

Effects of habitat degradation, microsite, and seed density on the persistence of two native herbs in a subtropical shrubland¹

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PREMISE OF THE STUDY: Species in degraded ecosystems may interact differently with their surroundings from those under historic conditions. Understanding factors affecting variation in early life history stages of plants is fundamental to assessing their persistence in intact and degraded habitats, and the value of degraded lands. We evaluated the effect of seed density on the seed dynamics of two herbaceous species (annual, biennial), and considered how seed availability may influence population dynamics in different habitats (degraded, intact Florida scrub) and microsites (bare sand, leaf litter, shrub).

METHODS: We used data on responses to experimental treatments (seed removal, seedling emergence, establishment) and models to evaluate how effects of these factors may change over time since the last disturbance.

KEY RESULTS: Probability of any seed removal, emergence, and establishment per unit increased with seed density, although proportion removal for *Chamaecrista fasciculata*, proportion emergence for *Balduina angustifolia*, and proportion establishment for both species decreased with density. When animals were given selective access to seeds, invertebrates were primarily responsible for seed removal of both study species. Models with dynamics changing with time-since-disturbance for both species predicted that population growth may decrease slightly if local available seed density increases.

CONCLUSIONS: Detailed demographic comparisons of populations in intact and degraded conditions can be used to understand the way that environmental conditions (habitat, microsite) combine with seed density effects to influence population dynamics of herb species. Degraded habitat may act as a transitional state in a trajectory toward intact conditions for some species, or as refugia for other native species.

KEY WORDS anthropogenic disturbance; Florida; plant populations; population dynamics; restoration

Habitat degradation can result in altered species abundance and composition, and can be associated with the formation of “novel” or “emerging ecosystems” (Milton, 2003; Hobbs et al., 2006). Since few, if any, ecosystems remain unaffected by anthropogenic activities (Marris et al., 2013), it is important to understand how species in degraded systems may interact differently with their surroundings from those under historic conditions. Demographic comparison of native species in degraded and intact habitats can help to discern changes in population dynamics, thereby providing insight into the ecological value of altered ecosystems (Marris et al., 2013). Such detailed studies should clarify ways to protect our remaining undeveloped lands and the native species they support.

Studies of early life-history stages in degraded and intact conditions can reveal potential changes in persistence patterns, especially for those species that rely on dormant seeds until conditions are favorable for germination and establishment (Auld et al., 2000; Holmes and Newton, 2004). These patterns may be most pronounced in short-lived species that have relatively little time to respond to environmental changes. Demographic drivers of species with seed banks may include seed availability, which affects seed dynamics as relatively larger groups of seeds can attract more seed predators (Brewer and Webb, 2001; Montesinos et al., 2006) and increase the chance of germination compared to smaller groups (e.g., Poulsen et al., 2007). Variation in habitat (Tallmon et al., 2003; Ronnenberg et al., 2008) and microsite characteristics (Oswald and Neuenschwander, 1993; Parent et al., 2006) regulate the abiotic (resource availability, e.g., Coop and Givnish, 2008; Ronnenberg et al., 2008) and biotic (competition, e.g., Liu et al., 2008; facilitation, e.g., Kellman and Kading, 1992; seed predation, e.g., Tallmon et al., 2003) conditions for germination and seedling establishment.

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Furthermore, it is important to consider how these potential environmental drivers might affect population dynamics over a longer time period (Oostermeijer, 2003; Levine and Rees, 2004; Pausas et al., 2005). Plant population dynamics in degraded habitats can mimic some effects of disturbance in intact habitats (Quintana-Ascencio et al., 2007). Successful habitat restoration may be possible if population dynamics of individual species are able to return to the dynamics in native habitats. This pattern would bode well for historical abundances and composition of species. Conversely, species in degraded habitats may remain trapped in an altered state of population dynamics.

The main goals of this study were to: (1) estimate the effects of seed density on seed removal, emergence, and survival of two short-lived species with seedbanks; (2) determine if these effects are dependent on habitat (intact, degraded) and microsite (under shrubs, in leaf litter, bare sand); and (3) evaluate whether these effects change with time-since-disturbance. We conducted this study in Florida rosemary scrub, a community that supports a large number of herb species with seedbanks, many of which are endemic (Quintana-Ascencio and Menges, 2000; Navarra et al., 2011). Previous data have indicated differences in community composition and structure between degraded and intact scrub (Navarra and Quintana-Ascencio, 2012). Intact and degraded scrub differ in habitat structure, and abundance and distribution of microsites; degraded scrub has more isolated patches of overgrown shrubs and continuous bare sand areas (Calabrese and Menges, 2007). Despite an overall negative effect of degradation on scrub ecosystems, increased open habitat and reduction in shrub cover may result, at least transiently, in greater herb recruitment.

We expected that greater seed densities of opportunistic herbs *Chamaecrista fasciculata* (Michx.) Greene (partridge pea) and *Balduina angustifolia* (Pursh) B. L. Rob. (coastal plain honeycombhead) would attract more seed predators and increase seed removal (Casper, 1987; Montesinos et al., 2006), as well as increase seedling emergence (Poulsen et al., 2007), relative to smaller seed densities. We expected density-dependent factors such as self-thinning to be minimal for seedling emergence because herb seedling mortality can be high in seasonally dry ecosystems regardless of density (Sacchi and Price, 1992; Carrington and Keeley, 1999; Maschinski et al., 2004). At each seed density, we expected both species to have more seedlings emerge in scrub degraded by mechanical disturbance because the more open habitat structure may reduce competition for resources and seed predation (Pugnaire and Lozano, 1997; Cole et al., 2004). We expected greater seed predation in intact than in degraded scrub because greater cover of low shrubs in intact scrub may protect seed predators from carnivores (Restrepo and Vargas, 1999; Weekley et al., 2008b); this is well known in deserts (e.g., Thompson, 1982; Longland, 1994). We anticipated greatest seedling emergence in bare sand microsites where there is less below-ground competition for resources (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernández, 1997; Petru and Menges, 2003). We expected that both species would decrease in population growth with time-since-disturbance as intact scrub conditions returned and frequency of bare sand microsites decreased.

MATERIALS AND METHODS

Study species—*Chamaecrista fasciculata* (Michx.) Greene is an annual legume with relatively sizeable and abundant seeds, and a fast

individual growth rate. Seeds of *C. fasciculata* are produced in late summer to early fall, and are eaten by birds and deer (Gee et al., 1994; Yarrow and Yarrow, 1999; Jones et al., 2010). *Chamaecrista fasciculata* is found throughout eastern North America (USDA, 2012); it occurs in open woodlands, old fields, roadsides, dunes, savanna (black oak, pine), and prairie (coastal, tall-grass, short-grass) (Fenster, 1997). This species has been described as self-compatible but predominately outcrossing (Fenster, 1991a, 1995), and dispersal limited (both via pollen and seeds, Fenster, 1991a) with a short-lived seed bank (Baskin and Baskin, 1988; Baskin et al., 1998; Fenster, 1991b). *Balduina angustifolia* (Pursh) B. L. Rob. is a biennial aster and widespread gap specialist. Its seeds are collected in quantity and primarily eaten by ants (*Pogonomyrmex badius* (Latreille); M. Deyrup, Archbold Biological Station, personal communication), but birds were observed eating seeds directly from the plant (C. Weekley, Archbold Biological Station, personal communication). Roots of *B. angustifolia* are colonized by arbuscular mycorrhizal fungi, and it has a greater mycorrhizal inoculum potential than co-occurring herbs (Anderson and Menges, 1997). *Balduina angustifolia* is found throughout the southeastern United States (USDA, 2012) in scrubby flatwoods, rosemary scrub, and along sand roads (Anderson and Menges, 1997; Petru and Menges, 2003), in sandhill (Grelen, 1962), and in mesic, coastal areas (Cane et al., 1996).

Study sites—We conducted this study in intact and degraded scrub habitat at the southern end of the Lake Wales Ridge in Highlands County (Township 38S, Range 30E, sections 5–8, 18, 19, 29–32), south-central Florida, USA (Weekley et al., 2008a). This ecosystem occurs on well-drained, nutrient-poor soils. Community composition and habitat structure depend on periodic fires (Abrahamson et al., 1984; Fernald and Purdum, 1992). Many Florida scrub plant species recover from fire and other disturbances by seedling recruitment, although most shrubs primarily resprout (Menges and Kohfeldt, 1995). Yearly temperatures ranged from 8.33°C (January mean-minimum) to 34.05°C (July mean-maximum), with mean annual rainfall of 136.4 cm (Archbold Biological Station weather data). Sites had sandy Satellite soils (elevation ~45 m).

Florida rosemary scrub is dominated by Florida rosemary (*Ceratiola ericoides* Michx.), oaks (*Quercus* spp.), palmettos (*Serenoa repens* (Bartram) J.K. Small and *Sabal etonia* Swingle ex Nash), *Lyonia* spp., and tough buckthorn (*Sideroxylon tenax* L.) (Abrahamson et al., 1984). Herbaceous species, many of them rare and endemic, and lichens grow in gaps of bare sand between shrubs (Abrahamson et al., 1984; Christman and Judd, 1990; Menges et al., 2008). Frequency of fires in Florida rosemary is moderate to infrequent (15–40 yrs) (Menges and Kohfeldt, 1995; Menges, 1999). We chose intact rosemary scrub in Archbold Biological Station (ABS; 2104 ha; Swain, 1998) burned between 8 and 27 yrs before study initiation.

The degraded Florida scrub of the Archbold Reserve (area of Reserve: 1476 ha) was subjected to roller chopping, and light cattle grazing until 2002. Fire frequency prior to management by Archbold Expeditions is unknown (Archbold Biological Station, unpublished data). Species composition in the degraded scrub was similar to the intact rosemary scrub sites aside from the presence of invasive nonnative grasses (*Digitaria eriantha* Steud., *Rhynchelytrum repens* (Willd.) C.E. Hubbard). However, vegetation structure, microsite, and species distributions often differed between the two land types (David and Menges, 2011; Navarra and Quintana-Ascencio, 2012). In degraded scrub, patches of shrubs were overgrown, while the same shrub species in rosemary scrub were

typically 2–5 m high (E. Menges and M. Rickey, Archbold Biological Station, unpublished data). Microsites differed in that bare sand areas surrounding shrubs were more extensive in degraded scrub (E. Menges and M. Rickey, Archbold Biological Station, unpublished data). Percent organic matter was significantly greater in intact scrub, but phosphorus and nitrogen were slightly greater in the degraded scrub (S. Hamman and P. Bohlen, Archbold Biological Station, personal communication; E. Menges et al., Archbold Biological Station, unpublished data).

Seed removal—We assessed effects of habitat (intact, degraded scrub), microsite (shrub, litter, bare sand), and seed density on seed removal in February to March 2009 (Winter Trial) and May 2010 (Spring Trial) (Stephens, 2013). We assumed that seed removal was representative of postdispersal seed predation in this system because seeds of the two study species do not have eliasomes (lipid attachments) or fleshy fruit, giving animals little incentive to move them without consumption. We evaluated the following treatments to filter animal access to seeds: (1) no-access control comprised of a wire mesh cage covered with clear plastic, rimmed with sticky nontoxic Tanglefoot, with a PVC ring; no animals could access seeds; (2) limited-access treatment comprised of a wire mesh cage with no plastic or Tanglefoot, with a PVC ring; only invertebrates could access seeds; (3) all-access treatment with no cage, only a PVC ring as a procedural control; invertebrates and vertebrates could access seeds; and (4) unmanipulated treatment with no cage or PVC ring; invertebrates and vertebrates could access seeds. PVC rings were 10.2 cm in diameter and 7.6 cm depth, buried approximately 3.5 cm, and were used to reduce the effects of wind / water displacement. We used removal from the limited-access treatment as an estimate of invertebrate-mediated seed removal, and the difference between removal from the all-access treatment and removal from the limited-access treatment as an estimate of vertebrate-mediated seed removal.

Each individual treatment location, in each habitat / microsite, was referred to as a unit. We randomly selected three intact and three degraded Florida scrub sites among the sites within the station where the study species were present. Within each site we used the following three microsites: (1) “shrub” with units placed under shrubs with leaf litter; (2) “litter” with units placed in leaf litter without shrub cover; and (3) “bare sand” with no shrub cover or leaf litter. We used seed densities of 1, 4, 8, and 24 seeds (per 82 cm²). These densities were chosen in an attempt to capture natural variation, from a minimum possible number, to some number beyond those observed in field (E. Stephens, University of Central Florida, personal observation).

Within each treatment unit, the assigned number of seeds was sprinkled on top of a Petri dish full of substrate taken from the immediate neighboring area (mostly sand); dishes were retrieved after 48 h to count remaining seeds. This time period was based on preliminary experiments with commercially available seeds, as well as our previous seed removal study of endemic scrub herbs (Stephens et al., 2012), and other previous seed removal studies (Fedriani et al., 2004). This interval was well suited to assess differential removal rates without compromising the quality of the enclosure devices. We observed that shorter trials did not provide sufficient time for animals to encounter seeds, and longer trials resulted in decreased effectiveness of Tangle-Trap Sticky Coating (Tanglefoot, Contech, Victoria, British Columbia, Canada, for the no-access treatment) due to adhesion and accumulation of litter and dead insects.

The experiment had a 6 • 3 • 4 • 3 replicated factorial design, where treatments were all possible combinations of site, microsite, seed density, and seed access treatment, respectively. We used 234 total treatment replicates (units, described in the paragraph below), including 3 additional control treatments per microsite in each site, and 2070 seeds. Locations of units were assigned using random coordinates generated in ArcMap, and were located using a Trimble Global Positioning System (Trimble Navigation Limited, Sunnyvale, California, USA), with submeter accuracy (GPS) (Archbold coordinates 27°11' N, 81°21' W).

Seedling emergence and establishment—We assessed the effects of habitat and microsite on seedling emergence and establishment in two trials, from April 2009 to April 2012, and from May 2010 to May 2012. We used a parallel experimental design to the seed removal study (Stephens et al., 2014): each unit in shrub, litter, and bare sand microsites, in both intact and degraded habitats, was assigned a planting density of 1, 4, 8, or 24. Controls with no planted seeds were used to assess emergence from outside sources (Turnbull et al., 2000). All planted and control experimental units were protected by vertebrate enclosures, mirroring the limited-access treatments from the seed removal study. As we intended this study to build upon insight gained from the seed removal study, we did not use the other treatments from the seed removal study to examine the mechanism of any potential seed removal. In addition, long-term use of the vertebrate / invertebrate enclosures (no access treatment) would have been impractical due to the requisite cleaning and reapplication of Tangle-Trap Sticky Coating every 48 hours. 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).

TABLE 1. Logistic regression model of proportion seed removal of *Chamaecrista fasciculata* across trials (seed removal ~ habitat • microsite • season / year + enclosure treatment + seed density).

Coefficients	Estimate	SE	Z value	Pr(> Z)
Intercept	-5.15	1.13	-4.54	< 0.001
Habitat (degraded)	0.41	0.65	0.63	0.530
Microsite (litter) ^a	-2.36	0.74	-3.20	0.001
Microsite (bare sand) ^a	-4.09	0.90	-4.55	< 0.001
Season / year	-0.36	0.35	-1.03	0.304
Treatment (limited access)	2.67	1.01	2.63	0.008
Treatment (all access)	2.84	1.01	2.80	0.005
Treatment (unmanipulated)	3.55	1.01	3.51	< 0.001
Seed density	-0.02	0.01	-2.60	0.009
Habitat (degraded) • microsite (litter) ^a	0.30	1.06	0.28	0.780
Habitat (degraded) • microsite (bare sand) ^a	-2.07	1.52	-1.36	0.173
Habitat (degraded) • season / year ^a	0.30	0.43	0.71	0.476
Microsite (litter) • season / year ^a	2.14	0.45	4.76	< 0.001
Microsite (bare sand) • season / year ^a	3.08	0.52	5.96	< 0.001
Habitat (degraded) • microsite (litter) • season / year ^a	-1.47	0.64	-2.29	0.022
Habitat (degraded) • microsite (bare sand) • season / year ^a	0.34	0.83	0.41	0.684

Note: Degrees of freedom = 16. SE = standard error.

^aMicrosites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter vs. bare sand microsites: model estimate = 1.72, SE = 0.89, Z = 1.93, $P = 0.053$; degraded habitat with litter vs. degraded habitat with bare sand microsites: model estimate = 2.37, SE = 1.61, Z = 1.47, $P = 0.14$; litter vs. bare sand microsites (and season / year): model estimate = -0.94, SE = 0.47, Z = -1.99, $P = 0.047$; degraded habitat with litter vs. degraded habitat with bare sand microsites (and season/year): model estimate = -1.80, SE = 0.85, Z = -2.11, $P = 0.035$.

Statistical analyses—We conducted analyses in R (2.7.2, R Development Core Team, 2013). We used logistic regression to evaluate whether habitat, microsite, exclosure treatment, trial season / year, and seed density were associated with seed removal. Habitat (2 levels), microsite (3 levels), exclosure treatment (4 levels), and trial season / year (2 levels) were categorical predictor variables and seed density was a continuous predictor variable. The response variables were presence (1) or absence (0) of seed removal per treatment unit, and proportion seed removal. We used Akaike’s Information Criterion corrected for small sample sizes (AICc) to select the most plausible model of the set (Appendices S1a, S1b, see Supplemental

Data with the online version of this article). For seedling data, we conducted logistic regression analyses using habitat (2 levels), microsite (3 levels), and trial year (2 levels) as categorical predictor variables and seed density as a continuous predictor variable. The response variables were presence (1) or absence (0) of seedling emergence per treatment unit, and proportion of seedling emergence. Plants were considered established if they grew to ≥ 30 cm or had reproductive structures. Microsites were compared in two tests to examine all microsite pairs (shrub vs. litter, shrub vs. bare sand, litter vs. bare sand). Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha' = 0.025$). Monte

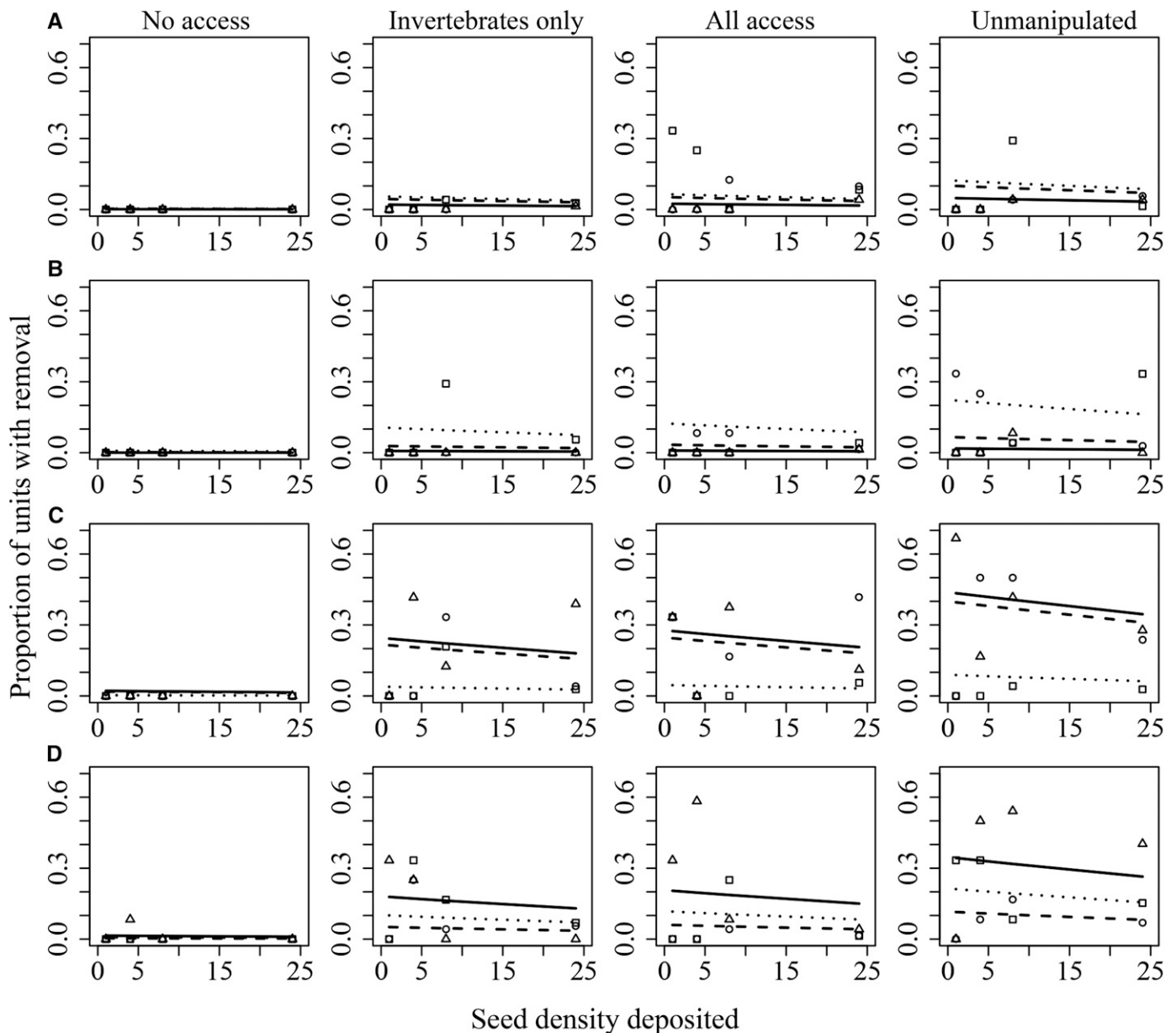


FIGURE 1 Predicted (lines) and observed (symbols) proportion seed removal of *Chamaecrista fasciculata* in each trial season / year, habitat, and exclosure treatment. Row A: removal from each exclosure treatment in intact habitat, Winter Trial, 2009; row B: removal from each exclosure treatment in degraded habitat, Winter Trial, 2009; row C: removal from each exclosure treatment in intact habitat, Spring Trial, 2010; row D: removal from each exclosure treatment in degraded habitat, Spring Trial, 2010. Solid lines and triangles represent bare sand microsites, dashed lines and circles represent litter microsites, and dotted lines and squares represent shrub microsites. Models were selected with AICc.

Carlo analyses were conducted to determine whether shrub species significantly affected emergence or establishment.

Models to evaluate change with time-since-disturbance—We simulated the effects of changes with time-since-disturbance associated with anthropogenic disturbance using population models based on our data (Stephens et al., 2014), and modified MATLAB code from Horvitz et al. (2010). Demographic models were created as periodic matrix models representing seasonal intervals, which were then combined into annual matrix models. These deterministic models included four stages (seed bank, small vegetative plants, large vegetative plants, reproductive adults) and three vital rates (survival, growth, fecundity). Models used habitat (intact, degraded scrub) and microsite-specific parameters (shrub, litter, bare sand). Population growth was calculated as the dominant eigenvalue for each matrix (deterministic λ), and the stochastic λ was calculated for successional simulated environments (Stephens et al., 2014).

Models for variable environments (Horvitz et al., 2010) were created by projecting the population matrices from one time to the next using sequences specified in an environmental matrix. Matrices were selected from the K possible states of the environment. In these models, the stochastic growth rate depended upon the frequency and sequence of environments. The elements in the environmental matrix determined the probability of going from one environmental state to another over one time step. Sample paths converged over time on an expected distribution of environments that was independent of the initial state, and the time average of cumulative population growth rate converged to the stochastic growth rate (Horvitz et al., 2010).

We created a time-since-disturbance environmental matrix comprised of transition probabilities from each habitat by microsite combination following an initially disturbed environment (Appendix 1). We used this environmental matrix in conjunction with six habitat by microsite matrices (Stephens et al., 2014), and a matrix representing a disturbance (e.g., fire, clearing) in which all plants died and only seeds in the seedbank remained (using the seed to seed transition, a_{11} , from the degraded model in Stephens et al., 2014).

We considered the above environmental matrix as a reference model because it did not incorporate particular seed densities or changes in availability of habitat by microsite combinations. We compared this model with scenarios in which only one habitat or microsite type was available, and considered the effect of seed density on survival in seed bank and emergence. We estimated approximately 10 seeds per m^2 in the degraded habitat ($0.04 \text{ plants} \cdot m^{-2} \cdot 240 \text{ seeds per plant}$; Stephens et al., 2014). We considered this number of seeds as the baseline density and associated to this number the estimated depredation and establishment of 10 seeds per PVC. We then compared the effects of seed densities greater and smaller than the baseline density.

RESULTS

Seed removal—*Chamaecrista fasciculata*—Proportion seed removal of *C. fasciculata* from individual units was best explained by the interactions among habitat, microsite and trial season / year and the additive effects of exclosure treatment and deposited seed density (Table 1, Fig. 1, Appendices S2a, S3; see Supplemental Data with the online version of this article). The occurrence or presence of seed removal for *C. fasciculata* was best explained by the additive

TABLE 2. Seed removal of *Chamaecrista fasciculata* per experimental treatment type (A) and per seed density deposited (B) in seed predation study (experimental units with removal, including percent of total units; seeds removed, including percent of total seeds deposited).

A) Treatment	Winter Trial (2009)		Spring Trial (2010)	
	Units with removal	Total seeds removed	Units with removal	Total seeds removed
Unmanipulated	17 (23.9%)	51 (7.7%)	34 (47.2%)	144 (21.7%)
All-access	16 (21.9%)	31 (4.6%)	26 (36.1%)	80 (12.0%)
Limited-access	7 (9.7%)	17 (2.6%)	26 (36.1%)	79 (11.9%)
No-access (control)	0	0	1 (5.6%)	1 (1.4%)

Note: Unmanipulated treatment provided seed access to vertebrates and invertebrates (72 units, 666 seeds per trial); all-access provided access to vertebrates and invertebrates but reduced wind / water displacement (72 units, 666 seeds); limited access gave seed access to invertebrates only (72 units, 666 seeds); no-access did not provide seed access to vertebrates or invertebrates (18 units, 72 seeds).

B) Density	Winter Trial (2009)		Spring Trial (2010)	
	Units with removal	Total seeds removed	Units with removal	Total seeds removed
1	2 (3.7%)	2 (3.7%)	8 (14.8%)	8 (14.8%)
4	3 (4.2%)	7 (2.4%)	20 (27.4%)	42 (14.4%)
8	10 (18.5%)	26 (6.1%)	27 (50.9%)	81 (19.1%)
24	25 (46.3%)	64 (4.9%)	32 (59.3%)	64 (4.9%)

model of all main factors studied (habitat, microsite, exclosure treatment, deposited seed density, trial season / year), along with the interaction of habitat and density (Appendices S4–S6, see Supplemental Data with the online version of this article). Seed density had a significant effect on seed removal in both assessments (Tables 1, 2, Appendix S5). As seed density increased, the proportion of seed removal decreased ($P = 0.009$), but the presence of seed removal increased ($P < 0.001$) (Table 1, Appendix S5). There was no overall effect of habitat type on seed removal ($P = 0.530$ for proportion, $P = 0.115$ for presence). There was a significant difference in proportion seed removal among some of the microsities (shrub vs. bare sand: $P < 0.001$; shrub vs. litter: $P = 0.001$; bare sand vs. litter: $P = 0.053$), but not presence of seed removal. There was the greatest

TABLE 3. Logistic regression model of proportion seed removal of *Baldouia angustifolia* across trials (seed removal \sim habitat + microsite + exclosure treatment + seed density + season / year + habitat \cdot exclosure treatment).

Coefficients	Estimate	SE	Z value	Pr(> Z)
Intercept	−3.52	1.02	−3.47	0.001
Habitat (degraded)	0.00	1.43	0.00	1.000
Microsite (litter) ^a	0.16	0.10	1.72	0.086
Microsite (bare sand) ^a	0.12	0.10	1.29	0.198
Treatment (limited access)	0.54	1.04	0.53	0.599
Treatment (all access)	2.97	1.01	2.93	0.003
Treatment (unmanipulated)	3.66	1.01	3.62	< 0.001
Seed density	0.01	0.00	2.94	0.003
Season / year	−0.63	0.08	−8.04	< 0.001
Habitat (degraded) \cdot treatment (limited access)	2.38	1.45	1.64	0.101
Habitat (degraded) \cdot treatment (all access)	−0.15	1.43	−0.10	0.919
Habitat (degraded) \cdot treatment (unmanipulated)	−0.22	1.43	−0.16	0.877

Note: Degrees of freedom = 12. SE = standard error.

^aMicrosites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter vs. bare sand microsities: model estimate = 0.04, SE = 0.09, Z = 0.43, $P = 0.665$.

proportion removal in shrub microsites in the Winter Trial in both habitats, and greatest proportion removal for bare sand microsites in the Spring Trial in both habitats ($P < 0.001$). For presence of removal, significantly fewer units had removal in the Winter Trial (4.8%) than in the Spring Trial (14.7%; Appendix S5, see Supplemental Data with the online version of this article; $P < 0.001$). Seasons / years did not exhibit the most removal in the same microsite (Winter: 8 units with removal in bare sand, 17 units in litter, 15 units in shrub; Spring: 35 units in bare sand, 29 units in litter, 26 units in shrub). Invertebrate-mediated seed removal (limited-ac-

cess treatment) was greater than vertebrate-mediated seed removal (all-access treatment—limited-access treatment) (Fig. 1, Tables 1, 2, Appendices S3–S5, see Supplemental Data with the online version of this article).

Seed removal—*Baldiuna angustifolia*—Proportion seed removal of *B. angustifolia* from individual units was best explained by the additive model of all main factors, plus the interaction between habitat and enclosure treatment (Table 3, Fig. 2, Appendix S2b, S7; see Supplemental Data with the online version of this article). The

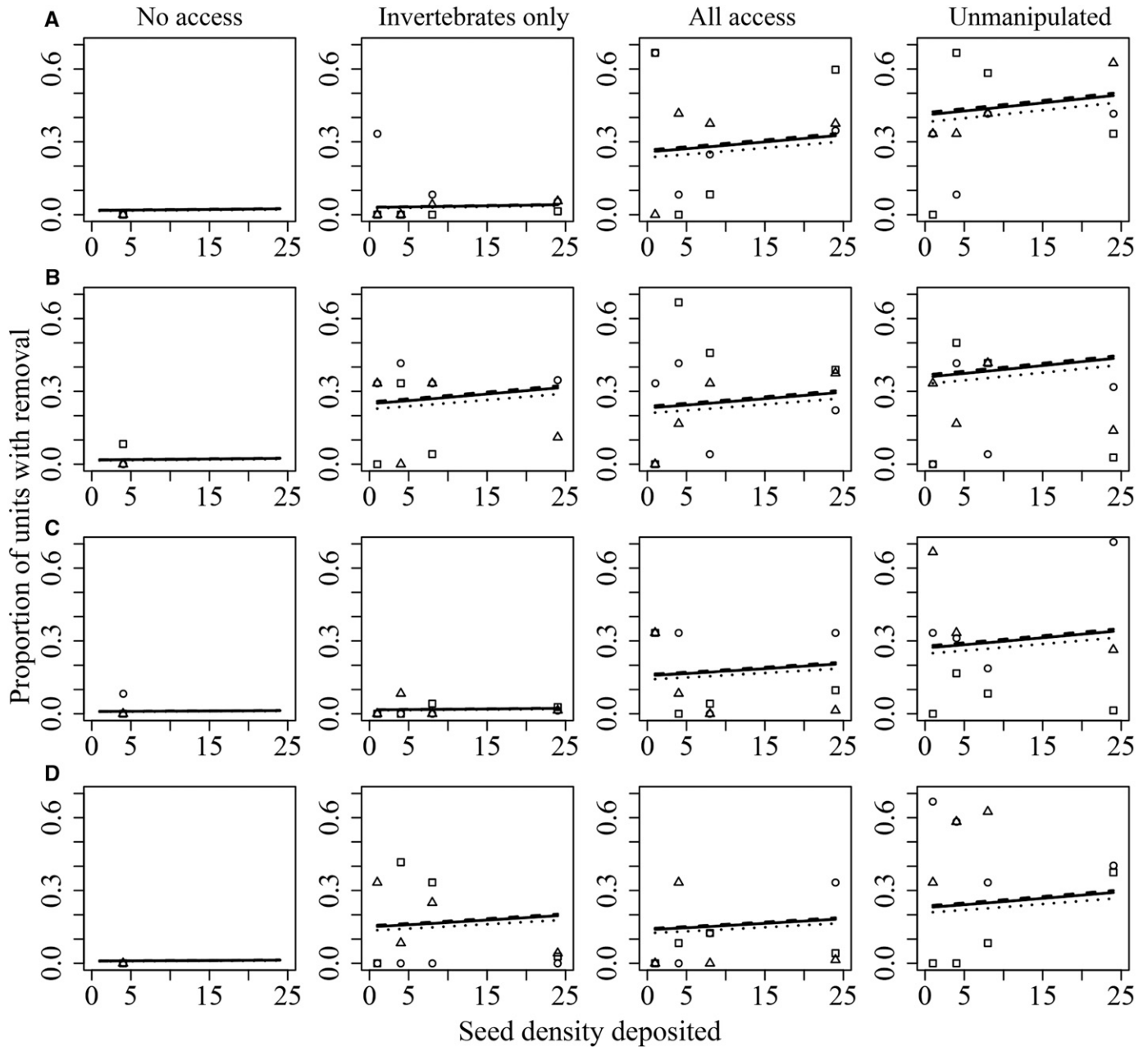


FIGURE 2 Predicted (lines) and observed (symbols) proportion seed removal of *Baldiuna angustifolia* in each trial season / year, habitat, and enclosure treatment. Row A: removal from each enclosure treatment in intact habitat, Winter Trial, 2009; row B: removal from each enclosure treatment in degraded habitat, Winter Trial, 2009; row C: removal from each enclosure treatment in intact habitat, Spring Trial, 2010; row D: removal from each enclosure treatment in degraded habitat, Spring Trial, 2010. Solid lines and triangles represent bare sand microsites, dashed lines and circles represent litter microsites, and dotted lines and squares represent shrub microsites. Models were selected with AICc.

presence of seed removal in individual units was best explained by the additive model of all main factors studied, plus the interaction between habitat and microsite (Appendices S8–S10; see Supplemental Data with the online version of this article). Deposited seed density had a significant positive effect on seed removal in both assessments (Tables 3, 4, Appendix S9); as seed density increases, proportion seed removal ($P = 0.003$) and number of units with seed removal ($P < 0.001$) increased (Table 3, Appendix S9). There was no overall effect of habitat type on seed removal. For microsite type, there was no significant difference in proportion removal, but more units in litter microsites tended to exhibit the presence of removal than in shrubs ($P = 0.025$, Appendix S9). Degraded habitat had a tendency for more removal in shrub than in litter ($P = 0.034$, Appendix S9) (with 33 units in degraded / shrub, 29 in degraded / litter, 34 units in degraded / bare sand. Intact habitat had a tendency for the most removal in litter (35 units in intact / litter, 32 in intact / bare sand, 23 in intact / shrub). Significantly fewer seeds were removed in Spring (18.3%) than in Winter (28.6%) (Table 3, Appendix S9) ($P < 0.001$ for proportion, $P = 0.019$ for presence). Invertebrate-mediated seed removal was greater than estimated vertebrate-mediated seed removal (Fig. 2, Table 4, Appendices S7, S8).

Seedling emergence and establishment—*Chamaecrista fasciculata*—Proportion emergence per unit for *C. fasciculata*, considered cumulatively during the first two years post seeding (2009–2011 and 2010–2012), was best explained by the additive model of habitat, microsite, seed density, and trial year, along with the interaction between microsite and trial year (Table 5A, Figs. 3A, B, Appendix S2c). Presence of emergence per unit was best explained by the interaction of seed density and trial year (Appendices S11–S13; see Supplemental Data with the online version of this article). Although planted seed density did not affect proportion emergence, there was an increasing chance of the presence of any emerged seedlings per unit ($P < 0.001$) with increasing planted

TABLE 4. Seed removal of *Balduina angustifolia* per experimental treatment type (A) and per seed density deposited (B) in seed predation study (experimental units with removal, including percent of total units; seeds removed, including percent of total seeds deposited).

A) Treatment	Winter Trial (2009)		Spring Trial (2010)	
	Units with removal	Total seeds removed	Units with removal	Total seeds removed
Unmanipulated	41 (56.9%)	218 (32.7%)	42 (58.3%)	266 (40.0%)
All-access	39 (54.2%)	229 (34.4%)	23 (31.9%)	80 (12.0%)
Limited-access	23 (31.9%)	144 (21.6%)	16 (22.2%)	32 (4.8%)
No-access (control)	1 (5.6%)	1 (1.4%)	1 (5.6%)	1 (1.4%)

Note: Unmanipulated treatment provided seed access to vertebrates and invertebrates (72 units, 666 seeds per trial); all-access provided access to vertebrates and invertebrates but reduced wind / water displacement (72 units, 666 seeds); limited access gave seed access to invertebrates only (72 units, 666 seeds); no-access did not provide seed access to vertebrates or invertebrates (18 units, 72 seeds).

B) Seed density	Winter Trial (2009)		Spring Trial (2010)	
	Units with removal	Total seeds removed	Units with removal	Total seeds removed
1	11 (20.4%)	11 (20.4%)	10 (18.5%)	10 (18.5%)
4	24 (33.3%)	57 (19.5%)	20 (27.4%)	43 (14.7%)
8	29 (53.7%)	112 (26.4%)	18 (34.0%)	72 (17.0%)
24	40 (74.1%)	412 (31.8%)	34 (63.0%)	254 (19.6%)

TABLE 5. Models of proportion seedling emergence (A) and proportion seedling establishment (B) of *Chamaecrista fasciculata* from logistic regression analysis. Proportion seedling emergence ~ habitat + microsite + seed density + year + microsite · year; proportion seedling establishment ~ habitat + seed density + density2.

A) Coefficients	Estimate	SE	Z value	Pr(> Z)
Intercept	0.24	0.22	1.09	0.276
Habitat (degraded)	−0.31	0.09	−3.43	< 0.001
Microsite (litter) ^a	−0.53	0.33	−1.61	0.107
Microsite (bare sand) ^a	−1.27	0.33	−3.90	< 0.001
Year	−1.27	0.16	−7.76	< 0.001
Microsite (litter) · year ^a	0.34	0.23	1.44	0.149
Microsite (bare sand) · year ^a	0.91	0.23	3.98	< 0.001

Note: Degrees of freedom = 8. SE = standard error.

^aMicrosites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter microsites vs. bare sand microsites: model estimate = 0.74, SE = 0.35, Z = 2.13, $P = 0.033$; litter microsites vs. bare sand microsites (year): model estimate = −0.57, SE = 0.23, Z = −2.48, $P = 0.013$.

B) Coefficients	Estimate	Std. Error	Z value	Pr(> Z)
Intercept	−6.44	1.17	−5.52	< 0.001
Habitat (degraded)	2.11	0.62	3.43	0.001
Seed density	0.28	0.19	1.46	0.144
Seed density2	−0.01	0.01	−1.85	0.064

Note: Degrees of freedom = 4. Plants were considered to be established if they grew to a height of at least 30 cm or were reproductive.

seed density for each year of the experiment, across habitats and microsites (Table 5a, Appendix S11). There was significantly greater proportion emergence in intact habitat than in degraded habitat ($P < 0.001$), less proportion emergence in bare sand than in the other microsites ($P < 0.001$ for bare sand vs. shrub, $P = 0.033$ for bare sand vs. litter), and significantly greater emergence in the trial initiated in 2009 than the trial initiated in 2010 ($P < 0.001$). In all but the smallest seed density, the 2010 trial had fewer units with emergence and fewer emerged seedlings compared to the 2009 trial (Appendix 2a).

Proportion establishment and presence of established seedlings per unit for *Chamaecrista fasciculata* (cumulative three years post seeding, 2009–2012) were each best explained by an additive model of habitat and planted seed density as a quadratic variable (Table 5B, Fig. 3C, Appendices S2d, S11, S12, S14; see Supplemental Data with the online version of this article). The presence and proportion of establishment was lowest for 1 seed, increased for 4 and 8 seeds, and decreased for 24 seeds (Table 5B, Fig. 3C, Appendices S2d, S11, S12, S14). For both assessments, there were significantly more established plants in degraded habitat than in intact (degraded: 24 plants, 3 units; intact: 3 plants, 2 units; $P < 0.001$ for proportion, $P = 0.002$ for presence) (Table 5B, Fig. 3C, Appendices S11, S12). Overall, we observed more emerged seedlings in intact scrub, but more established plants in degraded scrub (Fig. 4). Shrub species did not have a significant effect on emergence or establishment. We observed 41.7% germination in the growth chamber germination study.

Seedling emergence and establishment—*Balduina angustifolia*—Proportion emergence of *B. angustifolia* was best explained by the additive model of habitat, microsite, planted seed density, trial year, and the interaction between habitat and trial year (Figs. 5A, B, Table 6A, Appendix S2e, see Supplemental Data with the online version of this article). Presence of emerged seedlings per unit was best explained by the additive model of habitat, microsite, planted seed

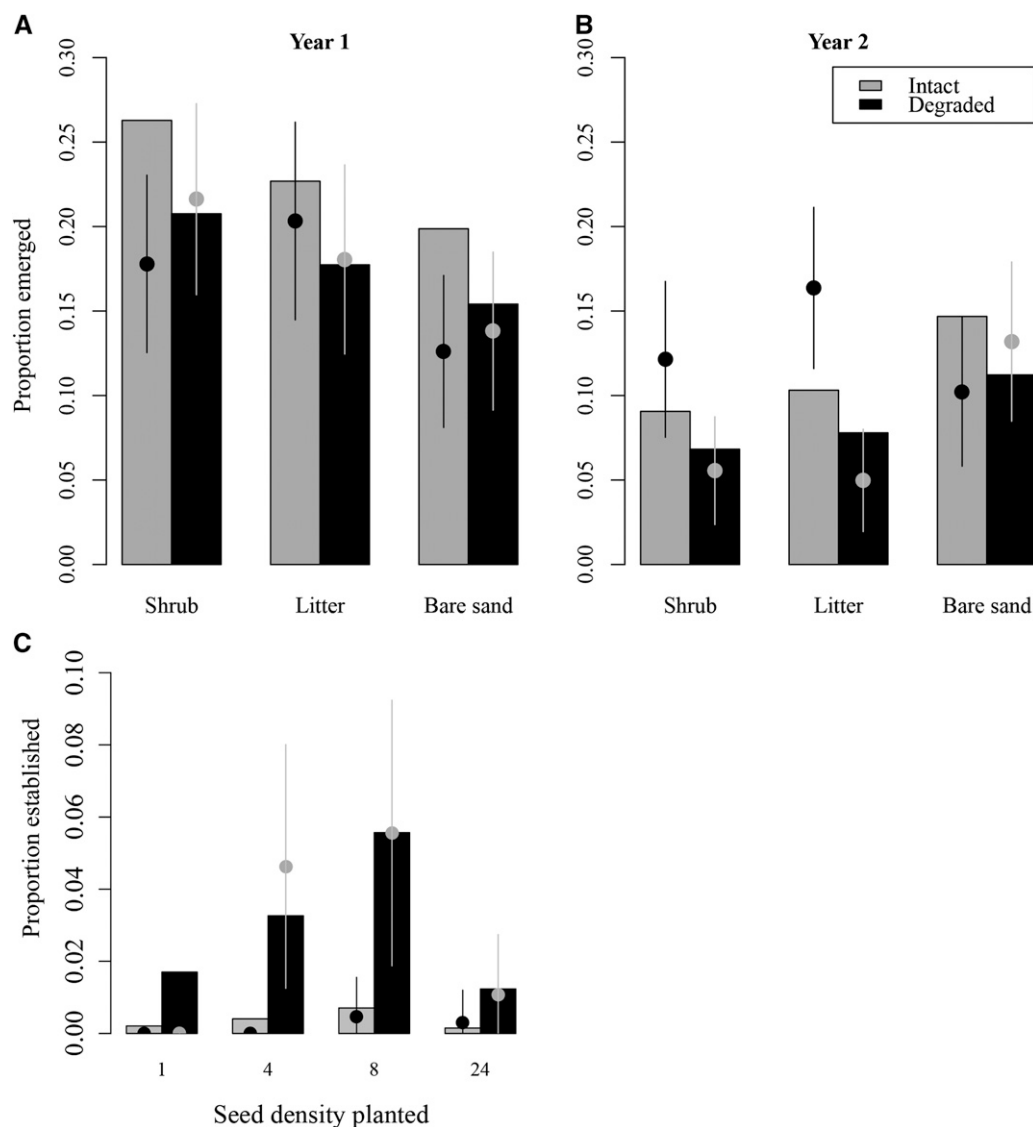


FIGURE 3 Predicted (bars) and observed (symbols) proportion emergence and establishment of *Chamaecrista fasciculata* in intact and degraded scrub. (A) Emergence from trial initiated 2009; (B) emergence from trial initiated 2010; (C) establishment from trial initiated 2009. Black bars represent degraded habitat, gray bars represent intact habitat. Models were selected with AICc. Error bars for observed proportions were estimated using the Wald interval (Brown et al., 2001).

density, and trial year (Appendices S15–S17; see Supplemental Data with the online version of this article). There was a decreasing proportion of emerged seedlings with seed density ($P = 0.006$), but an increasing presence of emerged seedlings with seed density ($P < 0.001$) (Table 6A, Appendices 2b, S16). There were significantly fewer treatment units with *B. angustifolia* seedlings in the degraded habitat (80 units, 109 emerged seedlings (years combined)) than in the intact habitat (in 207 units, 321 emerged seedlings (years combined)) ($P < 0.001$ for proportion, $P = 0.002$ for presence, Table 6A, Figs. 5A, B, Appendices S15, S16). For both proportion emergence and presence of emergence, there were significantly more emerged seedlings in bare sand than in the other microsites ($P < 0.001$ for each) (bare sand: 88 units, 299 seedlings; litter: 53 units, 123 seedlings; shrub: 48 units, 106 seedlings (years combined); Table 6A, Figs. 5A–D, Appendices S15, S16).

Proportion establishment of *Balduina angustifolia* seedlings per unit, and presence of established seedlings per unit, were best explained by an additive model of microsite and planted seed density (Table 6B, Fig. 5E, Appendices S2f, S15, S16, S18; see Supplemental Data with the online version of this article). As seed density increased, the proportion of establishment decreased ($P < 0.001$), but the presence of established seedlings increased ($P = 0.015$) (Table 6b, Appendix S16). For both assessments, there were significantly more established seedlings in bare sand than in the other microsites ($P < 0.001$ for each) (30 total units, 45 established plants with establishment in bare sand microsites vs. 8 units, 12 plants in shrub, and 5 units, 6 plants in litter). Overall, there were more emerged seedlings in intact scrub, but there was less of a distinction between habitats for established plants. Bare sand microsites, on the other hand, had the most emerged seedlings and established plants (Fig. 6). Shrub species did not have a significant effect on emergence or establishment. We observed 38.3% germination of *B. angustifolia* seeds in the growth chamber germination study.

Models to evaluate time-since-disturbance—Chamaecrista fasciculata—Stochastic population growth of *C. fasciculata* simulated under recovering successional conditions was less than 1

($\lambda = 0.58$; reference model). Population growth under continuously degraded habitat conditions was slightly greater than 1 ($\lambda = 1.04$), and that in continuously intact habitat conditions was less than 1 ($\lambda = 0.32$). Seed survival in the seedbank (a_{11}) had the greatest elasticity on stochastic lambda in all three models (Figs. 7A, B, Appendix 3, transition abbreviations from Stephens et al., 2014), followed by small vegetative survival to reproduction with seeds entering seedbank (a_{12}) in the reference model, reproduction by flowering adults with seeds entering seedbank (a_{14}) in the continuously degraded model and in the continuously intact conditions model. Stochastic population growth in the changing environment decreased with increasing seed density (density of 5: $\lambda = 0.55$; density of 10: $\lambda = 0.53$; density of 20: $\lambda = 0.45$). Elasticity of a_{12} and a_{14} increased and the a_{11} transition decreased in importance with increasing seed density (Figs. 7C, D, Appendix 3).

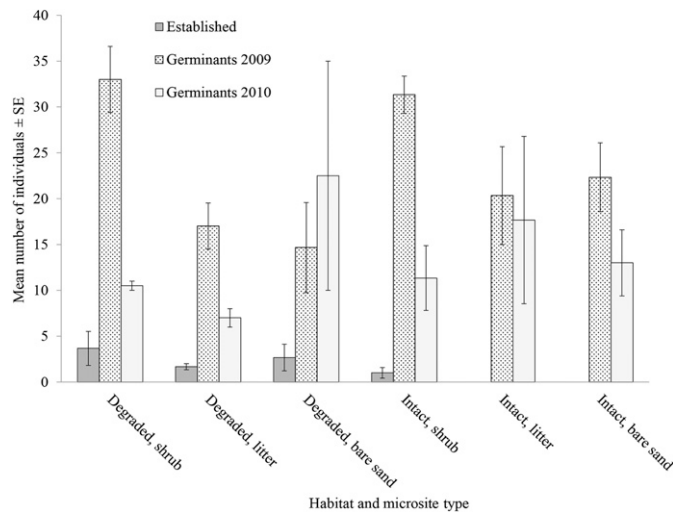


FIGURE 4 Emerged seedlings (2009, 2010 trials) and established individuals (2009 trial) per habitat and microsite for *Chamaecrista fasciculata*. Error bars represent standard error values for means of sites. Plants were considered established if they grew to ≥ 30 cm, or had reproductive structures (flowers, buds, seed pods).

Models to evaluate time-since-disturbance—Balduina angustifolia—Stochastic population growth of *B. angustifolia* in simulated changing conditions, continuously degraded habitat conditions, and continuously intact conditions was less than 1 (reference: $\lambda = 0.58$; degraded: $\lambda = 0.46$, intact: $\lambda = 0.45$). Reproductive adults with seeds entering the seedbank (a_{14}) had the greatest relative elasticity on stochastic population growth in the three models; reproduction with seeds surviving to the small vegetative stage (a_{24}) also had great elasticity values in the continuously intact and continuously degraded models (Figs. 8A, B, Appendix 4, transition abbreviations in Stephens et al., 2014). Stochastic population growth decreased with increasing seed density (density of 5: $\lambda = 0.58$; density of 10: $\lambda = 0.53$; density of 20: $\lambda = 0.37$). The importance of seed survival in the seedbank (a_{11}) decreased as seed density increased. At the highest seed density, reproduction by flowering adults with seeds entering seedbank (a_{14}) also decreased slightly (Figs. 8C, D, Appendix 4).

DISCUSSION

Habitat degradation had contrasting effects for the study species. We provided evidence for larger demographic changes for *Chamaecrista fasciculata* in degraded scrub habitat than for *Balduina angustifolia*. The significant differences in seed removal and establishment among microsites for *B. angustifolia*, but not for *C. fasciculata*, suggests that microsite may be more important for population dynamics of *B. angustifolia*. Habitat-associated microsite trends in *B. angustifolia* (degraded: greatest removal in bare sand, intact: greatest in litter) may also indicate that habitat degradation alters the abundances or distributions of seed predators (see also Restrepo and Vargas, 1999).

Seed removal—For both species, the presence of seed removal per unit increased with seed density as expected. This trend may be associated with increased likelihood of predators perceiving seeds in relatively denser patches of seeds (Brewer and Webb, 2001) and the

increased efficiency (reward for time and energy expended) of concentrating seed removal efforts on more plentiful seed sources (Bülow-Olsen, 1984). The decreasing proportion seed removal of *Chamaecrista fasciculata* with increasing density may indicate that once seeds were located, the number of seeds removed was limited by physical challenges associated with handling more seeds, or a higher risk of depredation associated with increased handling time (Brown et al., 1988; Garb et al., 2000). Seed predation theory also suggests that negative density dependence in seed removal may indicate satiation of seed predators (reviewed in Crawley, 2000). The increasing proportion seed removal with density for *Balduina angustifolia* suggests that seed predators were able to take relatively more seeds from denser patches of seeds, but the gradual degree of the increase suggests that these seed predators may still be limited by handling ability or time to a certain extent. Seed predator satiation may be less relevant for *B. angustifolia* at the seed densities tested. Differences in proportion seed removal between the study species could be associated with different species of seed predators for each plant. Other studies have focused on a range of factors affecting predator-induced seed mortality, such as spatial location, weather conditions, predator density, and availability of alternate foods (e.g., Ostfeld et al., 1997; Crawley, 2000; Benkman and Siepielski, 2004).

Contrary to our expectations, seed removal was not greater in intact scrub than in degraded scrub. The strong effects of seed density (seed perceptibility, efficiency of removal) may have dominated habitat effects on seed removal. However, habitat-associated microsite trends in *Balduina angustifolia* (degraded: greatest removal in bare sand; intact: greatest in litter) may indicate that habitat degradation can alter the abundances or distributions of seed predators (Restrepo and Vargas, 1999).

Invertebrates (likely ants, E. Stephens, University of Central Florida, personal observation; M. Deyrup, Archbold Biological Station, personal communication) were primarily responsible for removal of *Chamaecrista fasciculata* and *Balduina angustifolia* seeds in both Winter and Spring Trials. Similarly, invertebrates are important seed predators in xeric, nutrient-poor systems (Pirk and De Casenave, 2010; Arnan et al., 2011). Considering that the two study species differed in season of peak seed removal (Winter for *B. angustifolia*, Spring for *C. fasciculata*), this may further confirm that different invertebrates were responsible for seed removal of each species. Overall, while studies of seed predation are valuable in more fully understanding the dynamics of plant populations, and how these dynamics may change under different conditions, it is important to acknowledge that high seed removal rates will not necessarily translate into reductions in recruitment (Crawley, 2000).

Seedling emergence and establishment—The occurrence of emerged and established seedlings of each species increased with increasing density of planted seeds, as expected. More seeds enhances the chance of at least one emerged seedling in a given location (Poulsen et al., 2007). For *Chamaecrista fasciculata*, proportion emergence was not significantly affected by planting seed density, but proportion establishment decreased with increasing seed density. This suggests an absence of density-dependent effects at the emergence stage (individual seeds had the same chance of emerging whether they were planted in large or small groups), and negative density-dependent effects at the establishment stage. Initially, harsh abiotic environmental conditions could have overshadowed

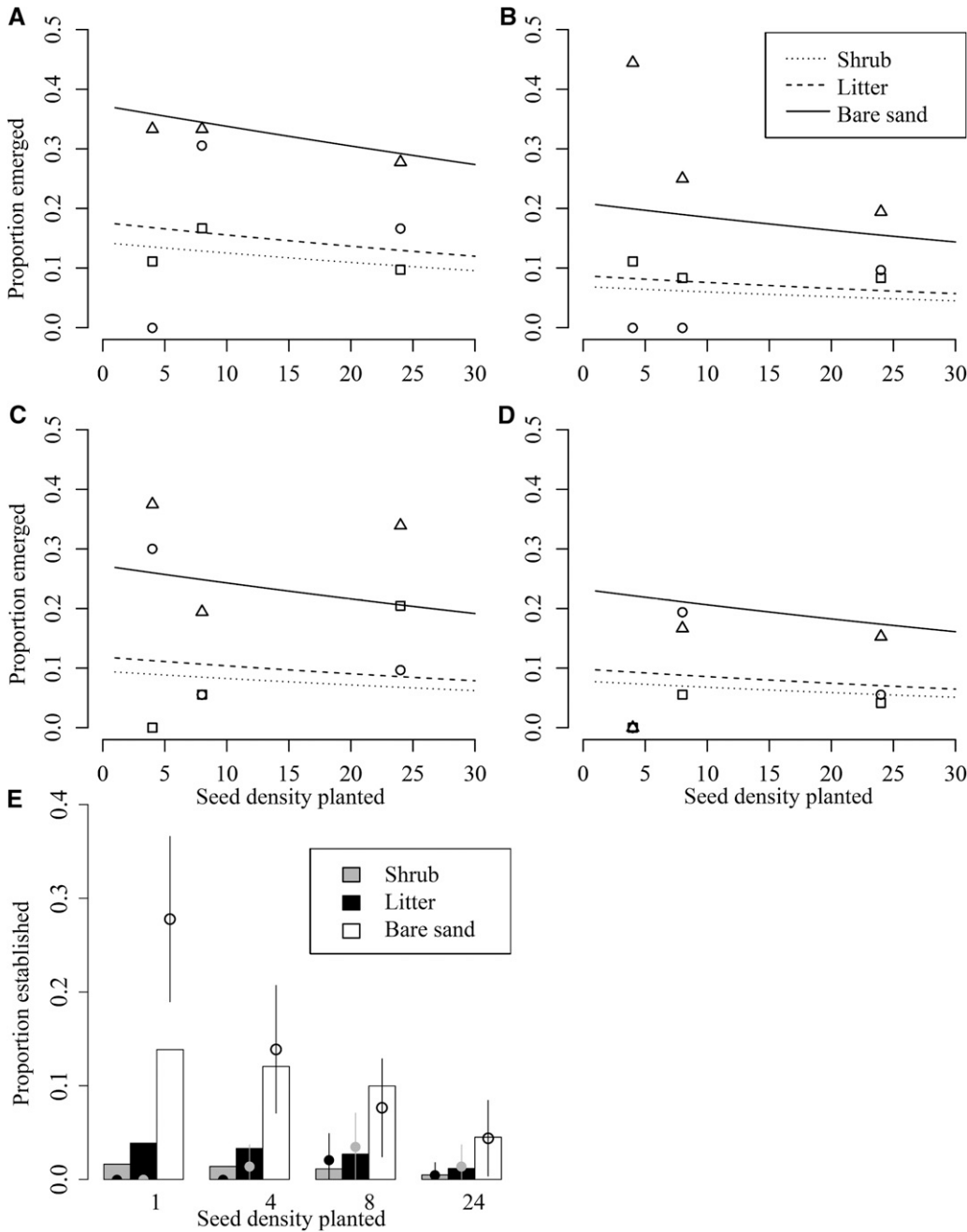


FIGURE 5 Predicted (lines) and observed (symbols) proportion emergence and establishment of *Balduina angustifolia* in intact and degraded scrub. (A) Emergence from trial initiated 2009 in intact habitat; (B) emergence from trial initiated 2009 in degraded habitat; (C) emergence from trial initiated 2010 in intact habitat; (D) emergence from trial initiated 2010 in degraded habitat; (E) establishment by microsite type, across trial season / year and habitat. For A–D, solid lines and triangles represent bare sand microsites, dashed lines and circles represent litter microsites, and dotted lines and squares represent shrub microsites. For E, gray bars = shrub microsites, black bars = litter microsites, white bars = bare sand microsites. Models were selected with AICc. Error bars for observed proportions were estimated using the Wald interval (Brown et al., 2001).

biotic factors such as early intraseedling competition, but as individuals grew larger, they began to compete more intensely for resources (moisture, nutrients, and space). In contrast, both the proportion emergence and establishment in *Balduina angustifolia* decreased with increasing seed density. This pattern implies nega-

tive density-dependent effects at both stages, likely due to early intraseedling competition and later competition among adult plants. We acknowledge that seedling herbivory by invertebrates may have decreased probability of early survival (e.g., grasshoppers; Squitier and Capinera, 2002), which may or may not (Russell et al., 2010) have been associated with seed density. Seedling mortality has been greatly attributed to seedling herbivory in other studies (Fenner, 1987); however, it is unlikely to have accounted for the majority of seedling mortality as we tracked the location of individual seedlings within experimental units, and seedling mortality was often marked by the presence of a desiccated seedling (E. Stephens, University of Central Florida, personal observation). The significantly greater establishment of *C. fasciculata* in the degraded habitat, and significantly greater establishment of *B. angustifolia* in bare sand microsites suggests that habitat may be more important for population dynamics of *C. fasciculata*, and microsite type may be more important for *B. angustifolia*.

Models to evaluate time-since-disturbance—The stochastic model of change associated with time-since-disturbance was consistent with much of the experimental data in that it projected that population growth of both species would decrease slightly as available seed density increased. In particular, this coincides with increased presence of removal for both species, increased proportion removal for *Balduina angustifolia*, decreased proportion emergence for *B. angustifolia*, and decreased proportion establishment for both species with increased seed density. In the stochastic models, the most influential transition for each species (*Chamaecrista fasciculata*: seed survival in seedbank; *B. angustifolia*: production of seeds with subsequent entry into seedbank) also decreased in relative importance with increasing seed density. These predictions suggest that, over time, conditions may be less favorable for populations producing

TABLE 6. Models of proportion seedling emergence (A) and proportion seedling establishment (B) of *Balduina angustifolia* from logistic regression analysis. Proportion seedling emergence \sim habitat + microsite + seed density + year + habitat \cdot year; proportion seedling establishment \sim microsite + seed density.

A) Coefficients	Estimate	SE	Z value	Pr(> Z)
Intercept	-1.33	0.23	-5.76	< 0.001
Habitat (degraded)	-1.41	0.31	-4.57	< 0.001
Microsite (litter only) ^a	0.25	0.14	1.80	0.071
Microsite (bare sand) ^a	1.27	0.12	10.40	< 0.001
Seed density	-0.02	0.01	-2.78	0.006
Year	-0.46	0.13	-3.65	< 0.001
Habitat (degraded) \cdot year	0.60	0.20	3.04	0.002

Note: Degrees of freedom = 7. SE = standard error. ^a Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter microsites vs. bare sand microsites: model estimate = -1.02, SE = 0.12, Z = -8.75, P = < 0.001.

B) Coefficients	Estimate	Std. Error	Z value	Pr (> Z)
Intercept	-4.05	0.49	-8.27	< 0.001
Microsite (litter) ^a	0.89	0.54	1.66	0.097
Microsite (bare sand) ^a	2.27	0.48	4.78	< 0.001
Seed density	-0.05	0.01	-3.71	< 0.001

Note: Degrees of freedom = 4. Plants were considered to be established if they grew to a height of at least 30 cm or were reproductive. ^a Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter microsites vs. bare sand microsites: model estimate = -1.39, SE = 0.33, Z = -4.19, P < 0.001.

greater densities of seeds. A biological explanation for this relationship between seed density and population growth may be: (1) a more than proportional increase in seed predation reduces the number of seeds available for germination (Janzen, 1971; Velho et al., 2012); or (2) greater competition results from an increasing number of germinants that suppresses (Clark et al., 2012) or delays (Hyatt and Evans, 1998) subsequent vegetative survival. In addition, if seeds were abundant, the population would likely already be

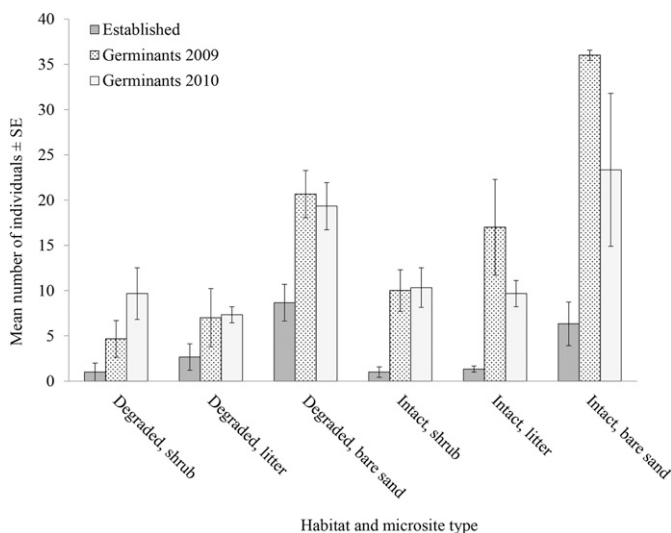


FIGURE 6 Emerged seedlings (2009, 2010 trials) and established individuals (2009 trial) per habitat and microsite for *Balduina angustifolia*. Error bars represent standard error values for means of sites. Plants were considered established if they grew to ≥ 30 cm, or had reproductive structures (flowers, buds, seed heads).

large and additional germination and survival may be constrained by competition with established adults (Ellner, 1986; Casper, 1990).

The low population growth rates with simulated vegetation recovery and continuously intact habitat conditions were consistent for *Chamaecrista fasciculata* considering that this species had significantly greater establishment in degraded habitat. This relationship could be explained by the negative effect of belowground competition for resources as intact scrub is reestablished. Intact scrub may be relatively less hospitable for establishment of *C. fasciculata* because this habitat contains most of its vegetative biomass belowground (Guerin, 1993; Schmalzer et al., 2002; Saha et al., 2010). While degraded scrub may have a similar proportion of below to above ground biomass, there is likely less total belowground biomass in degraded than in intact scrub. Previous studies in Florida scrub have attributed greater recruitment in anthropogenically disturbed scrub or scrub-like sites (vs. intact sites) to release from belowground competition (Petrů and Menges, 2003; Schafer et al., 2010). Other potential explanations for the greater establishment of *C. fasciculata* in degraded scrub may include competitive advantages conferred by an ability to fix nitrogen (Singer et al., 2009), a diminished dependence on soil microbes (e.g., soil crusts, Hawkes, 2000), or that root exudates and leaf leachates from allelopathic plants occur at lower concentrations in degraded scrub (Hewitt and Menges, 2008; Weekley et al., 2008b). Exudates and leachates are unlikely to explain the observed pattern as there was no relationship between shrub species and emergence and establishment in either habitat.

Balduina angustifolia appeared to be most affected by the presence of shrubs, regardless of habitat type. Seedlings of *B. angustifolia* may emerge and establish most easily in bare sand because of an increased distance from the resource-dominating root networks of shrubs. Seedling herbivory can also greatly affect establishment (Clark et al., 2012); herbivores of *B. angustifolia* seedlings may be more ubiquitous under shrubs and in litter. The great effect of shrubs on population dynamics of *B. angustifolia* may explain why population growth rates from the model were relatively similar among habitat conditions. Population growth rates in both habitats may have been low due to negative contributions from shrub microsites and litter microsites outweighing positive contributions from bare sand microsites (Stephens et al., 2014).

CONCLUSION AND APPLICATIONS

Remnant or intact ecosystems are essential for maintaining species diversity (e.g., Anand et al., 2010; McKinney, 2002), species interactions (e.g., Fagan et al., 1999), and ecological function / processes (e.g., Rathcke and Jules, 1993; Rosenberg et al., 1997; Belnap, 2002); however, our findings suggest that degraded scrub, as with other degraded habitat, also retains inherent ecological value in that it may act as a transient stage in a trajectory toward more intact conditions. With increasing time-since-disturbance, populations of certain native species such as *Chamaecrista fasciculata* in degraded habitat may behave more like those in intact habitat. Abundances and distributions among microsites of such native species and their representation in local assemblages may begin to mirror those in intact conditions. In addition, as we found that degraded scrub habitat may transiently increase bare sand areas for emergence and establishment of some species, and it may provide a release from belowground competition, degraded scrub may act as a temporary

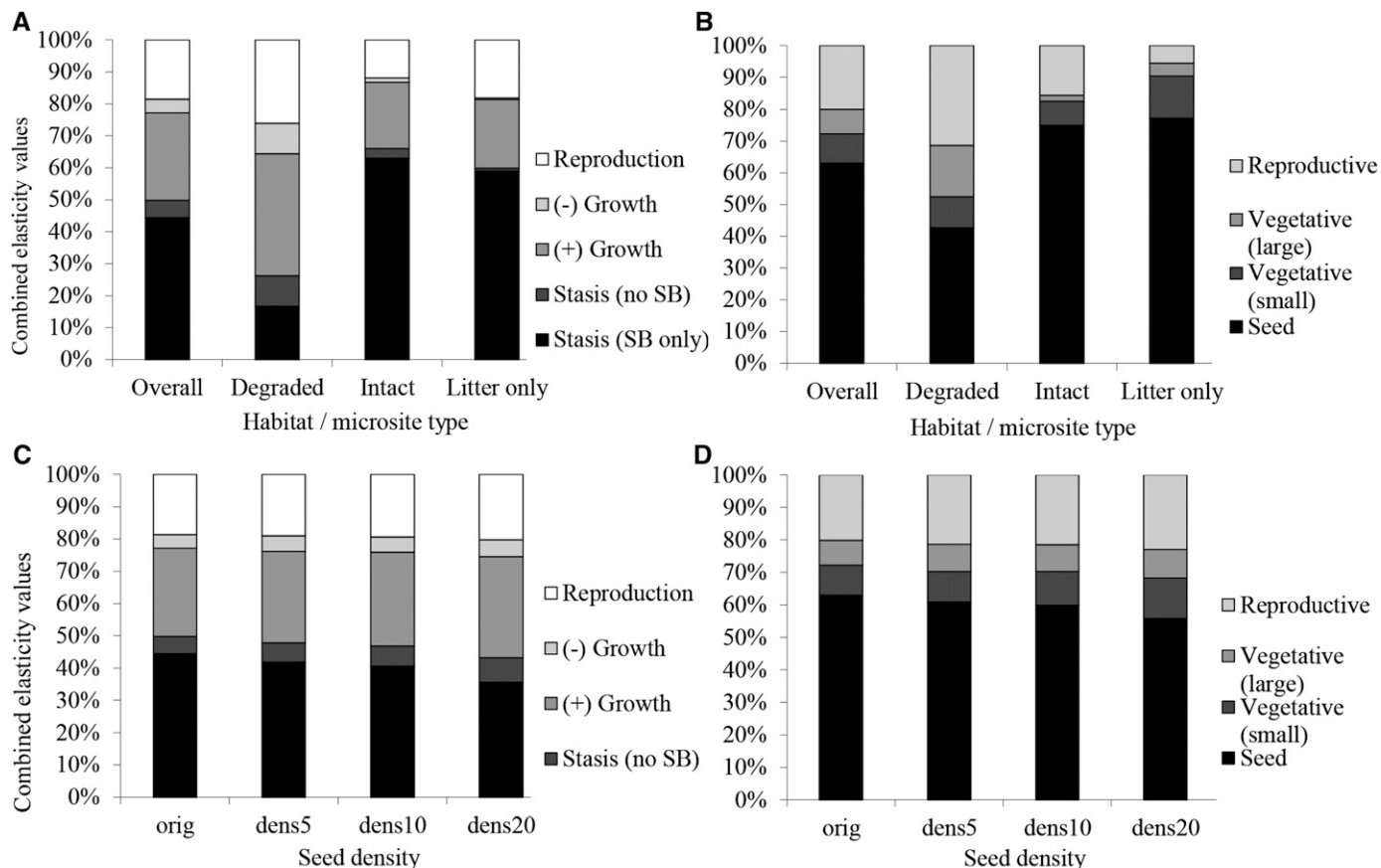


FIGURE 7 Combined elasticity values for time-since-disturbance models of *Chamaecrista fasciculata*. Unmanipulated (overall), individual habitat (degraded, intact), and microsite (litter) scenarios with elasticity values combined by transition type (A), and combined by life-history stage (B); various initial seed density scenarios (unmanipulated (orig), 5, 10, and 20 seeds) with elasticity values combined by transition type (C), and combined by life-history stage (D). Reproduction represents $a_{1,2'}$, $a_{1,3'}$, and $a_{1,4}$ transitions; negative (-) growth represents $a_{3,4'}$, $a_{2,3'}$, and $a_{2,4}$; positive or advancing (+) growth represents $a_{2,1'}$, $a_{3,1'}$, $a_{4,1'}$, and $a_{3,2'}$, $a_{4,2'}$, $a_{4,3'}$; stasis (no SB) represents $a_{2,2'}$, $a_{3,3'}$, $a_{4,4'}$; stasis (SB only) represents $a_{1,1'}$. SB = seed bank. See Stephens et al. (2014) for definitions of transition abbreviations.

source or refugia for some native plants. This role for degraded scrub was observed for an endemic scrub herb (Quintana-Ascencio et al., 2007), and is noted for other species on roadsides and utility corridors in developed areas (Andrews, 1990; Bennett, 1991). The above reasons for valuing degraded scrub should translate into consideration for conservation of degraded lands, and motivation to encourage land managers and the public to regard degraded, undeveloped lands as worth protecting and not to be dismissed as “trash ecosystems” (Marris et al., 2013).

However, degraded scrub should not be an acceptable end goal in land management. Our data indicate that individual species can react differently to habitat degradation; therefore, reoccurring mechanical disturbances are unlikely to result in stable population dynamics for a diversity of native species. Even after a single period of anthropogenic disturbance, it may be virtually impossible to reestablish all of the intricate belowground relationships between species found in intact scrub. Population dynamics of certain species, such as long-lived perennials with extensive root systems like palmettos, may be particularly affected by degradation (Breininger and Schmalzer, 1990). Overall, it is possible that with severe or repetitive anthropogenic disturbance, degraded scrub and other degraded habitats may become so different from their intact state that they could cross a threshold into a novel, stable state (Hobbs et al., 2006).

Therefore, while conservation of degraded land is important, such efforts must complement the essential protection of intact habitat.

This study should facilitate hypotheses about population dynamics of other scrub herbs and those in fynbos (Cowling and Campbell, 1983), heathland (Blanche, 2000), and chaparral (DeBano et al., 1979), as they all tolerate infertile conditions, they can survive seasonal dry periods in well-drained soils, and benefit from gap-generating disturbances. Research scientists must work with land managers to facilitate the understanding that most ecological systems have been transformed in some way, and continue to undergo changes (Seastedt et al., 2008). Comparisons of population and community dynamics before and after the disturbance, or in reference conditions and the degraded habitat, will help to identify what ecosystem changes have already occurred, how these have affected the system, what changes are likely to occur next (Seastedt et al., 2008), and what combinations of remedial measures may be necessary in the restoration process.

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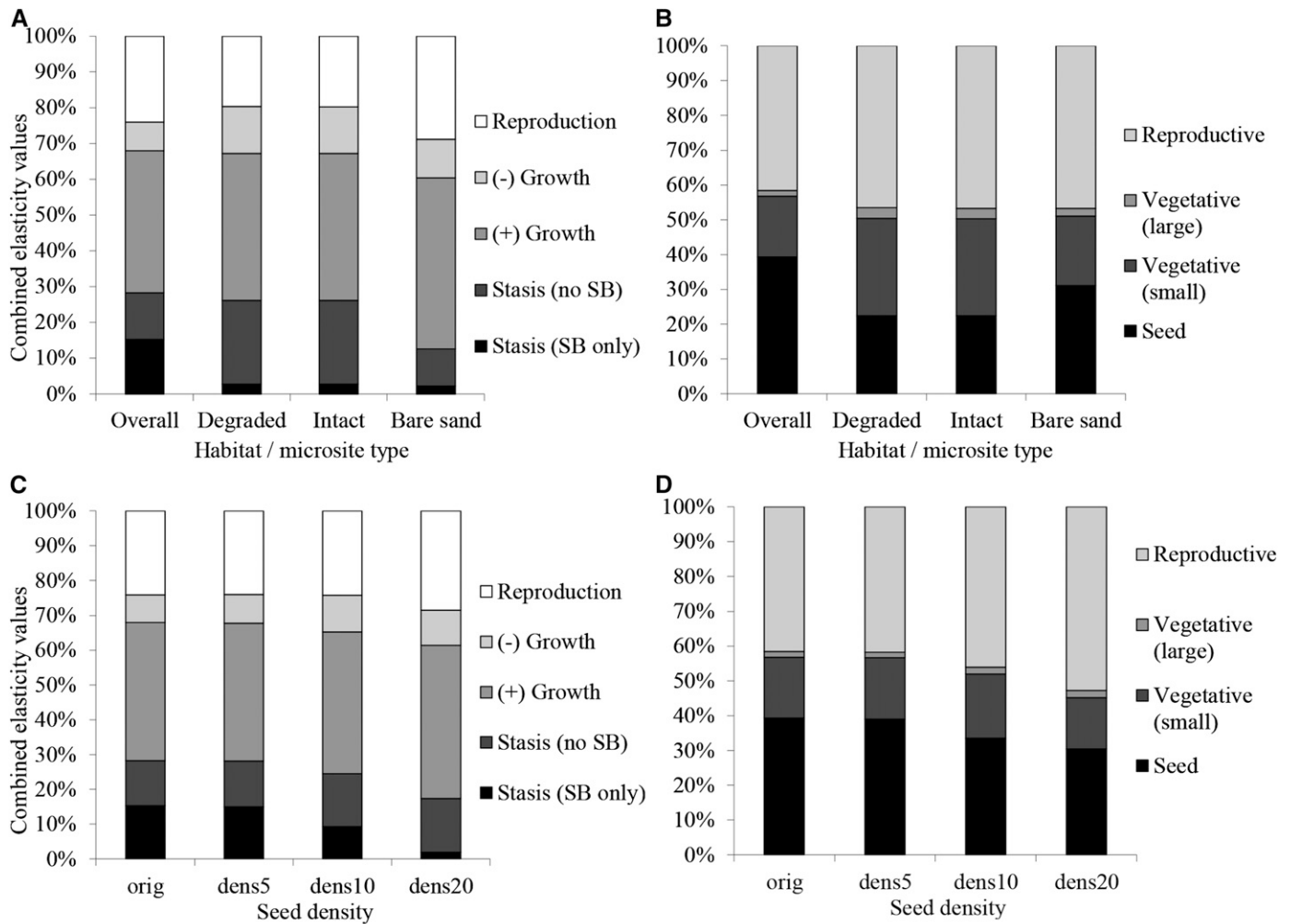


FIGURE 8 Combined elasticity values for time-since-disturbance models of *Balduina angustifolia*. Unmanipulated (overall), individual habitat (degraded, intact), and microsite (bare sand) scenarios with elasticity values combined by transition type (A), and combined by life-history stage (B); various initial seed density scenarios (unmanipulated (orig), 5, 10, and 20 seeds) with elasticity values combined by transition type (C), and combined by life-history stage (D). Reproduction represents the a_{14} transition; negative (-) growth represents $a_{34'}$, $a_{23'}$, and $a_{24'}$; positive or advancing (+) growth represents $a_{21'}$, $a_{31'}$, $a_{41'}$, and $a_{32'}$, $a_{42'}$, $a_{43'}$; stasis (no SB) represents $a_{22'}$, $a_{33'}$, $a_{44'}$; stasis (SB only) represents $a_{11'}$. SB = seed bank. See Stephens et al. (2014) for definitions of transition abbreviations.

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APPENDIX 1 Environmental matrix comprised of estimated probabilities of each habitat and microsite combination transitioning to other combination types.

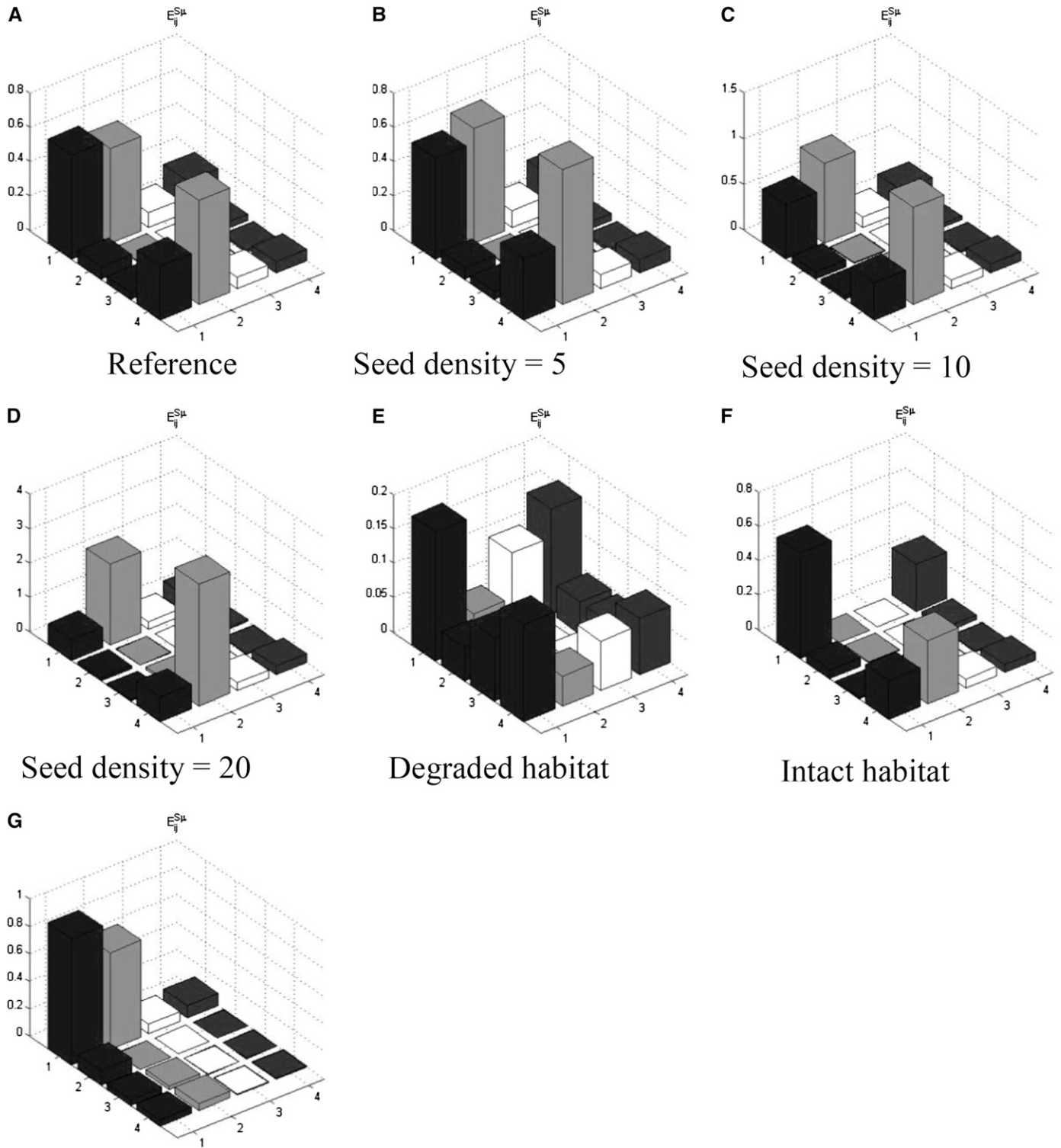
	DBS	DLIT	DSHR	IBS	ILIT	ISHR	DEG
DBS	0.30	0.25	0.05	0.05	0.05	0.05	0.50
DLIT	0.30	0.45	0.2	0.03	0.05	0.09	0.30
DSHR	0.15	0.10	0.5	0.01	0.04	0.09	0.10
IBS	0.10	0.09	0.01	0.50	0.31	0.11	0.01
ILIT	0.09	0.05	0.05	0.26	0.40	0.11	0.01
ISHR	0.01	0.01	0.14	0.10	0.10	0.55	0.03
DEG	0.05	0.05	0.05	0.05	0.05	0.05	0.05

Note: DBS = degraded habitat with bare sand microsite, DLIT = degraded habitat with litter microsite, DSHR = degraded habitat with shrub microsite, IBS = intact habitat with bare sand microsite, ILIT = intact habitat with litter microsite, ISHR = intact habitat with shrub microsite. DEG = degraded habitat.

APPENDIX 2 Counts of seedlings from emergence and establishment experiments for (A) *Chamaecrista fasciculata* and (B) *Balduina angustifolia*; habitats and microsites are pooled.

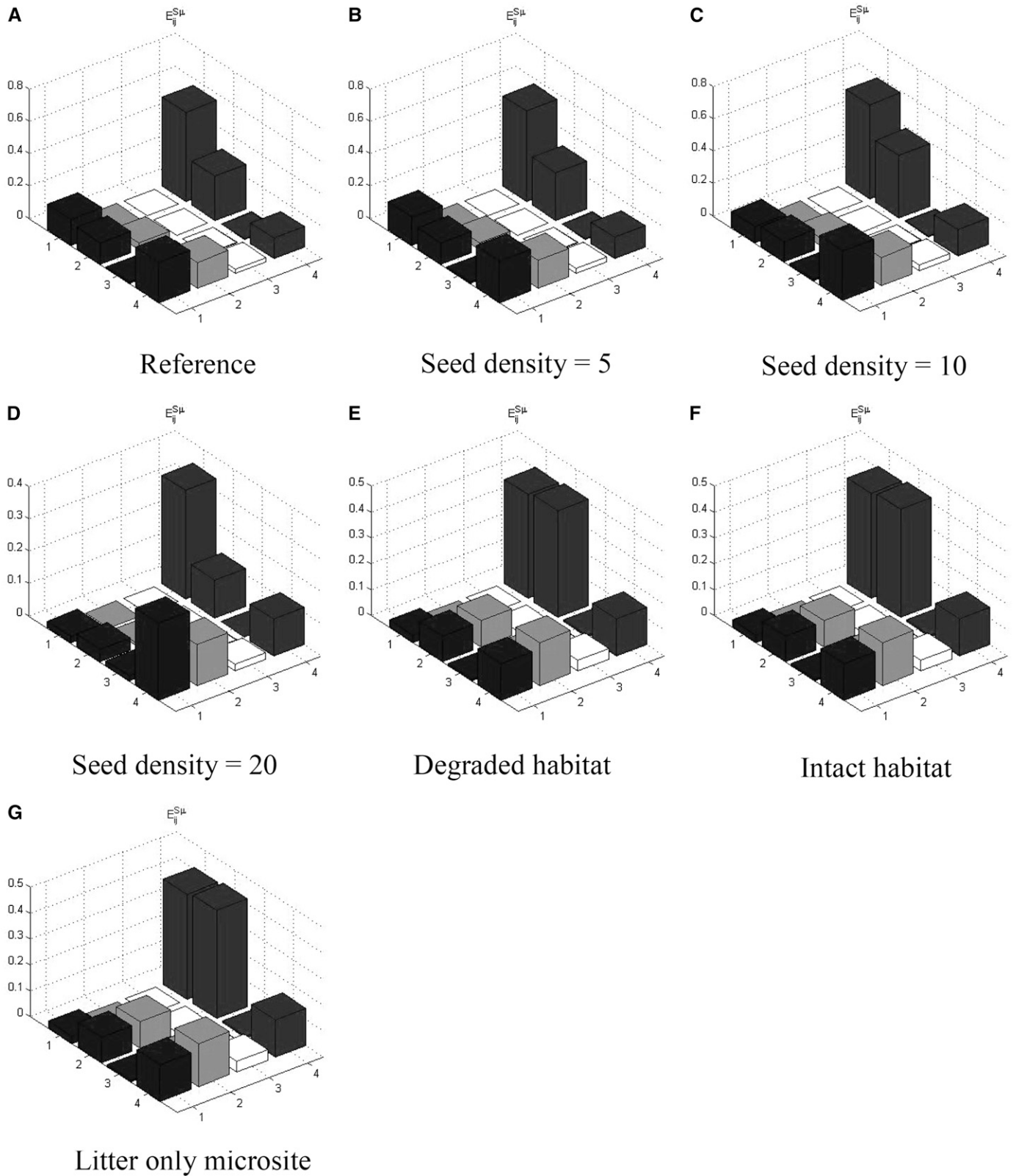
A) Seed density	Emergence 2009 (units, seedlings)		Emergence 2010 (units, seedlings)		Establishment (units, seedlings)	
1	7	9	4	5	0	0
4	16	24	28	42	3	5
8	22	37	46	89	9	13
24	43	136	53	280	7	9

B) Seed density	Emergence 2009 (units, seedlings)		Emergence 2010 (units, seedlings)		Establishment (units, seedlings)	
1	9	10	6	7	5	5
4	25	41	19	26	9	11
8	31	66	27	62	14	19
24	36	170	35	145	14	27



Litter only microsite

Appendix 3. Stochastic elasticity matrices for successional models of *Chamaecrista fasciculata* using pooled habitat and microsite combinations with perturbation of each mean transition. The reference model was a time-since-disturbance environmental matrix comprised of transition probabilities from each habitat by microsite combination following an initially disturbed environment (see Appendix 1). Axes along horizontal plane represent life history stage transitions. 1: seedbank; 2: small vegetative individual; 3: large vegetative individual; 4: reproductive. For example, a_{11} (far left bar in each figure) represents seedbank survival. See Stephens et al. (2014) for detailed definitions of transition abbreviations. Vertical axis represents elasticity values for each transition.



Appendix 4. Elasticity matrices for successional models of *Balduina angustifolia* using pooled habitat and microsite combinations with perturbation of each mean transition. The reference model was a time-since-disturbance environmental matrix comprised of transition probabilities from each habitat by microsite combination following an initially disturbed environment (see Appendix 1). Axes along horizontal plane represent life history stage transitions. 1: seedbank; 2: small vegetative individual; 3: large vegetative individual; 4: reproductive. For example, a_{11} (far left bar in each figure) represents seedbank survival. See Stephens et al. (2014) for detailed definitions of transition abbreviations. Vertical axis represents elasticity values for each transition.