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Habitat and microsite influence demography of two herbs in intact and degraded scrub

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Abstract Identifying environmental factors associated with vital rate variation is critical to predict population consequences of environmental perturbation. We used matrix models to explore effects of habitat and microsite on demography of two widespread herbs, *Chamaecrista fasciculata* (partridge pea) and *Balduina angustifolia* (yellow buttons). We evaluated models simulating population dynamics in common microsites (shrub, litter, bare sand) within two habitats (intact, degraded Florida scrub) using data on experimental populations initiated by sowing seeds, and natural seed production. Models included four stages (seed bank, small vegetative, large vegetative, reproductive) and three vital rates (survival, growth, fecundity), summarized in sixteen transitions. We conducted life table response experiments to assess contributions of each habitat and microsite to population growth rates. We found that (1) *C. fasciculata* had greatest population growth in degraded habitat and litter microsites, (2) *B. angustifolia* had similar population growth between habitats and greatest in bare sand microsites, (3) advancing growth transitions of *C. fasciculata* had greatest elasticity on population growth in degraded habitat, shrub, and litter, as did seed survival in intact habitat and bare sand, (4) seed survival and advancing growth transitions of *B.*

angustifolia had greatest elasticity on population growth in both habitats, as did seed survival in shrub and litter, and advancing growth in bare sand. Greater population growth of *C. fasciculata* in degraded scrub is probably explained by release from belowground competition; *B. angustifolia* may be most affected by competition with shrubs. Microsites in intact scrub were not ecologically equivalent to those in degraded scrub emphasizing that intact scrub is ecologically complex and critical to preserve.

Keywords Anthropogenic disturbance · Establishment · Florida · Germination · LTRE · Periodic matrix model

Introduction

Identifying environmental factors associated with variation in vital rates is critical to understanding population dynamics (Benton et al. 2006; Bakker et al. 2009; Crone et al. 2011), predicting consequences of environmental perturbation (Pollnac et al. 2014), and our ability to design better management plans (Miyashita et al. 2008). Studies of population dynamics that collect environmental data have the opportunity to examine the influence of these factors on vital rates particularly when proper experimental controls are utilized.

Demographic models considering environmental factors have demonstrated the importance of evaluating these variables to understand population dynamics. Examples of significant factors for plant species include vegetation cover and light availability (Valverde and Silvertown 1998; Jacquemyn et al. 2010), grazing (Bullock et al. 1994), time-since-fire (Menges and Dolan 1998; Satterthwaite et al. 2002; Quintana-Ascencio et al. 2003; Liu et al. 2005), hurricane damage (Pascarella et al. 2007), and levels of

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gap-opening (Sletvold and Rydgren 2007). These types of models have also identified the demographic effects of interactions between environmental factors (e.g., grazing and drought, Martorell 2007; temperatures and slope gradient, Nicolè et al. 2011; mowing and summer temperatures, Sletvold et al. 2013). Population growth in animals was notably affected by decreased predation and El Niño weather patterns (Bakker et al. 2009). Other models revealed only small effects of environmental factors such as canopy disturbance on population growth rates of understory plants (Cipollini et al. 1993) and particular chemical toxicants on some animals (Forbes et al. 2010).

Only two studies of plants evaluated the effect of anthropogenic habitat degradation on vital rate variation: one found negative effects (Martinez et al. 2010), while the other found similar population growth between degraded and intact habitats (Bell et al. 2003). It is important to study the influence of habitat degradation by mechanical disturbance on population dynamics because there may be effects on vital rates such as germination (Hellstrom et al. 2009), survival (Heelemann et al. 2012), or reproduction (Suazo et al. 2012). Degradation and disturbance could favor pioneer species such as opportunistic herbs (Brown and Schoknecht 2001; Feng et al. 2012). These effects may be particularly pronounced in specific microsites, such as bare sand gaps where there is more opportunity for recruitment and less competition.

We compared population dynamics of two common scrub herbs in degraded and intact habitats, using data from multiple sites per habitat, and examined the same three microsites in each site: shrub leaf litter located under shrubs with no nearby herbs ("shrub"), litter with no nearby shrubs or herbs ("litter"), bare sand with no nearby shrubs or herbs ("bare sand"). These microsites were typical in both habitats, and represented a gradient in plant structure and biomass. We tracked individual emerged seedlings of study species in each combination of habitat and microsite conditions. We used stage-based periodic matrix models to explore how population growth rate and the relative importance of stage transitions could be affected by successional changes in habitat availability and microsite abundance. We used both prospective (perturbation analyses) and retrospective (Life Table Response Experiments, LTRE) approaches to evaluate potential effects of habitat degradation and microsite on vital rate variation in these species.

We conducted our study in Florida scrub, an ecosystem recognized for its concentration of rare and endemic plants (Abrahamson et al. 1984). A number of these species are herbs that recruit seedlings in bare patches between shrubs (e.g., Menges and Kimmich 1996; Quintana-Ascencio and Morales-Hernández 1997; Petrů and Menges 2003; Schafer et al. 2010). We focused on experimentally initiated

populations of two herbs that grow in degraded and intact scrub: *Balduina angustifolia* (Pursh) B. L. Rob. (yellow buttons; semelparous) and *Chamaecrista fasciculata* (Michx.) Greene (partridge pea; primarily semelparous). We chose these two species because of characteristics conducive to manipulative experiments evaluating demographic effects of habitat and microsite: relatively sizeable and abundant seeds, fast growth rates, and widespread occurrence, relative to co-occurring species. We expected these species to be influenced to different degrees by the same environmental factors because of their different ecological relationships with soil microbes (*C. fasciculata* is a legume), and different life cycle (*B. angustifolia*: typically biennial, *C. fasciculata* typically annual).

For both species we predicted (1) greater population growth in degraded than in intact scrub because more isolated shrubs and extensive bare sand areas in degraded scrub (Navarra and Quintana-Ascencio 2012) may promote emergence and seedling establishment as for herbs in bare sand gaps in intact scrub (e.g., Menges and Kimmich 1996; Quintana-Ascencio and Morales-Hernández 1997; Petrů and Menges 2003; Schafer et al. 2010), (2) greater population growth in bare sand microsites than in microsites with shrubs or litter because of the open area available for recruitment, and (3) greater effects of individual growth (Cipollini et al. 1993; Silvertown and Franco 1993) and fecundity (Bullock et al. 1994; Silvertown et al. 1996) on population growth than survival, as was found in previous studies for plants in early successional habitats, gaps, increasing disturbance, and during early stages of colonization.

Methods

Study species and sites

Balduina angustifolia is an aster and a widespread gap specialist (Petrů and Menges 2004), with an annual or biennial life cycle, found in the southeastern United States (USDA, NRCS 2012). *Chamaecrista fasciculata* is an annual legume and a generalist (Foote and Jackobs 1966), found throughout eastern North America (USDA, NRCS 2012). The two species coexist in Florida scrub and have overlapping reproductive seasons: seeds of *C. fasciculata* are available in fall, while seeds of *B. angustifolia* are primarily available in fall to early winter. Both study species are a food source for wildlife: seeds of *C. fasciculata* are eaten by birds and deer (Gee et al. 1994; Yarrow and Yarrow 1999; Jones et al. 2010), and seeds of *B. angustifolia* are collected in quantity and primarily eaten by ants (*Pogonomyrmex badius*; M. Deyrup, personal communication), although birds were observed eating seeds

directly from the plant (C. Weekley, personal communication). Ants are also attracted to the extrafloral nectaries of *C. fasciculata* (Jezorek et al. 2011).

We conducted our study in the southern end of the Lake Wales Ridge in south-central Florida, a region characterized by some of the best remaining examples of intact Florida scrub (Weekley et al. 2008a). This ecosystem occurs on well drained, nutrient poor soils, and was historically maintained by lightning-ignited fires (Fernald and Purdum 1992). Many Florida scrub herbaceous species recover from fire and other disturbances by seedling recruitment, while shrubs primarily resprout (Menges and Kohfeldt 1995). We used intact scrub sites in Archbold Biological Station (ABS; 2,104 ha) and degraded scrub sites in the neighboring Archbold Reserve (Reserve; 1,476 ha), located in Highlands County. All sites shared Satellite soils and locally high elevations.

We chose intact scrub sites in rosemary scrub of ABS. Florida rosemary (*Ceratiola ericoides*) dominates the shrub layer of this open community, which is interspersed with patches of oaks (*Quercus* spp.), palmettos (*Serenoa repens* and *Sabal etonia*), *Lyonia* spp. and tough buckthorn (*Sideroxylon tenax*) (Abrahamson et al. 1984). Herbaceous species, many of them rare and endemic, and lichens grow in gaps of bare sand between shrubs (Christman and Judd 1990; Menges et al. 2008).

The degraded scrub of the Reserve was likely logged in the 1940s (determined by ABS staff using historical aerial photographs), and was roller chopped (date uncertain) and grazed by cattle until 2002 (Navarra and Quintana-Ascencio 2012). Roller chopping knocks down and breaks up ground vegetation (including shrubs and trees up to several inches in diameter) through the use of grader blades mounted on a large drum. This equipment is pushed or pulled by a tractor across the site, and it disturbs the top layer of the soil, severing shallow roots. Species composition in degraded scrub was similar to rosemary scrub, aside from the presence of nonnative grasses (*Digitaria eriantha* and *Rhynchelytrum repens*) in degraded sites. However, vegetation structure, microsite abundance, and species distributions differed between the two land types (Navarra and Quintana-Ascencio 2012). In degraded scrub, shrub patches were overgrown in height, while shrubs of rosemary scrub were typically only 2–5 m tall (Menges and Rickey unpublished data). Microsites differed in that bare sand areas surrounding shrubs were extensive in the degraded scrub (Navarra and Quintana-Ascencio 2012).

Seed collection and germination

We collected seeds at ABS and the Reserve in September to October 2009, prior to our population dynamics study. Intact, fully pigmented seeds were separated under a dissecting microscope; these were pooled to randomize seed source. Seed source randomization was intended to minimize any confounding effects of population genetics in the two habitats (e.g., Frankham et al. 2011). Seeds were stored in a refrigerator (4 °C) before use in the field and growth chamber. Background rates of germination were monitored in a growth chamber and considered as an upper boundary for expected germination of seeds in the field (Stephens 2013). We also conducted a preliminary study of seed production in natural populations in intact and degraded scrub (Stephens 2013).

Emergence and establishment

Each species was planted into three intact and three degraded sites in April 2009. We replicated experimental units in three microsites (litter under shrub ("shrub"), litter with no nearby shrub (units ≥ 1 m from shrubs, "litter"), bare sand with no nearby shrub ("bare sand"). Controls with no planted seeds were used to assess emergence from natural sources (Turnbull et al. 2000). Experimental units consisted of PVC rings (10.2 cm in diameter, 7.6 cm in depth, buried approximately 3.5 cm to keep seeds in place), each protected with a wire mesh vertebrate exclosure to reduce removal, and marked with wire-stake flags. Each experimental unit was randomly assigned a seed density (0, 1, 4, 8, 24; corresponded to approximately 0, 122, 490, 980 and 2,939 seeds per m^2). These densities were chosen in an attempt to capture natural variation, from a minimum possible number, to some number beyond those observed in field (Stephens 2013). Random seed density assignments were stratified by habitat and microsite. Seeds were deposited within a given PVC ring and sprinkled with sand until they were just covered. We monitored for seedling emergence and recorded plant survival, height and reproductive status once every week for the first month and monthly thereafter for 3 years. Treatment units were initially assigned locations based on coordinates of random points generated in ArcMap; coordinates were modified to correspond to the nearest (randomly) assigned microsite after each point was located using a Trimble Global Positioning System with sub-meter accuracy (GPS). Overall, there were 468 total units [units with seeds: 4 densities × 3 microsites × 3 replicates × 6 sites × 2 species; controls: 3 microsites × 6 sites × 2 (doubled to correspond to the two study species)] with 3,996 total seeds (Stephens 2013).

Modeling life cycles of *C. fasciculata* and *B. angustifolia*

Demographic matrix models

We built periodic matrix models representing seasonal intervals [summer (U) = June, July, August; fall

(F) = September, October, November; winter (W) = December, January, February; spring (S) = March, April, May] for each study species. Periodic models incorporate within-year data and examine between-year dynamics (Caswell 2001). Our models included four stages (seed bank, small vegetative plants, large vegetative plants, reproductive adults) and three vital rates (survival, growth, fecundity), summarized in sixteen transitions [Electronic Supplementary Material (ESM) S1].

We combined our four seasonal matrices into an annual matrix (ESM S2) using the fall to winter transition (B_{FW}) as the starting point in the cycle ($A = B_{UF} \times B_{SU} \times B_{WS} \times B_{FW}$; B_{UF} = summer to fall, B_{SU} = spring to summer, B_{WS} = winter to spring). B_{FW} was the most biologically appropriate choice as it was the seasonal transition during which the study species produced seeds. The starting point in the cycle was mathematically arbitrary because the annual population growth rate and associated sensitivity and elasticity values are not affected by this selection (Smith et al. 2005; Lesnoff et al. 2003). Due to the manner in which seasons are combined into an annual periodic matrix, a given transition represents strings of developmental steps occurring over multiple seasons. For example, depending of the number of seasons evaluated, a seedbank to seedbank transition (a_{11}, ESM S2) could represent a seed staying viable in the seedbank (from one season to the next), or a seed that germinates, survives to reproduce as an adult, with seeds that subsequently enter the seedbank (may take up to five seasons).

We constructed an overall matrix model (combining data pooled from all habitats and microsites), matrices for habitat-specific models (intact, degraded scrub), microsite-specific models (bare sand, litter, shrub), and habitat by microsite models (intact/shrub, intact/litter, intact/bare sand, degraded/shrub, degraded/litter, degraded/bare sand). Except as indicated, we built deterministic models with the following assumptions: (1) percent germination of seeds in the growth chamber represented initial viability of seeds produced by parent plants (V, Table 1), (2) all planted seeds were viable (probability of seeds surviving in the seedbank before germination (Ss) = 1, Table 1), (3) probability of survival in the seed bank in a given season was constant over time (Sb, Table 1; we fitted a survivorship curve to monthly emergence data from our field experiment and then extrapolated the likely number of seeds that survived in the seed bank each season after germination), and (4) individual seed production was estimated with the following equation:

$ph1 \times ph2 \times V \times Ss$

where $ph1$ = mean seeds per pod/head, $ph2$ = mean pods/heads per plant (Table 1).

Matrix stages were chosen based on biologically relevant morphological and life history data from our observations in the field. Seeds were considered part of the seed bank until emergence was recorded. Newly emerged plants ≤ 2 cm in height were considered small vegetative (non-reproductive) individuals, plants ≥ 2 cm without reproductive structures were considered large vegetative individuals, and plants displaying buds, flowers, or seed pods or heads were reproductive. These categories were appropriate because we observed a notable transition in each species between plants ≤ 2 and those >2 cm; individuals often remained ≤ 2 cm for many months, but grew more rapidly once they became >2 cm in height. *Balduina angustifolia* often bolted after exceeding 2 cm (Stephens 2013; *C. fasciculata* does not bolt).

We calculated population growth as the dominant eigenvalue for each matrix (deterministic lambda), and the stochastic lambda of successional simulated environments (Caswell 2000, 2001). We estimated deterministic and stochastic sensitivity and elasticity matrices (Caswell 2000, 2001) of population growth for each model. Sensitivity is the rate of change (or slope) of lambda with respect to a change in any given element of the matrix (Caswell 2000; Mills 2007). Sensitivity analyses identify the absolute effect of small perturbations in each stage transition probability on the overall population growth rate. Elasticity analyses provide sensitivity values proportional to the matrix element. These analyses were used to identify the transitions that had the greatest relative or proportional effect on population growth rate (de Kroon et al. 1986; Caswell 2000, 2001). We also examined the transition elasticities at individual seasons on population growth rate using the following equation (Caswell and Trevisan 1994):

$$E_{B_h} = \left(\frac{b_{ij}^{(h)}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}^{(h)}} \right)$$

The elasticities of λ to changes in the entries (b) of each (h) seasonal matrix **B** are given by Caswell (2001).

Bootstrapping

We used bootstrapping to estimate uncertainty in population growth of each matrix using sampling with replacement from the corresponding data subset (R Core Team (2013) 2.13.0; 1,000 iterations). Due to small sample size, values for fates of reproductive individuals were sampled from overall data for all matrices. We calculated mean and 95 % confidence intervals. Non-overlapping confidence intervals provided evidence of significantly different growth rates among treatment combinations.

Table 1 Vital rates and general seasonal matrix model of *C. fasciculata* and *B. angustifolia*

Vegetative				
	Seedbank	Small	Large	Reproductive
Seedbank	$[((ps \times Ss) - g) \times Sb]/ps$	–	–	$ph1 \times ph2 \times V \times Ss$
Small	$(Ss \times g)/ps$	$Sv1 \times (1 - Gs)$	$Sv2 \times Gl \times (1 - Fl)$	$Sr \times ph1 \times ph2 \times [(Ss \times g) / ps]$
Large	–	$Sv1 \times Gs \times (1 - Fs)$	$Sv2 \times (1 - Gl) \times (1 - Fl)$	$Sr \times (1-Fr)$
Reproductive	–	$Sv1 \times Gs \times Fs$	$Sv2 \times (1 - Gl) \times Fl$	$Sr \times Fr$

ps seeds in previous seasonal seedbank, *g* number of germinants, *Gs* probability of growth of small vegetative individuals (positive), *Gl* probability of growth of large vegetative individuals (negative), *Ss* probability of seed survival in seedbank (before germination), *Sb* probability of seed survival in seedbank (after germinants leave), *Sv1* probability of small vegetative survival, *Sv2* probability of large vegetative survival, *Sr* probability of survival for reproductive individuals, *Fs* probability of small individual becoming reproductive, *Fl* probability of large individual becoming reproductive, *Fr* probability of reproductive individuals remaining reproductive, *ph1* average seeds per pod/head, *ph2* average pods/heads per plant, *V* probability of seed viability

– structural zeros

Life table response experiments (LTRE)

We conducted LTREs to examine the effect of observed variation in vital rates by habitat, microsite, and habitat by microsite on population growth variation of each species using R (2.13.0, Popbio Package; Stubben and Milligan 2007). We examined summed contributions by habitat, microsite, and habitat by microsite to population growth. LTRE values are unitless and represent the relative contribution of each treatment (habitat, microsite) or transition to population growth rate (Caswell 1996).

Results

Vital rates of *C. fasciculata* and *B. angustifolia*

In natural populations across 2 years (2008–2009), we estimated 27.2 ± 3.8 pods of *C. fasciculata* per plant (mean ± SE per site) with 9.3 ± 0.7 seeds per pod in intact scrub, and 29.8 ± 0.1 pods per plant with 7.8 ± 0.5 seeds per pod in degraded scrub. We estimated 20.5 ± 2.2 heads of *B. angustifolia* per plant (mean ± SE per site) with 18.2 ± 2.2 seeds per head in intact scrub, and 20.3 ± 2.8 heads per plant with 21.2 ± 4.1 seeds per head in degraded scrub (Stephens 2013).

Of 999 seeds of *C. fasciculata* planted in each habitat, we observed a total of 256 emerged seedlings in intact scrub (mean ± SE per site: 85.3 ± 11.9) and 216 in degraded scrub (72.0 ± 10.1), with 3 total established plants (1.0 ± 0.6) in intact scrub and 24 established plants (8.0 ± 2.1) in degraded scrub (Stephens 2013). Mean lifespan of a *C. fasciculata* plant in intact scrub was 9.8 ± 0.2 months with a median of 2.0 and maximum of 28.0 months; mean lifespan was 7.7 ± 0.6 in degraded scrub with a median of 4.0 and maximum of 36.0 months. Of 999 seeds of *B. angustifolia* planted in each habitat, we observed 202 total emerged seedlings in intact scrub (67.3 ± 6.3) and 106 in degraded scrub (35.3 ± 7.8), with 26 total established plants (8.7 ± 2.3) in intact scrub and 37 (12.3 ± 3.8) in degraded scrub (Stephens 2013). Mean lifespan of a *B. angustifolia* plant in intact scrub was 9.8 ± 0.6 months, with a median of 6.0 months and maximum of 33 months; mean lifespan was 14.1 ± 0.9 in degraded scrub with a median of 14.0 and maximum of 36.0 months. Number of emerged seedlings and established plants increased with planted seed density (ESM S3a, b) (Stephens 2013).

Demographic matrix models of *C. fasciculata*

The overall model for *C. fasciculata* had a deterministic population growth rate (λ) of 1.65 (Fig. 1, ESM S4a). The degraded habitat model had a positive population growth rate ($\lambda = 1.88$), and intact habitat had a negative population growth rate ($\lambda = 0.315$) (ESM S4b, c). Population growth rate was most affected by changes in advancing growth transitions (ESM S2) in the degraded habitat (Fig. 2a, ESM S4b), which contrast with regressive transitions such as returning to a vegetative state from a reproductive state, or reduction in height. This trend was notable in the spring to summer season for large vegetative to reproductive plants (SS_{43}). Within the degraded habitat, production of seeds was notably greater in summer to fall (SF_{14}) than in other seasons. Changes in stasis transitions most affected population growth rate in the intact habitat (Fig. 2b, ESM S4c), particularly seed survival, especially in the winter to spring (WS_{11}), but also changes in vegetative survival in the spring to summer (SS_{33}).

Population growth rate was positive in the shrub ($\lambda = 1.135$, ESM S4d) and litter microsites ($\lambda = 1.52$, ESM S4e), and negative in bare sand ($\lambda = 0.62$, ESM S4f). As with the degraded habitat models, population growth rates in the shrub and litter microsite models were most

Fig. 1 Life cycle of *C. fasciculata*. Values correspond to overall annual matrix model (pooled habitats, microsites); labels correspond to generalized annual matrix model (ESM S2). *Broken lines* show transitions with values of less than 0.075
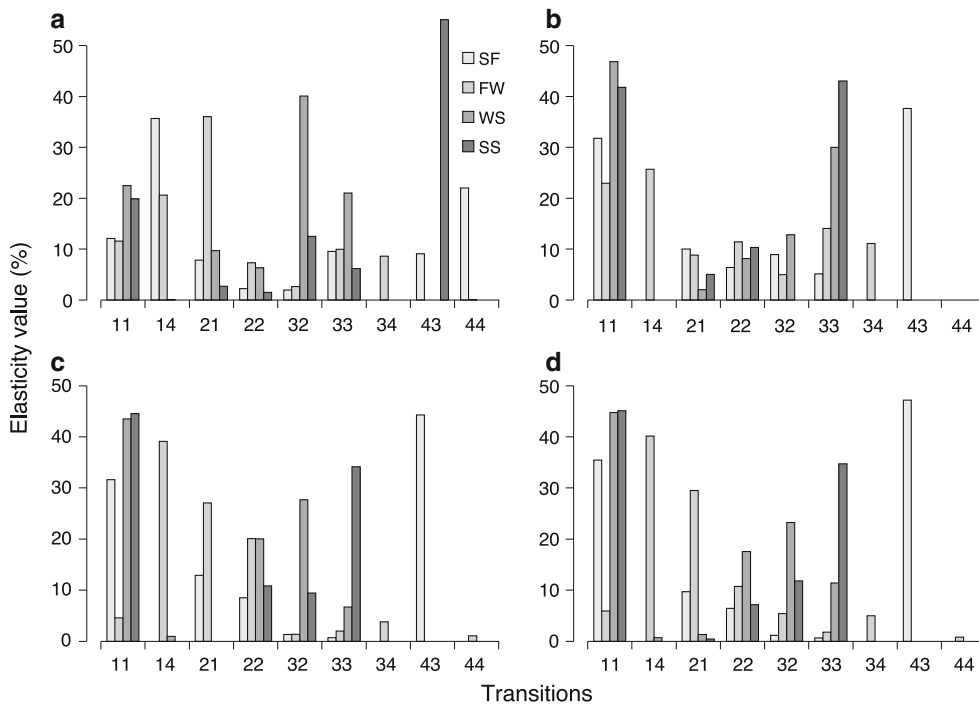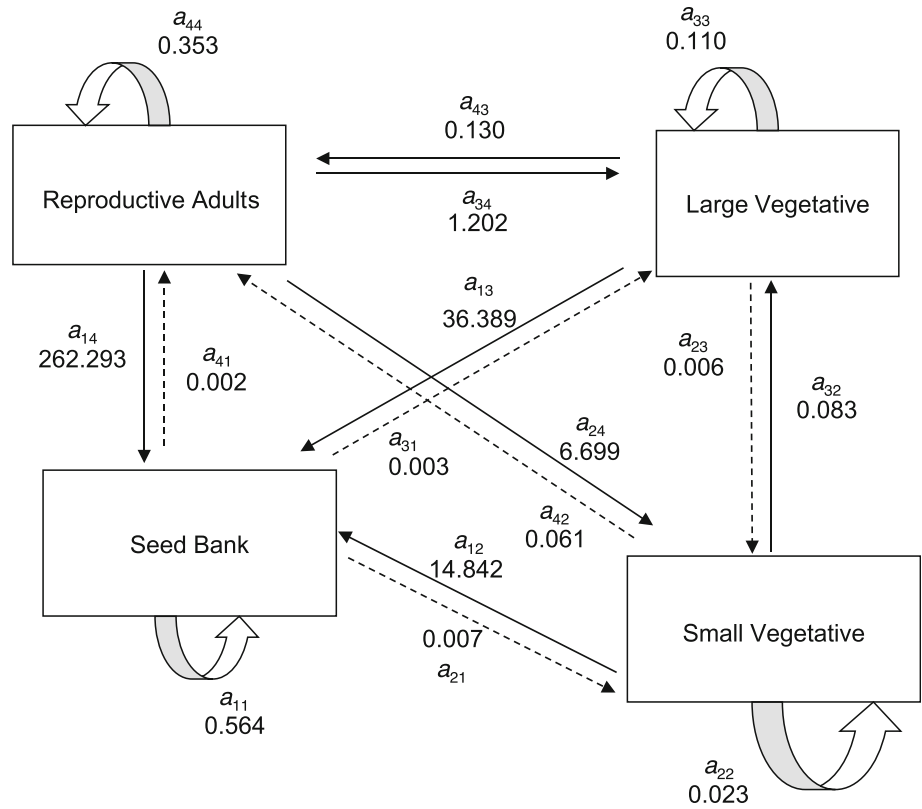

Fig. 2 Elasticity values for habitat matrix models with seasonal contributions to population growth rate. **a** *C. fasciculata* in degraded habitat, **b** *C. fasciculata* in intact habitat, **c** *B. angustifolia* in degraded habitat, **d** *B. angustifolia* in intact habitat. *SF* summer to fall, *FW* fall to winter, *WS* winter to spring, *SS* spring to summer. Transition numbers correspond to generalized annual matrix model (ESM S2). Other transitions are not shown because all four seasons had elasticity values of less than 0.02
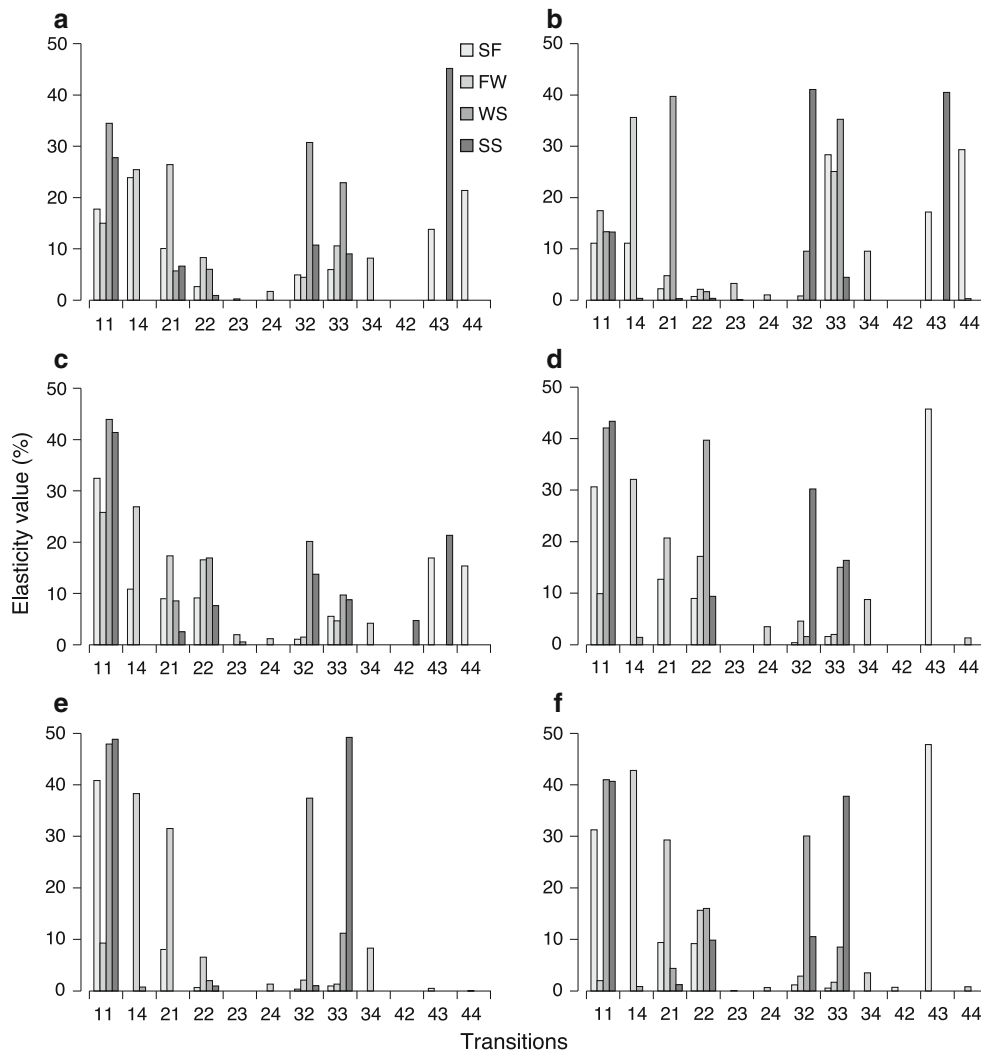
Fig. 3 Elasticity values for microsite matrix models with seasonal contributions to population growth rate. **a** *C. fasciculata* in shrub microsite, **b** *C. fasciculata* in litter microsite, **c** *C. fasciculata* in bare sand microsite, **d** *B. angustifolia* in shrub microsite, **e** *B. angustifolia* in litter microsite, **f** *B. angustifolia* in bare sand microsite. *SF* summer to fall, *FW* fall to winter, *WS* winter to spring, *SS* spring to summer. Transition numbers correspond to generalized annual matrix model (ESM S2). Other transitions are not shown because all four seasons had elasticity values of less than 0.02

affected by changes in advancing growth transitions (Fig. 3a, b), especially in the spring to summer in the litter microsite (SS_{32}, SS_{43}). Population growth in litter was much more affected by stasis transitions in summer to fall (SF_{33}, SF_{44}) than in the other microsites. Population growth rate in the bare sand microsite model (Fig. 3c) was most affected by seed bank survival as in the intact habitat model, especially in the winter to spring (WS_{11}).

Mean population growth rates from bootstrapped data were similar to those from observed data (Fig. 4). Bootstrapped lambdas had mostly normal distributions, with some bimodal distributions (Fig. 4). Confidence intervals in intact/bare sand and intact/litter combinations did not overlap each other or degraded/shrub, and those for intact/bare sand did not overlap degraded/bare sand. Those treatment combinations with the smallest deterministic

population growth rates had the narrowest confidence intervals (intact/litter, intact/bare sand); degraded/litter and degraded/bare sand had the widest confidence intervals (Fig. 4).

Demographic matrix models of *B. angustifolia*

The overall demographic matrix model for *B. angustifolia* had a deterministic population growth rate (λ) of 1.75 (Fig. 5, ESM S4g). Both habitat models had very similar, positive population growth rates (degraded: $\lambda = 1.49$, ESM S4h; intact: $\lambda = 1.43$, ESM S4i). Population growth rate in each habitat was most affected by changes in transitions of stasis especially in winter to spring (WS_{11}) and spring to summer (SS_{11}) and advancing growth transitions, especially large vegetative to reproductive in summer to
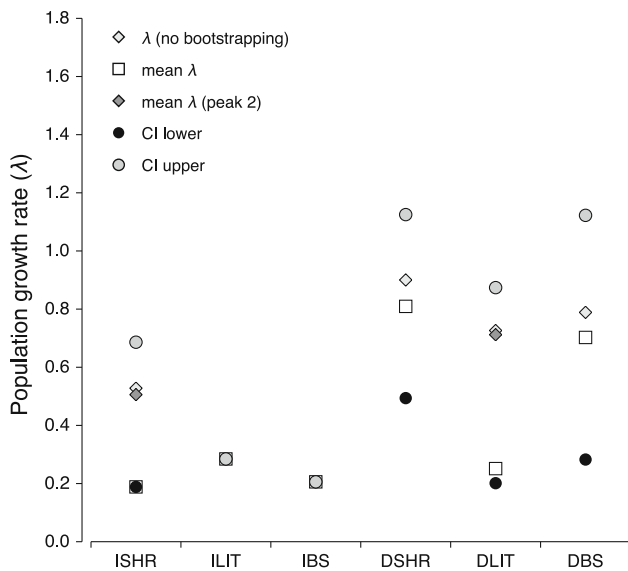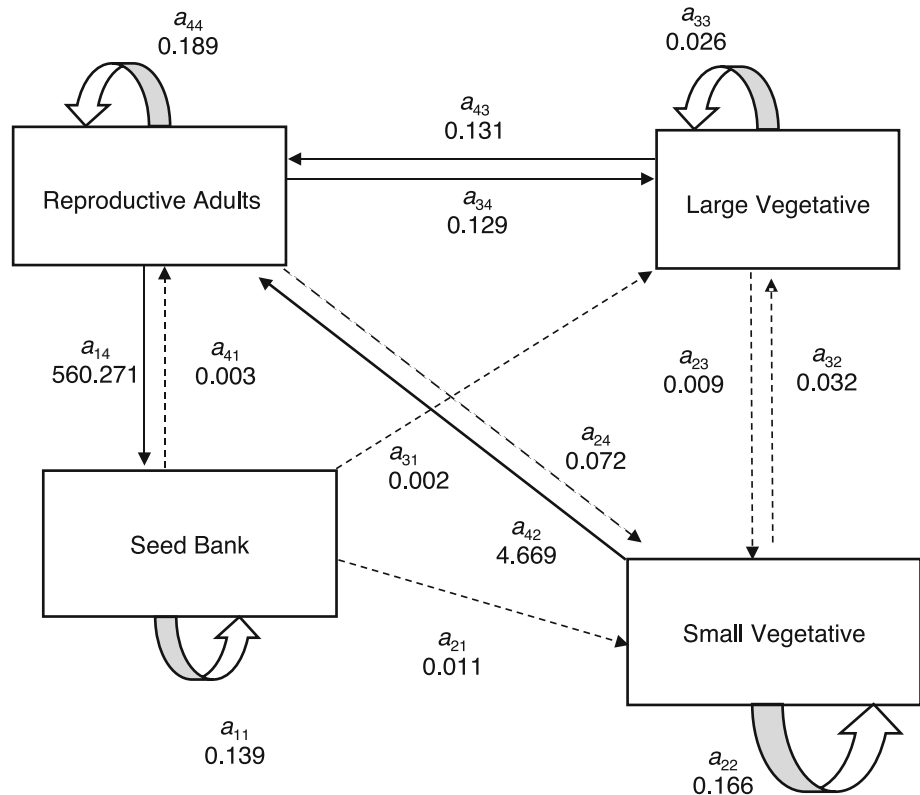
Fig. 4 Population growth rates (λ) for *C. fasciculata* with and without bootstrapping. Mean λ result of 1000 bootstrap iterations, *CI* confidence interval for mean λ. Normal distributions of bootstrapped λ are represented by one mean λ; bimodal distributions of bootstrapped λ values are represented by two mean λ values (mean λ: greater of the two λ values, mean λ peak 2: smaller of the two values). *ISHR* shrub microsite in intact habitat, *ILIT* litter microsite in intact habitat, *IBS* bare sand microsite in intact habitat, *DSHR* shrub microsite in degraded habitat, *DLIT* litter microsite in degraded habitat, *DBS* bare sand microsite in degraded habitat

fall (SF_{43}) (Fig. 2c, d, ESM S4h, S4i). Seasonal elasticity results exhibited less variation in *B. angustifolia* than in *C. fasciculata*.

The shrub microsite model had the smallest population growth rate ($\lambda = 0.56$, ESM S4j), followed by litter ($\lambda = 1.18$, ESM S4k) and bare sand ($\lambda = 1.71$, ESM S4l). Population growth rates were most affected by changes in stasis transitions in shrub and litter (a_{11}) (Fig. 3d, e). Within the shrub microsite, elasticity for vegetative regression was greatest in fall to winter (reproductive to large vegetative, FW_{34}), and vegetative stasis was greatest in winter to spring (WS_{22}). Within litter microsites, elasticity values for large vegetative stasis were greater in winter to spring (WS_{33}) and spring to summer (SS_{33}) relative to the other two seasons, and small vegetative to large vegetative growth was greatest in winter to spring (WS_{32}). Stasis in the seedbank was markedly lower in fall to winter (FW_{11}) than in the other seasons. Advancing growth transitions were most influential in bare sand microsites, especially large vegetative to reproductive plants in summer to fall (SF_{43}, Fig. 3f).

Mean population growth rates from bootstrapped data were similar to data without bootstrapping (Fig. 6). Bootstrapped lambdas had mostly normal distributions, with some bimodal distributions (Fig. 6). Only confidence intervals in intact/bare sand and degraded bare sand overlapped each

Fig. 5 Life cycle of *B. angustifolia*. Values correspond to overall annual matrix model (across habitats, microsites); labels correspond to generalized annual matrix model (ESM S2). *Broken lines* show transitions with values of less than 0.075. a_{12} and $a_{13} =$ zero
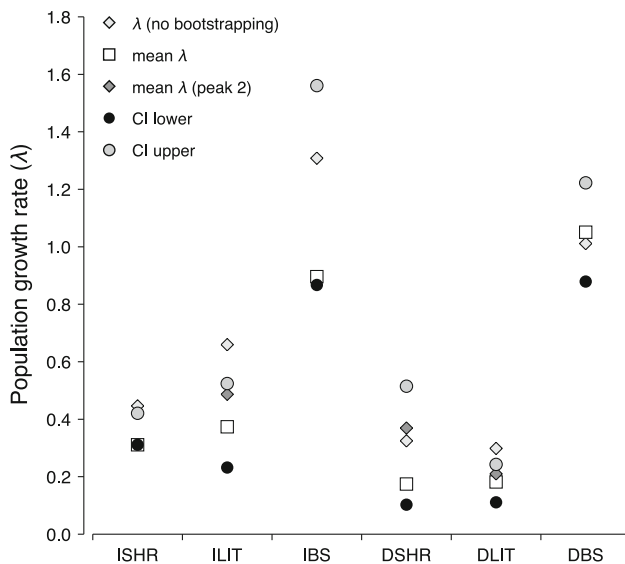
Fig. 6 Population growth rates (λ) for *B. angustifolia* with and without bootstrapping. *Mean λ* result of 1000 bootstrap iterations, *CI* confidence interval for mean λ. Normal distributions of bootstrapped λ are represented by one mean λ; bimodal distributions of bootstrapped λ values are represented by two mean λ values (mean λ: greater of the two λ values, mean λ peak 2: smaller of the two values). *ISHR* shrub microsite in intact habitat, *ILIT* litter microsite in intact habitat, *IBS* bare sand microsite in intact habitat, *DSHR* shrub microsite in degraded habitat, *DLIT* litter microsite in degraded habitat, *DBS* bare sand microsite in degraded habitat

other. Intact/shrub and degraded/litter treatment combinations had the smallest confidence intervals; intact/bare sand had the widest confidence intervals (Fig. 6).

Life table response experiments of *C. fasciculata*

Degraded habitat had a positive contribution to overall population growth of *C. fasciculata*, whereas intact habitat had a negative but greater absolute contribution to population growth of the overall model (Fig. 7a). Seed production (a_{14}, Fig. 7b) in intact habitat and germination from the seedbank in degraded habitat (a_{21}) had the greatest absolute contributions to population growth, but it was positive in degraded and negative in intact habitat.

The shrub microsite had a small negative contribution to population growth rate. Litter was the only microsite with a positive contribution to overall population growth rate and it had the greatest absolute contribution (Fig. 7c). Bare sand had a negative contribution to population growth (Fig. 7c). Survival of seeds in the seedbank (a_{11}, Fig. 7d) was the transition with the greatest contribution to population growth in all three microsites, but it was negative in the shrub and bare sand, and positive in litter.

All habitat by microsite treatment combinations in intact habitat were negative and those in degraded scrub were

positive (Fig. 7e). The degraded/litter treatment had the greatest absolute contribution, while the degraded/shrub treatment had the smallest absolute contribution to overall population growth rate. The intact/shrub and degraded/litter had the survival of seeds in the seedbank as the greatest individual contribution to population growth rate (a_{11}, Fig. 7f). Other important contributions were: production of seeds by reproductive adults in degraded/bare sand (a_{14}), survival of seeds in seedbank through germination to large vegetative survival in degraded/shrub (a_{31}), germination and survival to small vegetative in intact/litter (a_{21}), and reproduction through germination and small vegetation survival in intact/bare sand (a_{24}).

Life table response experiments of *B. angustifolia*

For *B. angustifolia*, both intact and degraded habitats had small contributions to overall population growth. Unlike in *C. fasciculata*, degraded habitat had a negative contribution and intact habitat had a positive contribution (Fig. 8a). Seed survival through germination and growth to reproductive adult was the transition with the greatest contribution in each habitat (a_{41}, Fig. 8b), but it was positive in intact and negative in degraded habitat (Fig. 8b).

Shrub and litter microsites negatively contributed to population growth; bare sand positively contributed and represented the greatest absolute contribution to population growth (Fig. 8c). Survival of seeds through the reproductive stage (a_{41}, Fig. 8d) was the transition with the greatest contribution to population growth in litter and bare sand microsites but it was negative in litter and positive for bare sand. For the shrub microsite, seed production by reproductive adults (a_{14}, Fig. 8d) was the transition with the greatest contribution to population growth rate.

All of the habitat by microsite treatment combinations in the shrub and litter microsites were negative and those in bare sand were positive (Fig. 8e). Intact/bare sand had the greatest absolute contribution, while intact/litter had the smallest absolute contribution. The greatest contribution by an individual transition to population growth in intact/litter, intact/bare sand, degraded/litter and degraded/bare sand was the survival of seeds in seedbank through germination to reproductive adults (a_{41}, Fig. 8f). In the intact/shrub treatment, the greatest contribution by a transition was in production of seeds by reproductive adults (a_{14}), and for degraded/shrub it was small vegetative survival to reproduction (a_{42}).

Discussion

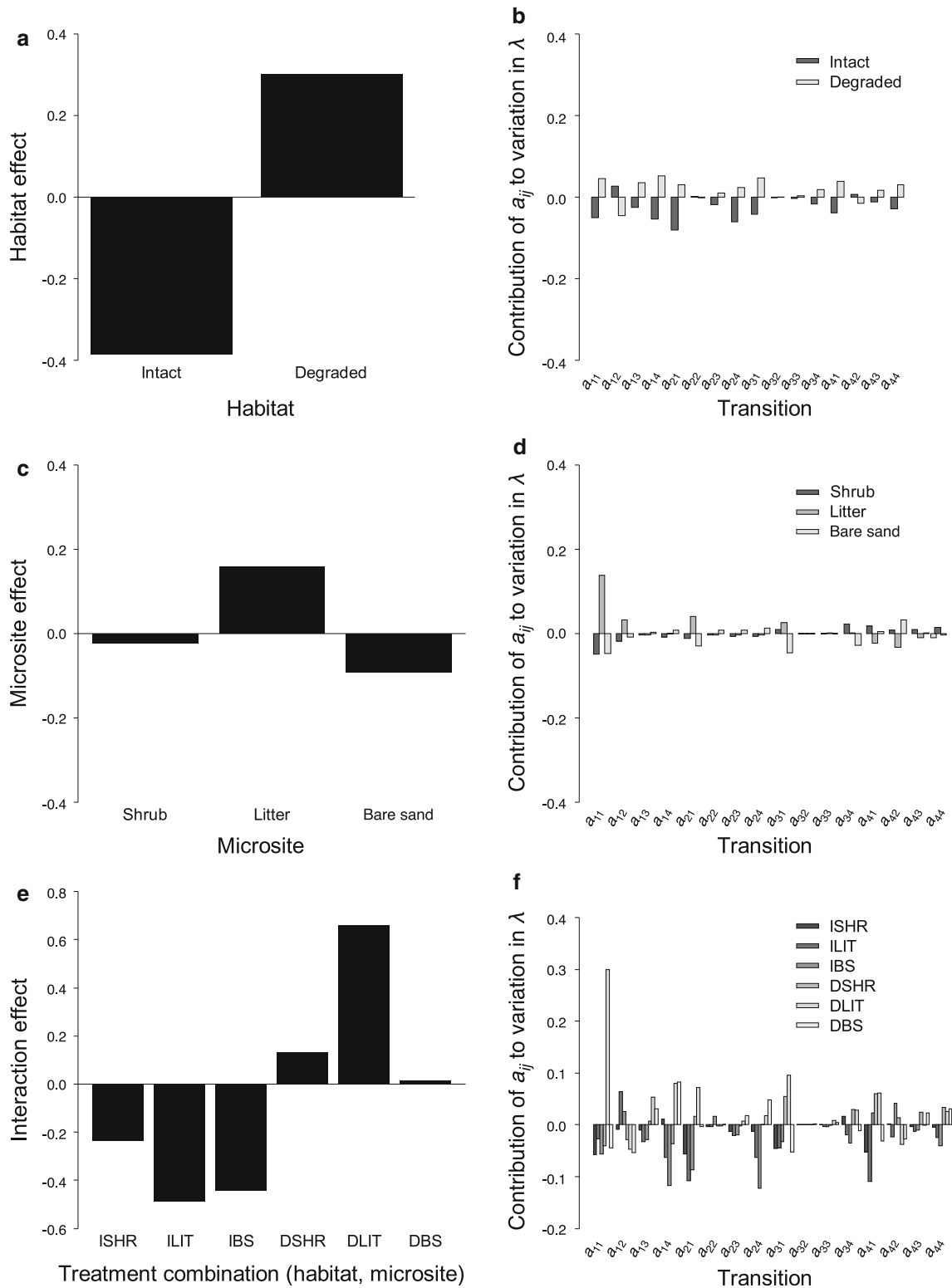The study of environmental factors associated with vital rate variation and demographic dynamics is essential to

Fig. 7 Results of LTRE for habitat of *C. fasciculata* (**a**, **b**), microsite (**c**, **d**) and habitat by microsite models (**e**, **f**). **a**, **c**, **e**: Contribution of each treatment to mean population growth rate. **b**, **d**, **f**: Contribution of each transition in each treatment to mean population growth rate; individual transitions represented by row, column numbers (i.e., a_{11} = seed survival in seedbank). For **f**: *ISHR* intact habitat/shrub microsite, *ILIT* intact habitat/litter microsite, *IBS* intact habitat/bare sand microsite, *DSHR* degraded habitat/shrub microsite, *DLIT* degraded habitat/litter microsite, *DBS* degraded habitat/bare sand microsite. *y*-axes of **e** and **f** are not equivalent in order to better display the contributions of the transitions
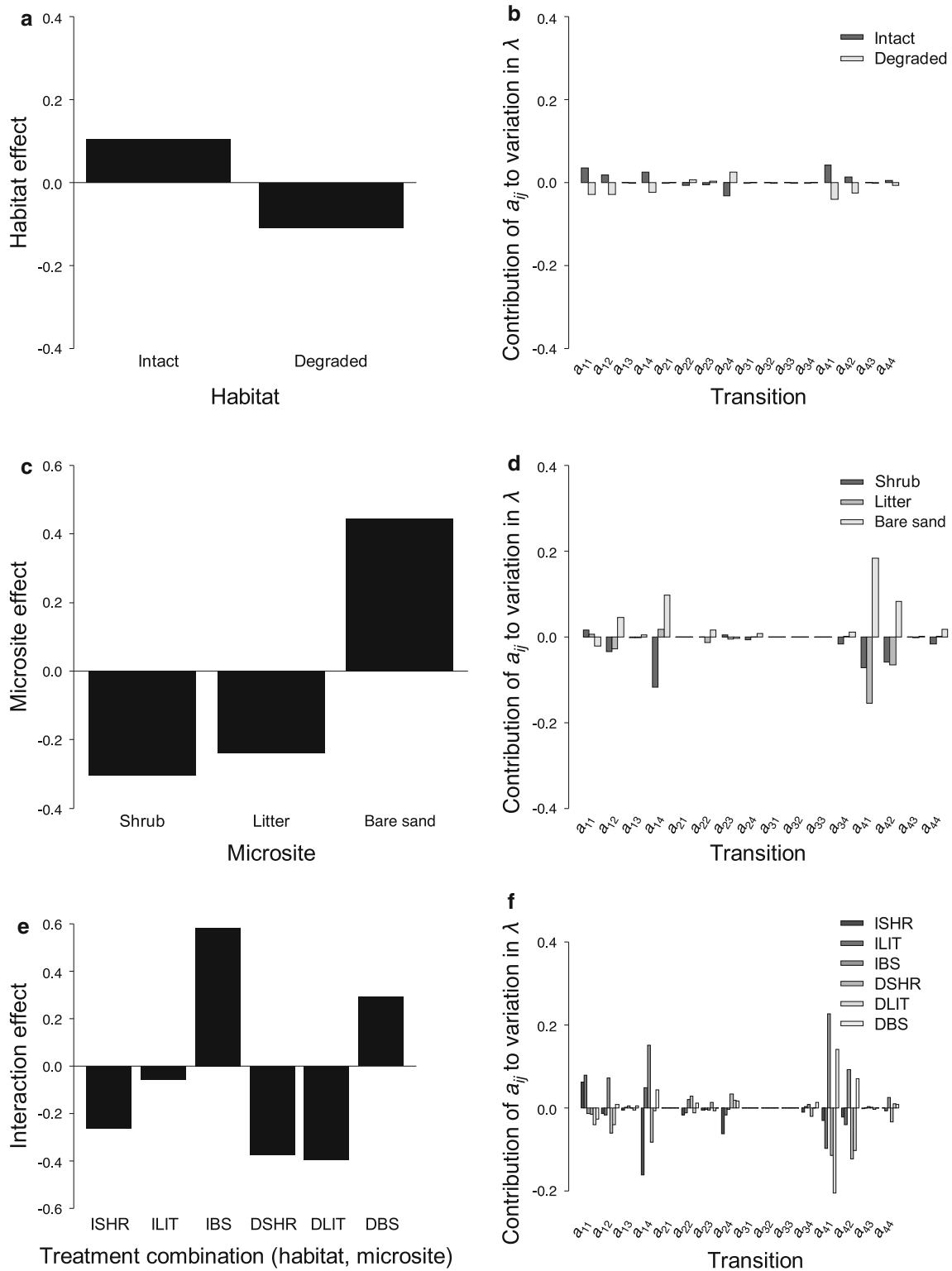
Fig. 8 Results of LTRE for habitat of *B. angustifolia* (**a**, **b**), microsite (**c**, **d**) and habitat by microsite models (**e**, **f**). **a, c, e**: Contribution of each treatment to mean population growth rate. **b, d, f**: Contribution of each transition in each treatment to mean population growth rate; individual transitions represented by row, column numbers (i.e., a_{11} = seed survival in seedbank). For **f**: *ISHR* intact habitat/shrub

microsite, *ILIT* intact habitat/litter microsite, *IBS* intact habitat/bare sand microsite, *DSHR* degraded habitat/shrub microsite, *DLIT* degraded habitat/litter microsite, *DBS* degraded habitat/bare sand microsite. *y*-axes of **c** and **d**, and **e** and **f** are not equivalent in order to better display the contributions of the transitions

understand the consequences of habitat change on species persistence (Crone et al. 2011). Comparative studies assessing responses of different species to habitat degradation and associated microsite variation help evaluate the effects of management actions. Results from our study of two short-lived herbaceous species suggest that particular habitat and microsite conditions can affect population dynamics of coexisting species in distinct ways. While degraded habitat conditions increased population growth for *C. fasciculata* across all microsites, there was little direct effect of habitat on population growth of *B. angustifolia*, which benefited from open sand in both degraded and intact habitat compared to the other microsites. Despite this microsite trend for *B. angustifolia*, population dynamics of our study species could not be explained by the presence of bare ground alone, as germination tended to be higher in intact habitats for both species, but fewer seedlings survived to become established plants.

Greater population growth rate of *C. fasciculata* in degraded habitats may be caused by reduced belowground competition for resources resulting from mechanical disturbance of root systems (Petrů and Menges 2003; Calabrese and Menges 2007; Breininger and Schmalzer 1990). Release from aboveground competition should not have influenced this experiment as planting locations were replicated evenly among microsites with and without shrubs in each habitat, and seeds were not planted near other herbs. Furthermore, we speculate that *C. fasciculata* may have a competitive advantage over co-occurring species in degraded scrub, but not in the intact scrub. Because it is a legume, *C. fasciculata* may have increased survival and reproduction associated with nitrogen fixation. This benefit may be obscured in intact scrub where features of other species confer more of a competitive advantage: extensive root systems enabling greater dominance of resource access in the densely colonized belowground environment, stronger relationships with soil microorganisms aiding in resource acquisition (e.g., soil crusts, Hawkes 2000), or greater tolerance of allelopathic shrub exudates (e.g., *Ceratiola ericoides*, Weekley et al. 2008b; Hunter and Menges 2002; Hewitt and Menges 2008) where distance-to-shrub is smaller than in degraded scrub. As certain *C. fasciculata* traits are plastic with respect to climate (rate of reproductive development, number of leaves, leaf thickness) (Etterson and Shaw 2001; Etterson 2004), there may be different interactions between this species and degraded vs. intact habitat conditions in other parts of its geographical distribution.

Variation in the relative importance of vital rates of *C. fasciculata* indicates demographic differences between habitats. Advancing growth transitions had a much greater effect on population growth rate in degraded habitat and had different seasonal contributions than in intact habitat.

The important transition from large vegetative to reproductive plants occurs in summer to fall in intact habitat; however, the same transition occurs earlier in spring to summer in degraded habitat. This pattern suggests that habitat degradation stimulates early reproduction in *C. fasciculata*, and reproductive phenology may be linked to population growth rate in this species. Seed survival was the most influential transition for long-term population growth in intact habitat; this was more pronounced in the winter to spring after reproductive plants died, and when seed predation may be most critical for this species. In general, seasonal elasticity values in *C. fasciculata* exhibited more variation than in *B. angustifolia*. This result was logical, as plants with relatively shorter life cycles tend to have less population stability (García et al. 2007).

Overall, population dynamics of *C. fasciculata* only partially supported our prediction that individual fecundity and growth would affect population growth more than individual survival. As there were significantly more established plants (large vegetative and reproductive plants) in degraded scrub (Stephens 2013), it is likely that the number of reproductive plants and associated seeds entering the seedbank were limiting in intact scrub. An increased number of seeds in the seedbank should increase number of emerging seedlings, as negative density dependence did not appear to limit emergence. Despite differences between habitats, we found that population dynamics of *C. fasciculata* were strongly influenced by seed dynamics. This pattern is also common among plants in arid habitats (Pico et al. 2003; Salguero-Gómez et al. 2012), in which seeds are ecologically important to survival in harsh abiotic conditions (Brown et al. 1979; Freas and Kemp 1983). Although Florida Scrub can have great annual rainfall (mean 1,300 mm), this is concentrated in summer months, and similarities between scrub herbs and arid habitat plants may be explained by the need for scrub herbs to survive seasonal dry periods in well-drained soils (Chen and Gerber 1990).

Similar population growth rates for *B. angustifolia* in intact and degraded conditions were reinforced by our observations that adult plant densities did not differ between habitats (Stephens 2013). Populations in bare sand exhibited the greatest population growth rate for *B. angustifolia*. *Chamaecrista fasciculata*, in contrast, had the poorest population growth in this microsite. The greater overall effect of microsites on population dynamics of *B. angustifolia* may reveal that this species is subject to biological trade-offs in shrub microsites that *C. fasciculata* is not (McPeek 1996); this may explain the more generalist nature of *C. fasciculata* (Foote and Jackobs 1966) and descriptions of *B. angustifolia* as more of a gap specialist (Petrů and Menges 2004). *Balduina angustifolia* was most affected by shrub presence, similar to scrub endemic *Paronychia chartacea* (Schafer

et al. 2010). Trade-offs under shrubs may include diminished shoot growth or reproduction in exchange for greater root growth for belowground resource competition. Or, *B. angustifolia* may have reduced reproduction or root growth due to more investment in longer and thinner or branched shoots resulting from competition for light. Such competition would be more intense with shrubs than with smaller herbs or grasses found in open areas. Other negative effects of shrubs may include an increased presence of herbivores or seed predators (Weekley et al. 2008b). Herbivores or other factors may have a more pronounced effect on *B. angustifolia* than seed predators in shrub microsites, as seed predation was less intense under shrubs than in litter or bare sand microsites (Stephens 2013). The greater values for vegetative regression in the fall-winter transition, and greater values for vegetative stasis in the subsequent winter-spring transition, provide support for the idea that large vegetative individuals in shrub are indeed experiencing a negative pressure such as herbivory during this period. Such effects of shrubs may also reduce the likelihood of subsequent reproduction. Positive effects of bare sand gaps on *B. angustifolia* population growth could include the presence of beneficial soil microorganisms such as soil crusts (Hawkes 2000) that may be absent or less abundant under shrubs.

Seed survival in the seedbank was the most influential transition in the majority of models of *B. angustifolia*. It was only in bare sand where individual growth had the greatest influence on population growth rate that *B. angustifolia* partially supported our prediction about the relative importance of vital rates. Trends in *B. angustifolia* in bare sand microsites were consistent with studies of plants during early stages of colonization (Silvertown et al. 1996) and those exposed to relatively greater levels of disturbance (Bullock et al. 1994). Despite differences in which seed-related transitions are most important, the significance of seed dynamics for population persistence of both study species is similar to plants that recruit from seeds in dry ecosystems (Brown et al. 1979; Freas and Kemp 1983; Pico et al. 2003; Salguero-Gómez et al. 2012).

The strong effect of habitat on *C. fasciculata*, but not *B. angustifolia*, suggests that only *C. fasciculata* is directly affected by time-since-disturbance. In a recovery trajectory from an anthropogenic (mechanical) disturbance event to relative restoration of intact scrub conditions, we expect that *C. fasciculata* would have an initially positive population growth rate that would gradually decline to a negative rate. We expect that the change in these rates would mirror the establishment of competing plant species or recovery of soil microbes. Periodic disturbance events (especially belowground) would likely be required to maintain positive *C. fasciculata* population growth. In contrast, we expect very little direct effect of a transition from degraded to intact scrub for *B. angustifolia* within a given microsite. However, habitat type or quality may still affect *B. angustifolia* populations indirectly through microsite abundance or proportion within the habitat. The greater extent of bare sand gaps in degraded scrub may actually result in more *B. angustifolia* plants in degraded than in intact habitat. Also, the decreasing availability of bare sand gaps in intact scrub with increasing time-since-fire (Menges et al. 2008) would likely cause *B. angustifolia* populations to decline with fire suppression. Interactions between habitats and microsites suggested by our LTRE analysis (e.g., litter/degraded for *C. fasciculata*, intact/bare sand for *B. angustifolia*) could be studied in more detail to further identify likely population trends over the course of a habitat restoration. For example, if particular microsites in each habitat have very local differences in soil composition or allelopathic exudates, this may affect reproduction (Abdala-Roberts and Marquis 2007) or growth.

Our study links data from field experiments and matrix models in a way that clarifies the role of environmental factors in population growth and provides context for analyzing seed dynamics of our study species. We demonstrate how co-occurring species can be affected differently by habitat and microsite, and identify how available seed density may be relevant to the demography of these species. Our results suggest that for some species, bare sand gaps in intact scrub are not equivalent to the extensive bare sand areas in the degraded scrub. This conclusion is supported by the juxtaposition of a strong positive effect of degraded scrub and a negative effect of bare sand microsites on *C. fasciculata* population growth, as well as the lack of a specific effect of intact scrub vs. the strong positive effect of bare sand on *B. angustifolia* population growth. These trends further emphasize that intact scrub is ecologically complex and critical to preserve. Restoration efforts, while helpful in ameliorating some biotic and abiotic aspects of a habitat, may never achieve exact pre-degradation conditions (Schmalzer et al. 2002). Due to the intricate and often subtle ways that organisms are affected by their environments, it will be difficult to reestablish typical population dynamics of some species in habitat undergoing restoration. We strongly advocate for the protection of intact habitat whenever possible.

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