to the proportion of palms that were browsed. The demography of browsed palms was based on data from a burro browse experiment conducted August 2003. These palms were protected from subsequent herbivory for one additional year after the experiment to estimate recovery from browse. Confidence intervals obtained from bootstrap analyses ($n = 1,000$)

Fig. 6 Patterns of seedling recruitment in *C. radicalis*. Reported are mean seedling recruitment distances (±SD) based on a census of new seedlings within a 10-m radius for each of *n* females that fruited during the previous year

Fig. 5 Comparison of the observed proportion of *C. radicalis* (excluding seeds) on each substrate with the projected stable stage distributions from single-substrate population matrix models (Appendix 2). Control models were parameterized based on substrate-specific annual demographic rates from protected palms for 2003–2004 and 2004–2005. Demographic data for $\mathbf{B}_{f(browse)}$ and $\mathbf{B}_{f(browse\ recovery)}$ were collected from palms during the year of a burro browse experiment (2003–2004) and 1 year of recovery after the experiment (2004–2005). Observed proportions were calculated from sampling data reported in Endress et al. (2004a). Abbreviations are as defined in Fig. 1

both browsed and non-browsed individuals, the negative impact of herbivory on the browsed palms was so great that the entire forest floor subpopulation was projected to decline ($\lambda < 1$). The projected population growth rate for

palms recovering from browse ($\mathbf{B}_{f\ (browse\ recovery)}$) was more similar to values for browsed populations ($\mathbf{B}_{f\ (browse)}$) than to non-browsed populations ($\mathbf{B}_{f\ (control)}$), but not significantly below the replacement rate of $\lambda = 1$. As with the control models, the projected stable stage distribution for the browse recovery model overestimated the relative proportion of seedlings and underestimated the proportion of both adult stages (Fig. 5). Stable stage distributions for browsed palms more closely predicted the observed proportions, and accurately projected the relative proportion of seedlings and juveniles on the forest floor.

Seed dispersal and source-sink dynamics

Patterns of seedling recruitment were very similar for 2003–2004 and 2004–2005, and revealed that most *C. radicalis* seeds disperse within a few meters of their parent plant (Fig. 6). Although we were unable to quantify the fate of the few seeds that dispersed beyond our study plots, results from seed traps showed that nearly all seeds produced within our plots (>95% of all seeds) on both substrates dispersed to the forest floor. During 2003–2004, palms on rock outcrops dispersed 92% (±SE 4.6%, $n = 24$ females) of their seeds to the forest floor, while 99% (±SE 0.1, $n = 30$ females) of all seeds produced by palms on the forest floor remained on that substrate. Likewise, during 2004–2005, palms on rock outcrops dispersed 83% (±SE 1.5%, $n = 30$ females) of their seeds to the forest floor and 96% (±SE 2.5%, $n = 30$ females) of seeds produced by palms on the forest floor remained on the forest floor. These seed dispersal values were used to parameterize submatrices $\mathbf{M}_{f\rightarrow r}$ and $\mathbf{M}_{r\rightarrow f}$, and were incorporated into the two-substrate population models $\text{A}_{control}$ and A_{browse} with the substrate-specific demographic data in submatrices $\mathbf{B_r}$ and $\mathbf{B_f}$ (Fig. 2).

Table 2 Comparison of the observed proportion of *C. radicalis* on two substrates with the observed proportion of each substrate type and the projected distribution of palms from population matrix models

	Substrate		χ^2	P	Δ
	Rock outcrops (%)	Forest floor (%)			
Observed palm distribution[a]	28.3	71.7	–	–	–
Observed substrate distribution[b]	18.1	81.9	2.8	0.093	36.2
2003–2004 projections					
Two-substrate model (A), control	0.8	99.2	35.3	<0.005	55.0
Two-substrate model (A), browse experiment	23.8	76.2	0.8	0.362	9.0
2004–2005 projections					
Two-substrate model (A), control	4.8	95.2	19.2	<0.005	47.0
Two-substrate model (A), browse recovery	12.0	88.0	8.0	0.005	32.6

Projected distributions were stable stage distributions generated from two-substrate matrices that linked palms on rock outcrops to those on the forest floor by seed dispersal. Palm distributions on each substrate type include all stages except seeds

P values are from Pearson's chi-square tests. Δ is Keyfitz's index of dissimilarity

[a] Calculated from sampling data reported in Endress et al. (2004a; $n = 922$)

[b] From 2003 sampling data based on ten 50-m line transects placed near the permanent plots in Cañon del Diablo ($n = 86$ rock outcrops)

Fig. 7 Comparison of the observed proportion of *C. radicalis* (excluding seeds) on each substrate with the projected stable stage distributions from the two-substrate, source-sink population matrix models (Fig. 2). For each model and the observed proportions, the size of each *pie chart* is proportional to the projected number of individuals on each substrate. Matrix models $A_{control}$ and A_{browse} were parameterized based on substrate-specific demographic rates from 2003 to 2004. Model $A_{browse\ recovery}$ was parameterized with 2004–2005 data based on the demography of palms after 1 year of recovery from burro browse. Results from model $A_{control}$ for 2004–2005 were not included, as they were very similar to the 2003–2004 control results. Observed proportions were calculated from sampling data reported in Endress et al. (2004a). Abbreviations are as defined in Fig. 1

Matrix model $A_{control}$, which was based on the demography of non-browsed palms, projected an overall positive rate of population growth for both 2003–2004 and 2004–2005 (Table 1). For each of these control models, the stable stage distribution predicted that nearly all palms will be on the forest floor, and therefore the proportion of palms predicted to be on rock outcrops was much lower than that observed in wild populations (Table 2). This model was also a poor predictor of the relative abundance of each stage on a given substrate, as projected stable stage distributions were very different from observed proportions on each substrate (Fig. 7).

The two-substrate projection matrix A_{browse}, which incorporated the demography of browsed palms on the forest floor (Fig. 2), projected an overall population growth that was not significantly different than from the replacement rate of $\lambda = 1$, indicating a population in stasis (Table 1). Population growth rates from $A_{browse\ recovery}$, which incorporated the demography of palms after 1 year of recovery from browse, however did project positive population growth at a
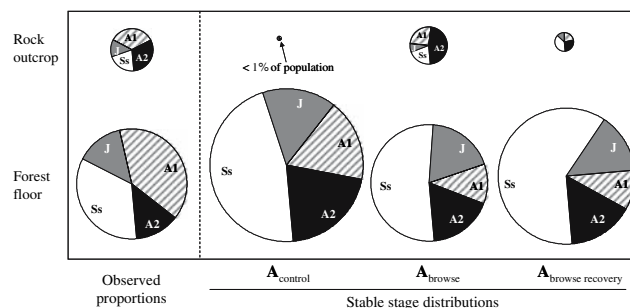
rate intermediate between browsed and non-browsed populations. Stable stage distributions of both of these browse models more closely approximated the relative abundance of palms on the two substrates than the stable stage distribution of $A_{control}$, but only A_{browse} projected substrate distributions that were statistically similar to observed palm distributions (Table 2). A_{browse} also projected stable stage distributions that most closely predicted observed stage distributions, where seedlings comprise a much greater proportion of the population on the forest floor than on rock outcrops (Fig. 7). This pattern contrasts with the single substrate model projections (Fig. 5) that predicted proportionally more seedlings on rock outcrops; a difference explained by incorporating seed migration into the two-substrate models.

Discussion

The impact of substrate and herbivory

Despite observed differences between rock outcrops and the forest floor in palm distribution, abundance, and fecundity (Endress et al. 2004a; Berry and Gorchov 2006), substrate was not the direct cause of spatial demographic variation in *C. radicalis*. Instead, this demographic variation was due to differences in herbivory from free-range livestock, which in turn was related to substrate. In the absence of livestock browse, palms on rock outcrops and forest floor had similar demographic rates, and matrix models incorporating these rates projected nearly identical finite rates of population growth (λ), both of which were significantly above the

replacement rate of 1. These estimates of population growth were also very similar to λs previously reported for *C. radicalis* in populations protected from leaf harvest and livestock browse (Endress et al. 2004a: $\lambda = 1.18$; Endress et al. 2006: $\lambda = 1.06$–1.18), and were well within the range of $\lambda = 0.98$ (Zuidema 2000) to $\lambda = 1.26$ (Silva Matos et al. 1999) that has been reported for other palms in undisturbed populations.

Unlike substrate alone, herbivory did have a negative impact on *C. radicalis* by reducing the survival and growth of each stage, except large adults. These low rates of mortality for large individuals are perhaps not surprising, as this trend has been observed in several other long-lived understory palm species (Piñero et al. 1984; Oyama and Mendoza 1990; Pinard 1993; Olmsted and Alvarez-Bullya 1995; Endress et al. 2004a). And while the effects of herbivory on survival and growth were more modest for adult palms than for the smaller stages, browsed female adults did show a sharp decline in fruit production, an effect that persisted into the year following browse, when other vital rates recovered toward pre-browse levels. These demographic impacts after one full year of recovery from browse, when incorporated into a matrix model, projected a population growth rates well below that for non-browsed palms on the forest floor. These findings are consistent with experimental data from a related understory palm, *C. elegans* that showed a significant decrease in resource allocation to reproductive structures in response to artificial defoliation (Anten et al. 2003).

In the absence of seed dispersal from rock outcrops, this loss of fecundity contributed to the projected population decline of forest floor palms exposed to livestock browse. For single-substrate population models, the contrast between the projected population decline of browsed palms on the forest floor and the positive population growth of non-browsed *C. radicalis* on rock outcrops highlights the importance of substrate heterogeneity in mediating the impact of herbivory.

Similar natural features of the landscape such as bolder tops (Rooney 1997) and barriers formed from tree-falls (Schreiner et al. 1996; Long et al. 1998) have been shown to deter ungulate herbivory in temperate forests. Within our study areas, the karst limestone outcroppings and very steep slopes (>20%; Endress et al. 2004a) that characterize much of El Cielo limited the accessibility of free-range livestock to some palms, particularly those on rock outcrops. And although burros are generally better able to navigate this rugged terrain than horses or cattle (E.J. Berry, personal observation), the burro in our experiment did not browse on rock outcrops, which effectively made these areas a refuge from herbivory. Therefore, differences in *C. radicalis* demography between the two substrates were due to differences in accessibility.

Source-sink population dynamics

Our results indicate that the criteria for source-sink dynamics on two substrates apply to *C. radicalis*: (1) rock outcrop subpopulations ($\mathbf{B_r}$) are sources, where in the absence of migration $\lambda > 1$, (2) forest floor subpopulations ($\mathbf{B_f}$) are sinks, where in the absence of migration $\lambda < 1$, and (3) there is net positive migration from rock outcrop to forest floor (i.e., $\mathbf{M_{r \to f}} > \mathbf{M_{f \to r}}$). However, criterion (2) applies only in the presence of free-range livestock. The overall positive rate of population growth on both substrates projected for the populations exposed to free-range livestock indicates that seed migration from sources is more than sufficient to sustain subpopulations in sink areas. Such asymmetric migration fits the third condition listed above for a source-sink population, which is a criterion that has most often been left unexamined in similar studies of plant populations (Pulliam 1996; Eriksson 1996).

This finding is particularly important to our study of *C. radicalis*, because in addition to confirming the dependence of forest floor areas on seed dispersal from rock outcrops, these results highlight the importance of seed dispersal in shaping the distribution of *C. radicalis* across the landscape. Plant ecologists have long recognized that such patterns of seed dispersal can have a significant effect on plant population dynamics (Kadmon and Shmida 1990), but relatively few studies have examined these processes based on field data from real populations (e.g., Platt 1975; Werner 1975; Keddy 1982; Hanzawa et al. 1988; Watkinson et al. 1989; Valverde and Silvertown 1997; Kadmon and Tielbörger 1999). This lack of quantitative field data is most likely due to the difficulty of measuring seed dispersal in the field. While individuals of *C. radicalis* produce few fruits (32 per female; Berry and Gorchov 2004), most of which disperse a short distance from the parent plant, quantifying dispersal for plants with much greater seed production or longer distance dispersal is more difficult. However, creative advances in field techniques for monitoring seed dispersal (Wang and Smith 2002) have made it more feasible to collect field data required to test some of the expectations from models of seed dispersal.

For *C. radicalis*, the asymmetric pattern of seed migration also helps explain why, at stable stage distribution, approximately three-fourths of the individuals (excluding seeds) were projected to occur on the forest floor, despite the fact that demographic rates on that substrate were significantly reduced due to herbivory. This projection is consistent with observed palm distributions on the two substrates within El Cielo (Table 2). Like the observed distribution, the projected distribution by the browse model includes slightly fewer palms on the forest floor than one would expect based simply on observed substrate distribution. While the difference was not statistically significant, this trend is consistent with the

higher palm density in rockier areas previously reported for *C. radicalis* within El Cielo (Jones and Gorchov 2000), providing further support that rock outcrops are important refuges from livestock herbivory in El Cielo. This explanation is consistent with other studies that documented the impact of herbivory on the demography of *C. radicalis* (Endress et al. 2004a), as well as on the population structure and abundance of several other species (e.g., Anderson and Loucks 1979; Allison 1990; Sullivan et al. 1995; Schreiner et al. 1996; Rooney 1997).

Patterns of seed migration also help to explain observed stage distributions of *C. radicalis* on rock outcrops and the forest floor (Fig. 7). More specifically, the asymmetric pattern of seed migration provides an explanation for why there are proportionally more seedlings on the forest floor than on rock outcrops, even though fruit production on rock outcrops is greater and there is no difference in rates of seed germination between the substrates. Our models showed that in the absence of seed migration (i.e., single substrate models), projected stable stage distributions tended to overestimate the proportion of seedlings relative to larger palms on rock outcrops. When seed dispersal was included in the two-substrate models, projected stable stage distributions were a much closer fit with the observed population structure. This is important because the closer the match between current stage structure and the projected stable structure, the more closely the short-term population dynamics will reflect long-term (asymptotic) estimates of population growth (Caswell 2001; Koons et al. 2005).

Population model strengths and limitations

Although the population matrix models used in our study were parameterized from the specific demography of individuals on rock outcrops and the forest floor, these models were not spatially explicit; meaning that they did not directly incorporate the area or distribution of the two substrates throughout the forest. The accurate prediction of the proportion of palms that occur on each substrate type within El Cielo by the two-substrate model incorporating livestock browse provides evidence that the demographic and dispersal data used to parameterize these models accurately reflected patterns found in natural populations. However, a limitation of these models is that they do not provide information about how *C. radicalis* population dynamics might change, if for example the landscape included proportionally more or less rock outcrops. This model also assumed that rates of seed migration were uniform throughout the population, regardless of the proximity, number, or size of rock outcrops. One could imagine instances where this

assumption might be violated, such as if more seeds fall off small rock outcrops to the forest floor than on very large outcrops or if there were reduced seed recruitment in forest floor areas with fewer rock outcrops. Incorporating some of these spatially explicit variables into future population models for *C. radicalis* can add to our understanding of how palm population dynamics might be influenced by changes in the type or arrangement of rock outcrops within the landscape. Such spatially explicit models have proven useful in studying mobile animal populations (Pulliam et al. 1992), and have even produced results that would otherwise not be observed by a nonspatial approach (Wiegand et al. 1999).

The population matrix models used in this study proved to be very useful as an effective test for source-sink dynamics in a plant population. As reviewed in the Introduction, very few studies of plant populations have been designed to specifically test the source-sink concept. Our study documented source-sink dynamics within *C. radicalis* populations by extending the idea of source-sink regional dynamics between populations to include the spatial demographic variation that is observed within populations of *C. radicalis*. In addition to testing the more general source-sink concept, results from this study also provide a more specific understanding of how landscape heterogeneity within El Cielo interacts with herbivory to produce spatial variation in palm demography.

Implications for palm conservation

The impact of livestock browse on palm distribution and abundance is of particular concern in areas where *C. radicalis* leaves are harvested. These leaves are sold to international floral and horticultural markets, and in El Cielo are the only forest products residents are authorized to harvest, providing the main source of income for most families (Peterson 2001). Due to a large and increasing demand for *Chamaedorea* leaves (CEC 2002), there is a concern that over-harvesting of leaves will lead to a decline in palm abundance, threatening the long-term economic sustainability of leaf harvest. These concerns apply to *Chamaedorea* spp. populations throughout Mexico and Central America, which has generated interest in certification programs as a means of promoting sustainable harvest practices. However, results from this study and others (Sullivan et al. 1995; Endress et al. 2004a) suggest that livestock herbivory may have a greater effect than leaf harvest on palm demography and population growth. Although leaf harvest has been shown to reduce *C. radicalis* population growth, the effect of leaf removal is not dramatic enough to reduce λ

significantly below 1, which implies that current leaf harvest practices are ecologically sustainable (Endress et al. 2004b; Endress et al. 2006).

In contrast, population projections from the same study (Endress et al. 2004b) that were based on the demography of browsed palms did result in a projected population decline consistent with our population projections for the forest floor subpopulation exposed to burro browse. Our two-substrate model also indicates that seed dispersal from the more fecund large adult palms on rock outcrops is sufficient to sustain the forest floor subpopulation. Thus, the survival and fruit production of these few large adults on rock outcrops is crucial to population persistence, even though they comprise only a small minority proportion of the entire population. Furthermore, because most seeds disperse to forest floor areas, seedling recruitment on rock outcrops is naturally low, which can make these subpopulations more vulnerable to unexpected palm mortality than those on the forest floor. For example, if large adults on rock outcrops were to experience a 5% increase in mortality, the overall finite rate of population growth (both substrates) in areas exposed to free-range livestock would fall below the replacement rate of 1 ($\lambda = 0.997$). With this in mind, management strategies that are designed to promote population persistence and sustainable leaf harvest should consider the important reproductive contribution of this subset of individuals, for example by restricting the harvest of their leaves.

In conclusion, the interaction between substrate and herbivory to produce source-sink population dynamics in *C. radicalis* highlights the importance of environmental factors in determining population dynamics. Future assessments of harvest sustainability of non-timber forest products (NTFP) should consider these factors as an important source of demographic variation within palm populations. Indeed, recent papers that examined NTFP sustainability have called for more studies to incorporate landscape heterogeneity into population models (Endress et al. 2004a; Ticktin 2004). Our results show that such modified models better incorporate processes that are important to population dynamics. Identifying the factors, both natural and anthropogenic, that most influence the population growth of harvested species will aid governmental agencies and non-governmental organizations involved in their conservation and management. For the specific case of *Chamaedorea* palms, certification programs to promote conservation and sustainable leaf harvest should consider livestock browse in addition to leaf harvest practices.

Appendix 1

Table 3 Proportion of adult *C. radicalis* fruiting, and mean fruits per fruiting adult for rock outcrops versus forest floor

	Rock outcrop	Forest floor	Test statistic	*P* value
August 2003–2004				
Number of adult palms	150	136	–	–
Percentage of adults fruiting	9.3	11.8	0.74[a]	0.390
Mean fruit per fruiting adult	44.8	32.5	1.00[b]	0.318
August 2004–2005				
Number of adult palms	159	138	–	–
Percentage of adults fruiting	8.2	7.2	0.09[a]	0.765
Mean fruit per fruiting adult	64.6	72.3	0.02[b]	0.877

Values for each substrate were calculated from pooled data for both reproductive sizes of small adults and large adults

[a] Likelihood-ratio chi-square (G^2)

[b] Kruskal–Wallis statistic (H)

Appendix 2

Table 4 Single-substrate projection matrices for browsed and non-browsed (control) *C. radicalis*

Model	Stage	S	Ss	J	A1	A2
2003–2004						
Control, rock outcrop	S	0.00	0	0	0.35	8.11
	Ss	0.13	0.79	0.08	0	0
	J	0	0.17	0.39	0.05	0
	A1	0	0	0.47	0.70	0.10
	A2	0	0	0	0.24	0.89
Control, forest floor	S	0.06	0	0	0.10	6.67
	Ss	0.16	0.62	0.00	0	0
	J	0	0.29	0.50	0.03	0
	A1	0	0	0.45	0.66	0.05
	A2	0	0	0	0.26	0.90
Browse experiment, forest floor	S	0.06	0	0	0.02	1.24
	Ss	0.16	0.58	0.08	0	0
	J	0	0.20	0.44	0	0.00
	A1	0	0	0.20	0.53	0.09
	A2	0	0	0	0.27	0.86

Table 4 continued

Model	Stage	S	Ss	J	A1	A2
2004–2005						
Control, rock outcrop	S	0.01	0	0	0.62	7.69
	Ss	0.25	0.73	0.04	0	0
	J	0	0.19	0.48	0.03	0
	A1	0	0	0.44	0.77	0.05
	A2	0	0	0	0.18	0.93
Control, forest floor	S	0.02	0	0	0.62	7.69
	Ss	0.25	0.67	0.04	0	0
	J	0	0.24	0.43	0.04	0
	A1	0	0	0.43	0.65	0.06
	A2	0	0	0	0.24	0.92
Browse recovery, forest floor	S	0.02	0	0	0.23	3.20
	Ss	0.25	0.75	0.13	0	0
	J	0	0.15	0.36	0.10	0
	A1	0	0	0.30	0.54	0.06
	A2	0	0	0	0.27	0.91

Each model assumes no seed migration between substrates. Models for populations exposed to livestock browse incorporated the demography of both browsed and non-browsed palms weighted according to the proportion of palms that were browsed. The demography of browsed palms was based on data from a burro browse experiment conducted August 2003. These palms were protected from subsequent herbivory for one additional year after the experiment (2004–2005) to estimate recovery from browse. Abbreviations represent life history stages as described in Fig. 1

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