Received: 18 October 2017 | Accepted: 16 March 2018

DOI: 10.1111/1365-2745.12985

RESEARCH ARTICLE

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

Predicting landscape-level distribution and abundance: Integrating demography, fire, elevation and landscape habitat configuration

Pedro F. Quintana-Ascencio[1,2] | **Stephanie M. Koontz**[2] | **Stacy A. Smith**[2] | **Vivienne L. Sclater**[2] | **Aaron S. David**[3] | **Eric S. Menges**[2]

[1]Department of Biology, University of Central Florida, Orlando, Florida, USA

[2]Plant Ecology Program, Archbold Biological Station, Venus, Florida, USA

[3]Department of Biology, University of Miami, Coral Gables, Florida, USA

Correspondence
Pedro F. Quintana-Ascencio
Email: pedro.quintana-ascencio@ucf.edu

Funding information
Division of Environmental Biology, Grant/Award Number: NSF-DEB 0812753 and NSF-DEB 1347247

Handling Editor: Shurong Zhou

Abstract

1. Demography varies in response to multiple interactive drivers at varying scales. However, these relationships are often assessed piecemeal, particularly without consideration of drivers at the landscape level.
2. We developed a model to predict population dynamics of an endangered, perennial herb *Hypericum cumulicola* across a range of landscape drivers. We estimated vital rates using 22 years of annual census data from 15 populations (10,910 and 38,313 unique observations) and additional seeding experiments, considering four landscape drivers (time-since-fire, patch area, patch aggregation and patch elevation).
3. We combined these models into integral projection models to assess population parameters. Predictions of occupancy and density were compared with an independent dataset of 33 habitat patches. We also evaluated the effect of fire-return interval on population persistence.
4. The landscape drivers had interactive effects on vital rates and demography. Occupancy was predicted for most patches, including many that were unoccupied. Abundances were poorly predicted, primarily because projections were unreliable for patches having intermediate areas and aggregation. When these patches were removed, the model explained 42% of the variance in abundance. Projected population growth was greater and extinction risk lower under more frequent fire-return intervals, at higher elevations, and in larger and more aggregated patches. Our modelling suggests that fire can be prescribed less often in larger than smaller patches to support a viable metapopulation of *H. cumulicola*.
5. *Synthesis*. The integration of landscape-level drivers and detailed demographic data is a valuable tool for understanding species abundances, distributions and dynamics at large scales. We evaluated the effect of interactions among fire, patch elevation, area and aggregation on the demography of a rare and endangered plant. Our findings reinforce the importance of regional dynamics. These drivers and their interactions suggest locations that can support higher vital rates, occupancy and abundance, and what fire-return intervals are optimal depending on landscape characteristics. This approach demonstrates a link between plant demography and landscape variables, although further work is needed to improve ecological predictions.

KEYWORDS
Florida scrub, habitat patches, *Hypericum cumulicola*, integral projection models (IPMs), landscape demography, metapopulations

1 | INTRODUCTION

Population dynamics result from the interplay between individual organisms and their environment. Yet, our ability to adequately predict population dynamics is limited, particularly over large spatial scales and long timeframes in which environmental factors vary widely (Gurevitch, Fox, Fowler, & Graham, 2016). Although there are thousands of studies of plant population dynamics, many involving the use of matrix or integral projection models to analyse life histories and compare treatments (Crone et al., 2011; Merow et al., 2014), most occur at small spatial scales and span few years (Crone et al., 2011; Menges, 2000; Salguero-Gómez et al., 2015). Advancement in this area will require understanding demographic effects of drivers over larger spatiotemporal scales that will improve predictions of the distribution and viability of populations in the face of global change mediated by human exploitation (Buckley et al., 2010; Csergő et al., 2017; Ulrey, Quintana-Ascencio, Kauffman, Smith, & Menges, 2016).

Most demographic models, including those at the landscape level, overlook environmental drivers and their interactions (Ehrlén, Morris, von Euler, & Dahlgren, 2016). Incorporating the effects of multiple, interactive landscape drivers into demographic models can provide better understanding and lead to realistic projections of population dynamics across landscapes that better explain the complex population dynamics than single factors (e.g. Mande, Ticktin, & Zuidema, 2015; Tye, Menges, Weekley, Quintana-Ascencio, & Salguero-Gómez, 2016). In this paper, we define landscape drivers as the habitat requirements, disturbances and spatial structure among patches that contribute to population dynamics. For example, ecological disturbances can facilitate or disrupt population growth, and the disturbances themselves can be affected by landscape structure (Turner, 2010). In particular, fire is a predominant ecological disturbance world-wide (Bond & Keeley, 2005), and landscape features (e.g. vegetation, elevation) contribute to the spatial patterning of fire's effects (Turner & Romme, 1994). Fire plays a fundamental role in the demography of many species which display strong ecological and evolutionary responses to fire (Hoffman, 1999; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011; Menges & Hawkes, 1998). However, effects of disturbance regimes on population dynamics can be challenging to study because of the large amount of longitudinal data required. Long-term studies may be necessary to avoid misleading conclusions built on chronosequence-based short-term studies (Pickett, 1989). Even when such long-term data are available, decoupling the effects of time since disturbance from year and population effects (e.g. climate, biotic interactions) requires datasets with replication across space and time.

The distribution of species across landscapes ultimately reflects the interaction of demography (vital rates such as survival, growth, fecundity and recruitment) with landscape and disturbance properties. However, both demographic inertia (e.g., long life span, dormant stages) and landscape history (e.g. environmental legacies) may create lags in responses. Therefore, realized species distributions (reflecting past interactions) may have different patterns than current vital rates. Assessing the relationships between demography and landscape-level drivers using detailed long-term monitoring can help to disentangle the causes of realized species distributions.

We assess the effects of landscape factors varying temporally and spatially on the population dynamics of *Hypericum cumulicola*, a pyrogenic, endangered Florida scrub endemic plant species. We take advantage of an ongoing 22-year study that has monitored many populations (sampled in 15 independent habitat patches) with a rich disturbance history (14 independent fires), well-described habitat requirements (for open gaps in Florida scrub dominated by *Ceratiola ericoides*; Quintana-Ascencio & Morales Hernández, 1997; Quintana-Ascencio & Menges, 2000) and a strong spatially patterned landscape (Miller, Quintana-Ascencio, Maliakal-Witt, & Menges, 2012). Past work has demonstrated critical roles of fire and human disturbances as drivers of individual *H. cumulicola* populations (Quintana-Ascencio, Menges & Weekley, 2003, Quintana-Ascencio, Weekley, & Menges, 2007) and the distribution of the species in the landscape (Miller et al., 2012; Quintana-Ascencio & Menges, 1996). However, we lack a comprehensive understanding of the interplay between *H. cumulicola* demography and landscape drivers, and this information is critical for proper habitat management for this species. We evaluate the following questions: (1) How will *H. cumulicola* vital rates change as a function of spatial and temporal variation of landscape variables? (2) How does the spatial and temporal variation of landscape variables affect abundance, occupancy, growth and persistence among populations of this species?

We built population models to evaluate the interactive effects of drivers on *H. cumulicola* population dynamics at the landscape level. We used integral projection models (Easterling, Ellner, & Dixon, 2000) incorporating submodels of vital rates based on stage, plant size, year, population and four landscape drivers: time-since-fire, patch elevation, patch area and patch aggregation. We recognize that while other components such as dispersal and metapopulation dynamics are important to population dynamics, we focus here on the temporal and spatial variation of habitat suitability and will address these other components in future work. Relative elevation, patch area and patch aggregation, which can affect both resource availability and local biotic interactions, were evaluated as measures of habitat suitability that could be characterized across the landscape

TABLE 1 Rosemary scrub patch-identification number (id) of populations studied for demography, and their patch area (ha), patch aggregation index, burned years (1967–2014), number of studied gaps and permanent quadrats

Id	Area (ha)	Aggregation	Fire years	Gaps	Quadrats
1 North	0.56	2.85	<1966, 1999	3	9
1 South	1.31	2.96	<1966	3	10
29	1.40	3.68	1985, 1997, 2015	1	20
32	0.22	4.83	1985, 1997	1	20
42	1.70	7.66	1993, 2010	3	20
45 (103)	0.23	5.37	1986, 1996, 2010	2	20
50	0.38	10.70	1968, 1993, 2010	1	20
57	0.09	11.80	1967, 1968, 1993, 2010	2	20
59	0.37	9.67	1968, 1991, 2010	7	20
62	0.55	11.50	1967, 2004, 2010	3	20
67	0.60	11.50	1972, 1986, 2008	1	20
87	0.17	9.33	1972, 1986, 2008	1	50
88[a]	0.27	10.30	1972, 1986, 2008	1	20
91	0.81	8.37	1972, 1986	1	40
93	0.70	6.86	1972	9	20

[a] We have not found any *Hypericum cumulicola* above-ground individuals in this patch since 2008.

(Bradley & Mustard, 2006). This landscape IPM approach allows us to model not only censused populations, but also *other* populations occurring in patches that were not sampled but for which we have spatiotemporal data. We evaluated the ability of our model to predict *H. cumulicola* occurrence across the landscape by comparing our model results (constructed from census data of 15 populations) to abundance and occurrence data from an independent sample of 33 habitat patches. Finally, we used our model to simulate population growth and extinction under various fire frequencies in order to evaluate different management options.

2 | MATERIALS AND METHODS

2.1 | Species natural history

Our model system was the Highlands scrub hypericum, *H. cumulicola* (Small) P. Adams. This short-statured perennial herbaceous species is endemic to Polk and Highlands Counties in central Florida, USA. (Christman & Judd, 1990; Estill & Cruzan, 2001) and listed as endangered by the US Fish and Wildlife Service (US Fish and Wildlife Service, 1999) and the state of Florida (Coile & Garland, 2003). Reproduction predominantly occurs between June and September. Its flowering branches are many flowered and indeterminate. It is self-compatible but depends on pollinators to set seed (Evans, Menges, & Gordon, 2003). Above-ground individuals are killed by fires (Dolan, Yahr, Menges, & Halfhill, 1999; Menges & Kohfeldt, 1995; Quintana-Ascencio & Morales Hernández, 1997), but seeds in the soil survive fire and form long-lived seed banks (Quintana-Ascencio, Dolan, & Menges, 1998). Fire suppression threatens this species because it depends on disturbances to reduce competition from dominant shrubs (Quintana-Ascencio & Menges, 2000; Quintana-Ascencio et al., 2003; Quintana-Ascencio & Morales Hernández, 1997). This species has a high degree of genetic differentiation (Dolan et al., 1999) and a distribution consistent with metapopulation dynamics (Miller et al., 2012; Quintana-Ascencio & Menges, 1996).

2.2 | Study site and environmental context

We conducted this study at Archbold Biological Station, Highlands County, Florida (USA).

Detailed community descriptions are given by Abrahamson, Johnson, Layne, and Peroni (1984), Menges and Kohfeldt (1995), and Menges (1999). The Archbold property contains a complex mosaic of habitats with different fire histories, including areas not burned since the late 1920s (Menges, Main, Pickert, & Ewing, 2017). Fire frequency varies among habitats due to different community structure, chances of ignition, rates of fuel accumulation and fire propagation (Abrahamson et al., 1984; Menges, Main, et al., 2017). Our focal community, the Florida rosemary scrub is an open shrub-dominated community that occurs on sandy, well-drained soils on ridges and knolls in central and coastal Florida and southeastern United States (Abrahamson et al., 1984). Florida rosemary occurs as patches at the highest elevations within a matrix of denser oak dominated communities and seasonal wetlands. The Florida scrub patches themselves are composed of several gaps of bare sand surrounded by a variable, but generally sparser matrix of shrubs. In central Florida, stands of uneven-aged Florida rosemary (*C. ericoides*) often dominate the shrub layer (Gibson & Menges, 1994; Johnson & Abrahamson, 1990). Other common shrubs in this community are xeromorphic oaks (*Quercus* spp.) and palmettos (*Serenoa repens* and *Sabal etonia*). Ground lichens (*Cladonia* spp. and *Cladina* spp.) and several herbaceous species, many of them endemic, proliferate in the open areas among the shrubs. Fire-return estimates for this community range between 10 and 100 years (Menges, Main, et al., 2017). Fires merge gaps and increase gap sizes, increasing occupancy of gap specialist herbaceous plants (Dee & Menges, 2014; Gibson & Menges, 1994; Menges, Crate, & Quintana-Ascencio, 2017; Young & Menges, 1999). *Hypericum cumulicola* is mostly limited to gaps between vegetation patches in Florida rosemary scrub.

2.3 | Demographic data

We recorded 38,313 unique observations from a sample of 10,910 individuals of *H. cumulicola*, from 15 independent Florida rosemary scrub patches (Table 1). Plants were censused during their peak of reproduction annually in July and August between 1994 and 2015. Annually, in every population, we tagged and evaluated *c.* 100 plants. In years when <100 plants were found, new tagged plants were added (*c.* 20–40 individuals) to the existing sample. Plants were classified into six possible stages: dead, alive, yearling (new plants just reaching its first census), new plant (plants of unknown age), missing and previously dead. For each tagged plant, we measured maximum height and recorded reproductive status annually. We counted total number of reproductive structures (flowers and fruits) for every plant in 1994–1999, 2001, 2002, 2010–2012 and counted reproductive structures for a sample of individuals in other years. Each year, coinciding with the annual census, we counted the number of plants in 0.5 × 1 m quadrats which summed area represented *c.* 2% of the open area in each focal patch (Table 1). Additional plant counts were performed in these plots in February of each year until 2008. Plants were classified by stage (yearling vs. adult) according to their recruitment year, but new plants outside of permanent density plots with unknown recruitment year at the census time were classified as adults if height >15 cm and number of stems >1, otherwise they were considered yearlings. We checked the location of previously dead plants after a year of first detection

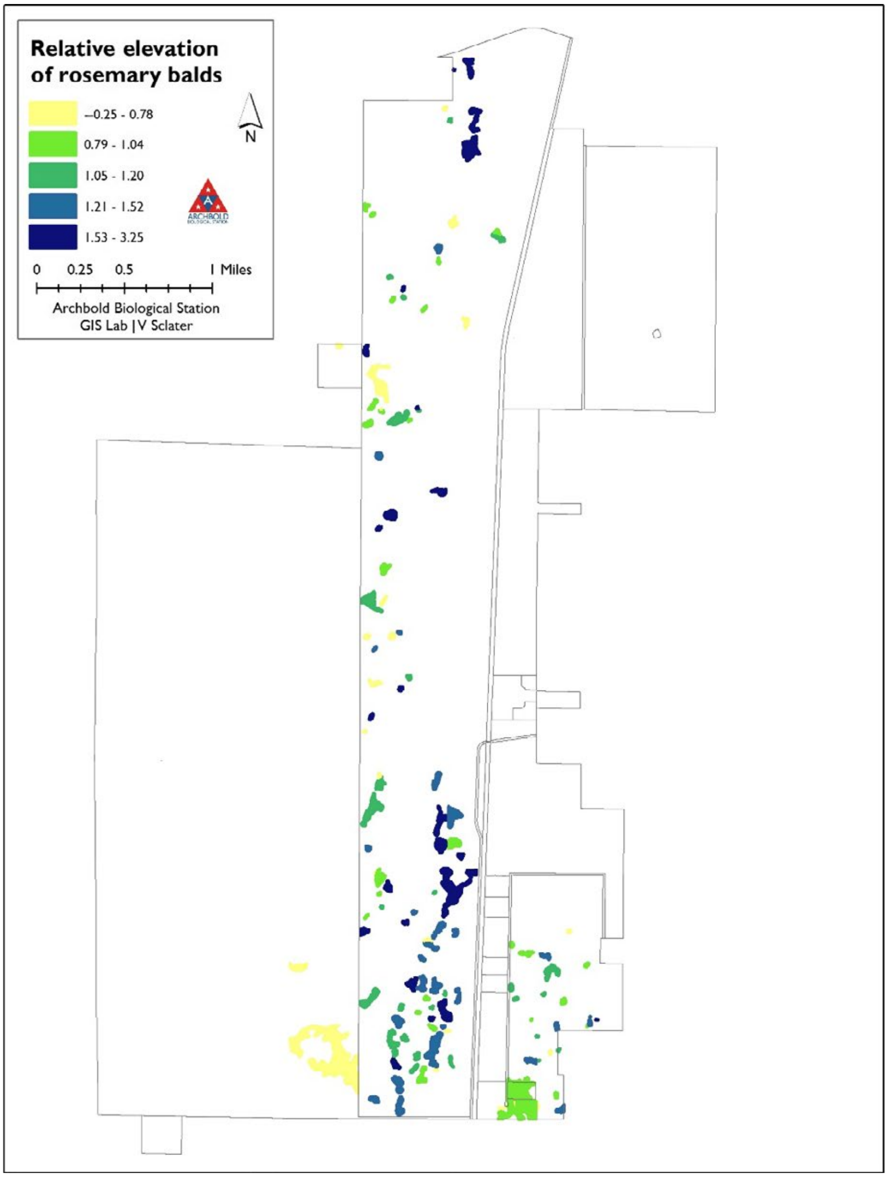

FIGURE 1 Map of Florida rosemary patches at Archbold Biological Station ($n = 92$). Approximate mean relative elevation (m) for each habitat patch is indicated with different colours

to assess possible plant dormancy. Less than 0.01% of previously declared dead plants were found subsequently alive and we did not include any plant dormancy.

Several reproductive metrics (fruiting, seed production, seed germination, seedling survival and seed dormancy) were quantified separately from the annual census. From observations of 20 plants that were visited once a week during the whole flowering season in 1995, we estimated that 55% of the flowers become viable fruits and produce seeds (P. F. Quintana-Ascencio & E. S. Menges, unpublished data). We estimated recruitment in the permanent quadrats in each site. We evaluated seed germination in burned and unburned microsites (Quintana-Ascencio & Menges, 2000) and survival of seedlings from February to August (1994–2008) in permanent plots within each studied patch (P. F. Quintana-Ascencio & E. S. Menges, unpublished data). For our models, we used seedling survival multiplied by 1.5 to produce estimates consistent with counts of yearlings in the field (Figure S16). We evaluated long-term seed dormancy of seeds in nylon mesh bags buried 5–10 cm for 1 and 2 years (Quintana-Ascencio et al., 1998). In 1995, 1996, and 1998, we counted under a microscope the number of visually viable seeds in a sample (n = 20) of fruits randomly taken from plants in every population (n = 15) studied for demography.

2.4 | Rosemary scrub patch data

We characterized Florida Rosemary scrub patches at Archbold and validated our models comparing the model output to occurrence data generated from broad surveys of these patches (Miller et al., 2012; Quintana-Ascencio & Menges, 1996). We identified 92 Florida rosemary scrub patches using available Archbold vegetation maps (Abrahamson et al., 1984; Figure 1). We surveyed for all vascular plant species in each rosemary patch in June 1988 and August 1989 and again in November 2004 and March 2005 (Miller et al., 2012; Quintana-Ascencio & Menges, 1996). There were 52 patches occupied by *H. cumulicola* in the first survey and 53 patches in the second. Between surveys, 11 patches changed status; 6 gained *H. cumulicola* occupancy and 5 lost it. We used historical records to document the occurrence of multiple natural, accidental and prescribed fires since 1967 (Menges, Main, et al., 2017). We used available GIS polygons to obtain data on patch area and geographic coordinates of each patch centroid to estimate patch aggregation with the index of Hanski and Thomas (1994).

$$S_i = -\left(\sum_j^n \exp(-ad_{ij}) * A_j\right) \tag{1}$$

where d_{ij} is the distance in kilometres from focal patch i to patches j to n and A_j is patch area in hectares. We used ∞ = 1 as in Quintana-Ascencio and Menges (1996) to facilitate comparisons between studies. In 2016, total counts of reproductive plants in a sample of 33 of these patches were used to validate model projections (see below; Table S7).

For each patch, we calculated relative elevation using ESRI's ArcGIS 10.3.1. We used zonal statistics and an existing Lidar dataset (flown in April, National Center for Airborne Laser Mapping, 2005) to calculate relative elevation for each studied gap and the mean elevation of all 92 rosemary scrub patches. Buffers at 50 m intervals were constructed around each rosemary scrub patch and searched for intersecting wetlands or seasonal ponds. The relative elevation for each patch was calculated as the average elevation of the rosemary scrub patch minus the average elevation of the wetland edges within the selected buffer surrounding the rosemary scrub patch. A 50-m buffer was used for the majority of the patches; however, some required searching up to over 150 m. The relative elevation was similarly calculated for gaps (as defined in Menges, Crate, et al., 2017) within studied rosemary scrub patches as the elevation of the gap point minus the average elevation of the wetland edges within the selected buffer surrounding the rosemary scrub patch. We used the relative elevation at the gap level to assess vital rate variation but the patch level elevation for modelling.

2.5 | Evaluating drivers of vital rates

The integral projection model was comprised of submodels that estimated vital rates as a function of the different drivers. In these models, we recognized three life-history stages (seed, yearling and adult) and used the natural logarithm of individual height (size) as the continuous state variable (with a quadratic response). We modelled vital rate variation using GLMM. Variation of population within year was included as a random effect in all models when data permitted ($\alpha_{s(y_i)}$). We used binomial error distributions for survival (σ) and probability of reproduction (φ_0), and normal distributions for changes in size of yearlings and adults (γ), and counts of reproductive structures (φ_1). We preferred a normal distribution instead of Poisson or negative binomial for reproductive structures because of the large number produced per plant ($\bar{x} = 124$, SE = 2.5; up to 6,000 structures, n = 7,055 plants; data were transformed with natural logarithms). We replaced models of yearling fecundity with those for adults when generated unreliable results associated with low sample sizes. The hierarchical models describing survival (σ), growth (γ), probability of flowering (φ_0) and fecundity (φ_1) of yearlings and adults were defined as:

$$\begin{aligned} \mathrm{G}(\mu_{j(i_y)}) = {} & \alpha_0 + \left(\alpha_1 \times \mathrm{size}_j + \alpha_2 \times \mathrm{size}_j^2\right) * \alpha_3[\mathrm{stage}_j] * \beta_k \\ & \times \mathrm{elevation}_i * \beta_k \times \mathrm{TSF}_i + \sum (\beta_{k_v} \times \mathrm{patch}_i) + \alpha_{s(y_i)} \end{aligned} \tag{2}$$

where α and β are coefficients for data at individual (j) and patch (i) levels for each driver (k) and their interactions (*). The term ($\beta_{k_v} \times \mathrm{patch}_i$) included the additive and interactive effects of patch size and aggregation (v). Data for all independent variables, except plant size, were scaled to facilitate model convergence. We used model selection based on Akaike Information Criterion corrected for small sample sizes (AIC$_c$; Burnham & Anderson, 2002) to identify the most plausible combination of landscape drivers (time-since-fire, relative elevation, patch area and patch aggregation) and their interactions explaining variation of each vital rate of above-ground individuals (survival, growth, probability of reproduction and fecundity).

Annual individual seed production was partitioned among deceased seeds, seeds that remained dormant and seeds that germinated and survived through the annual census. We evaluated the variation of these seed and seedling vital rates as function of time-since-fire and relative elevation and identified the most plausible models. Seed germination proportions in burned and unburned microsites were point estimates (Quintana-Ascencio & Menges, 2000). We used a linear model with quadratic response of time-since-fire for seed dormancy, and seed survival.

$$g(\mu_j) = \alpha_0 + \alpha_1 * \mathrm{TSF}_i + \alpha_2 \mathrm{TSF}_i^2 \qquad (3)$$

where α are coefficients for data at patch (i) level used for each individual seed (j). We used a general additive model (procedure GAM in package R mgcv, Wood, Pya, & Saefken, 2016) with cubic regression splines and normal distributed errors to assess the variation in seedling survival as a function of time-since-fire. Using AIC to compare models with a range of values (4–12) for the smoothing term, we identified the most likely term (6).

2.6 | Implementing the integral projection model

We used the fixed effects of vital rate models to build the kernels of integral projection models (Easterling et al., 2000; Ellner, Childs, & Rees, 2016; Ellner & Rees, 2006) summarizing the *H. cumulicola* life cycle (Figure 2a) for each rosemary patch's specific combination of time-since-fire, relative elevation, patch area and patch aggregation. The mid-point rule approximation to the continuous form of these IPMs (from Ellner et al., 2016) was a Goodman matrix (Goodman, 1969) model (with 301 × 301 cells, Figure 2b) that describes the population dynamics of three stages, one discrete (dormant seeds) and two continuous (yearlings and adults). Every IPM consisted of two merged rectangular matrices (of 300 × 150 cells each for yearlings and adults, respectively), one vector for germination of dormant seeds and their survival to census, another vector for recently produced seeds (150 × 2 cells each) and one scalar describing long-term seed dormancy. The responses of coupled equations are integrated over $L = -2.3$ and $U = 4.5$ (logarithm values of 0.1 to 90 cm in height, respectively) using the mid-point approximation into $m = 300$ size classes of width $h = (U-L)/m$. Models with 200 bins per stage were commensurate and we kept 150 because computation ease. The discrete form of the IPM is described as:

$$n(z_{jk}, t+1) = h \sum_{i=1}^{m} \mathrm{K}(z_{jk}, z_{ik}) n(z_{ik} t) \qquad (4)$$

where $n(z_{jk}, t+1)$ is the number of individuals in size class j and stage k at time $t + 1$ from individuals in size class i and stage k at time t given the matrix kernel (K) and number of individuals at time t $n(z_{jk} t)$. We defined two continuous kernel functions for yearlings and adults, one including survival and growth ($P_{j,i}$) and another for recruitment ($F_{j,i}$; as surviving dormant seeds [$Seed_{(j,i)}$] and yearling recruitment [$Yearling_{(j)}$]).

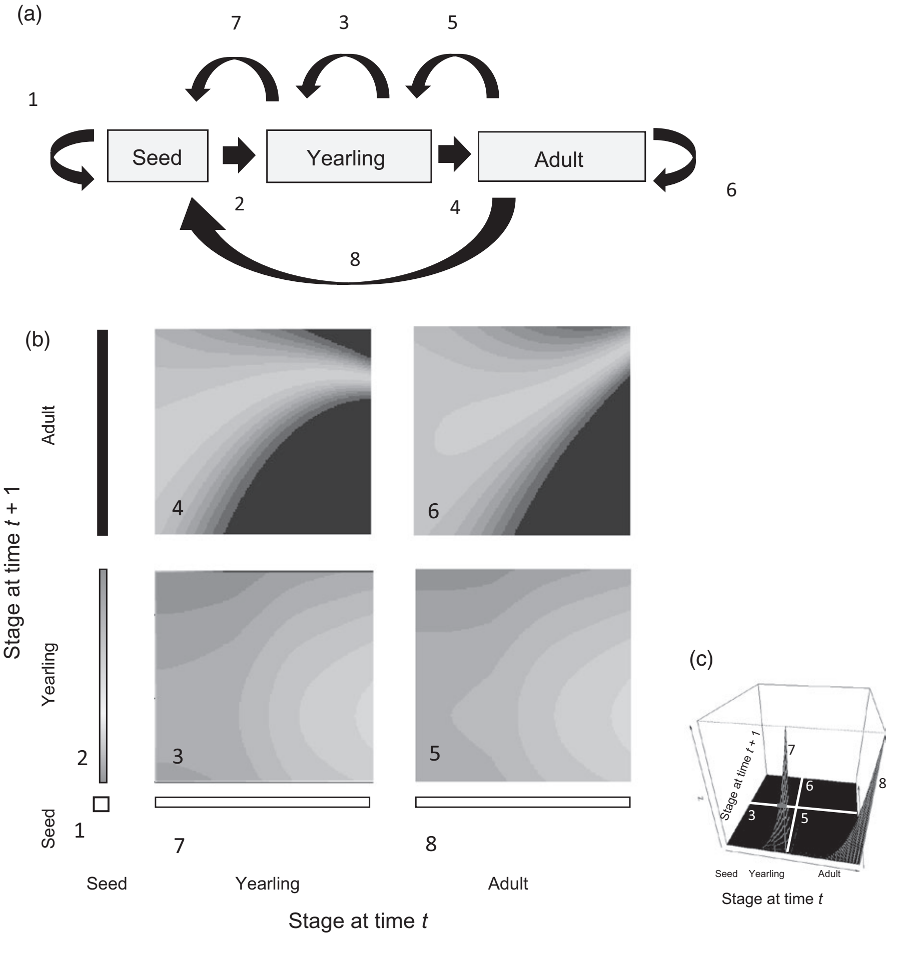

FIGURE 2 (a) *Hypericum cumulicola* life cycle diagram. Stage transitions are indicated with wide arrows. Labels 1–8 relate these transitions across panels. (b) Demographic transitions are depicted as a Goodman's matrix incorporating the kernels of the integral projection model. Lighter colours denote higher values. Transitions 3–7 are size-based, with larger plants to the right and towards the top of each box. The axes are relative encompassing a matrix of 301 by 301 bins. The width of the vectors for new produced dormant seeds (rectangles at the bottom), yearlings germinating from the seed bank (left rectangles; seeds do not produce adults directly) and dormancy (bottom left square) are exaggerated. (c) 3-D depiction of the Goodman's matrix in (b) that better illustrates seed production by yearlings (7) and adults (8) along the Z-axis

$$K_{z(j,i)} = P_{(j,i)} + F_{(j,i)} \tag{5}$$

$$P_{(j,i)} = \sigma_{(i)} \times \gamma_{(j,i)} \tag{6}$$

$$F_{(j,i)} = \mathrm{Seed}_{(j,i)} + \mathrm{Yearling}_{(j)} \tag{7}$$

where j is the index for the vector of size classes n at $t + 1$ and i the one of time t. Recruitment as seeds included estimates of probability of seed survival (s), reproduction (φ_0), number of reproductive structures (φ_1), fruit set (φ_2), number of viable seeds per fruit (φ_3) and proportion going dormant (δ).

$$\mathrm{Seed}(y, t+1) = s(x, t) + \int_L^U \varphi_0(x)\varphi_1(x)\varphi_3 s\delta dx \tag{8}$$

Recruitment as new yearlings (seedlings surviving until the annual summer census) included estimates of germination from the seed bank (Seed(x, t)ξ), probability of reproduction (φ_0), number of reproductive structures (φ_1), fruit set (φ_2), number of viable seeds per fruit (φ_3), germination probability ($\xi = 1 - \delta$) and seedling survival (φ_4).

$$\mathrm{Yearling}(y,t+1) = \mathrm{Seed}(x,t)\xi\varphi_4 + \int_L^U \left[\varphi_0(x)\varphi_1(x)\varphi_2(x)\varphi_3(x)\xi\varphi_4\right] \mathrm{d}x \tag{9}$$

Yearlings were assigned initial heights using normal distributions of logarithmic plant height with a common mean (log [6 cm]) but time-since-fire specific standard deviations. We used the eigen structure of our models to quantify the population growth rate (λ) for each population with specific time-since-fire, patch relative elevation, patch size and patch aggregation. We calculated 100 bootstrap iterations for eight scenarios bracketing observed variation with lambda as a function of time-since-fire, relative elevation, patch size and patch aggregation to obtain 95% CI and minimum and maximum λ.

We used the IPM to obtain predictions of the number of above-ground adult (flowering) individuals, comparing predictions to numbers counted in 33 randomly chosen rosemary scrub patches in 2016. Simulations started in the year 1964 and followed patch specific historical burn frequencies, each initiated with a common vector (271,170 seeds, 2,809 yearlings and 10,749 adults). The absolute numbers in the vector are subjective (50% of all observed plants) and were used to obtain relative assessments among patches, not absolute estimates. We used the overall data to establish the relative abundance of yearlings and the number per size bin in the initial vector (Figure S1). We used an estimate of 20/1 seeds per plant in the initial vector based on the mean ratio in the simulated data. We assumed all simulated populations started 9 years since the last fire. We compared predicted numbers to observed complete patch counts of above-ground adult plants in 2016 year. We focused on adult plants because they are conspicuous in the field, providing accurate density estimates. We considered the patch to be occupied if the number of above-ground individuals at the end of the simulation was >1. We calculated the Yule coefficient, a test of association between two binary variables (Yule, 1912; using R package PSYCH; Revelle, 2017), to assess the overall agreement between observed and expected occurrences in these patches.

2.7 | Fire simulations

We evaluated the effect of different fire frequencies on population dynamics with simulations. We used Weibull functions to model the probability of fire as a function of time-since-fire. Each fire occurrence was simulated collecting uniform random numbers and comparing them to the value of the function. If the function generated value was higher it was presumed that a fire would happen. The mean fire returns used were at 20, 40 and 60 years (Figure S17). These values bracket current prescribed time-since-fire at Archbold Biological Station (Menges, Main, et al., 2017). Cumulative probability of quasi-extinction (n < 1 above-ground individuals) after 200 years was estimated for 200 simulations of each combination of fire frequency, relative elevation (0.5 and 1.5 m), patch area (small = 0.08 ha and large = 10 ha) and patch aggregation (isolated with index = 5 and aggregated with index = 10). All populations started with the same vectors and 9 years post-fire (see Figure S17 for the shape of functions determining simulated fire returns).

3 | RESULTS

We monitored *H. cumulicola* in 15 populations, all of which have unique burn histories (Table 1). Between 1966 and 2015, individual populations burned 1–5 times during 14 different years, creating many combinations of calendar year and time-since-fire (TSF). *H. cumulicola* occurs over several metres of relative elevation, but tends to have its highest occupancy at intermediate elevations (Figures 1 and 3). All plausible models for annual vital rate variation of above-ground individuals included plant stage (whether plants were adults or yearlings [1 year old plants]), quadratic terms for size (natural logarithmic plant height) and several landscape drivers: TSF, patch relative elevation, patch area, patch aggregation and multiple interactions (Tables S1 and S2–S5 with the significance of the coefficients for each vital rate).

3.1 | Summary of vital rates

Survival: *H. cumulicola* was characterized by extremely low seedling (newly recruited plants found prior to census) survival. Estimated seedling survival was highest in recently burned patches (0.006), decreasing at intermediate TSF and long-unburned patches (0.001; Figure S16). Most yearlings (new plants reaching their first census) were shorter than 15 cm, the threshold for reproduction, and had a log-normal distribution in height while adult heights were normally distributed with a mean of 32 cm (*SE* = 0.1; Figure S1). Annual transitions indicated more yearlings and adults survived than died (overall 0.649 and 0.790, respectively; Figures S2–S4). In general, adult survival was highest for smaller and intermediate plant heights, lower TSF and relative elevations, and larger and more aggregated patches

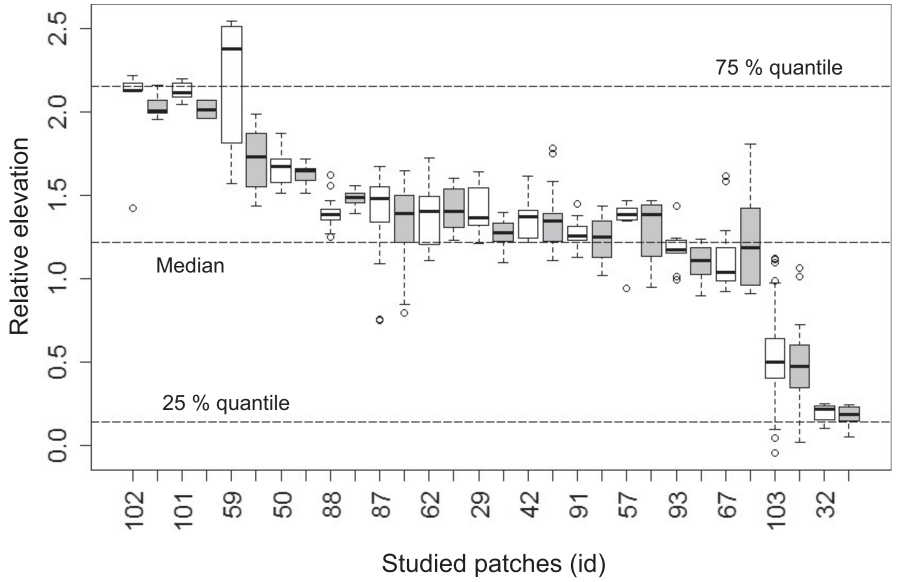

FIGURE 3 Relative elevation (m) of gaps among censused rosemary scrub patches (the abscissa is patch-identification number) ordered from higher to lower relative elevation. Gap occupancy, within the patch, by *Hypericum cumulicola* is indicated by colour (white was unoccupied, grey was occupied). The dotted lines mark the median, 25th and 75th percent quantiles for relative elevation for all Florida rosemary scrub patches in Archbold Biological Station (n = 92)

(Figures S2 and S4), with clear interactions (e.g. large plants had relatively higher survival than small plants in smaller patches and at lower elevations; [Figure S4]; survival for small plants decreased faster with TSF in lower elevations [Figure S4]). Yearling data, based on smaller sample sizes, was more uncertain but indicated a decrease in survival with TSF and patch area at higher relative elevations (Figures S3 and S4).

Growth: *H. cumulicola* had consistent growth patterns from year to year (Figure 4). Yearlings and small plants tended to grow while adults were more stable in height. Plant growth (change in height) decreased with size particularly among large adults (Figures S5–S7). Both adult and yearling growth decreased with time-since-fire at lower relative elevations. At intermediate elevations, fire had little effect on growth (TSF lines very close together; Figure S7), and at higher elevations growth increased with TSF (Figure S7).

3.1.1 | Reproduction

Most plants taller than 15 cm (91%) produced fruits, with the number of fruits increasing exponentially with height (Figure 4 and Figure S8–S13). Time-since-fire effects on fruit production were relatively subtle, especially for yearlings, and interacted with elevation, patch area and aggregation (Figure S10). Reproduction started at smaller plant sizes for adults than yearlings, and at higher elevations and in larger patches for both adults and yearlings (compare levels in Figure S10). Fecundity of adult plants was higher in long-unburned sites with lower elevations and less affected by TSF at intermediate and higher relative elevations. Adult fecundity for small plants was higher in recently burned sites at lower elevations and lower in recently burned sites at higher elevations (Figure S13, left panels). Across all sizes of yearlings, fecundity increased with TSF in lower elevation patches but decreased with TSF in higher elevation patches (Figure S13, right panels).

3.1.2 | Seed production

We estimated an average of 13 (*SD* = 0.97; Table S8) viable seeds per fruit. Most seeds (60%–80%) became dormant for one year or more (Figure S14). Approximately 30–50% of the dormant seeds remained dormant each year with higher dormancy at intermediate TSF (Figure S15). Variation in height for yearlings at census time decreased with time-since-fire.

3.2 | Integral projection modelling of growth rates

Population growth (λ) increased during the first few years post-fire with a peak around 5–6 years, then quickly declined, reaching its lowest values between 10 and 20 years post-fire. Our models projected higher population growth at higher elevations and in larger and aggregated patches. There was more variation in λ among bootstrap projections with higher elevation during the first few years post-fire but this pattern reversed in long-unburned conditions (Figure 5).

We found no evidence of overall agreement between observed and projected occurrences (−0.12; CI = −0.87, 0.80; Yule association coefficient, alpha = 0.05; Yule, 1912; Figure 6). Our model was biased towards predicting occurrences (30 out of 33 patches were predicted having *H. cumulicola*). Predictions of occurrence were particularly unreliable for patches with small patch area and small aggregation (the lower and left sections in Figure 6). Our models also did not predict overall abundance of plants in occupied patches (Figure 7, n = 23 patches). Predictions of abundance were particularly unreliable for patches with intermediate areas and aggregation (Figure 6). However, when these patches (those with asterisks in Figures 6 and 7) were removed, our model explained 42% of the variance in plant abundance within occupied patches in 2016 (log of observed count = 2.4 + 0.49 × log of predicted count (*SE* = 0.86 and 0.19, respectively; n = 10).

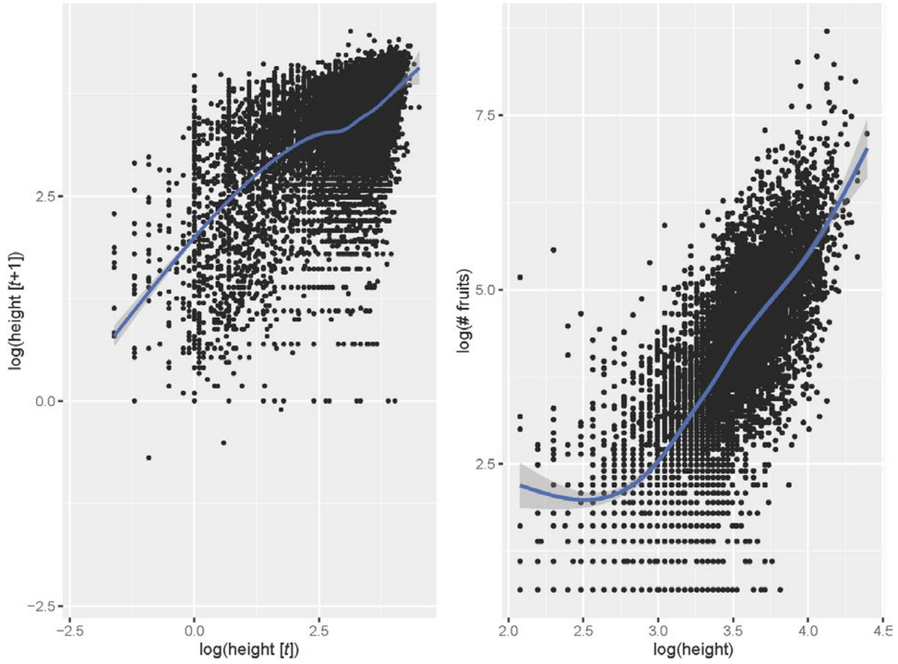

FIGURE 4 Plot of (a) individual heights from 1 year to the next and (b) numbers of fruits as function of height. All variables were natural log transformed. All studied *Hypericum cumulicola* observations were included in this plot

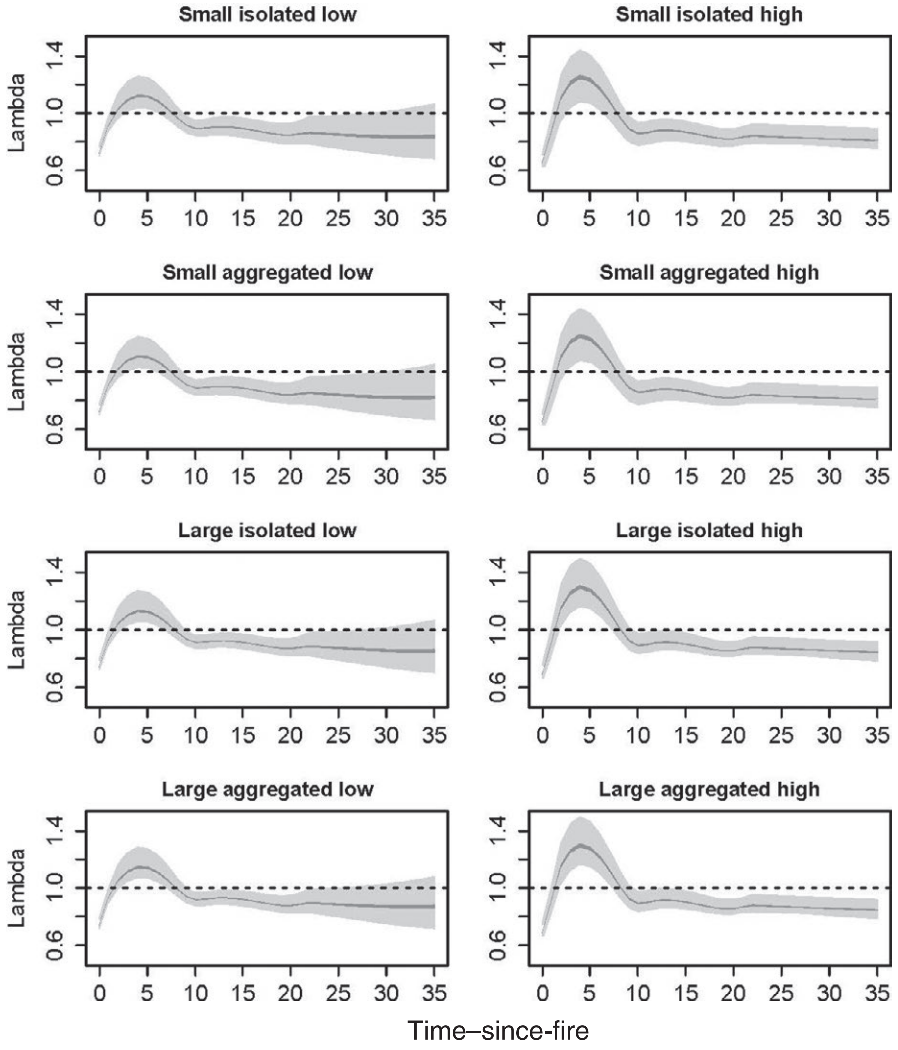

FIGURE 5 Lambda as a function of time-since-fire, patch size (small = 0.08 ha; large = 1.0 ha), patch aggregation (isolated = 5, aggregated = 10) and relative elevation (low = 0.5 m; and high = 2.5 m). Dark grey areas are 95% CI and light grey polygons are limited by minimum and maximum values both from bootstrapped data (n = 100 iterations). The line at $\lambda = 1.0$ is provided as a reference

Cumulative probability of extinction increased with TSF and decreased with patch area and patch aggregation (Figure 8). The model predicted the lowest extinction probabilities for the fire-return intervals of 20 years (close to the lower limit for Florida rosemary scrub; Menges, Main, et al., 2017) and a fast escalation of extinction probabilities with longer fire intervals. Changes in extinction probability with time-since-fire were less marked between 0.5 and 1.5 m of elevation. Our model predicted that *H. cumulicola* populations in the smallest and more isolated patches are the most prone to extinction, with population under fire-return intervals of >40 years becoming extinct in less than 50–90 years and those with fire every 20 years becoming extinct in 100–200 years (Figure 8). Populations in large aggregated patches with fire-return intervals around 40 years could persist 70–150 years before becoming extinct and could persist >200 years with more frequent fires. Small, aggregated patches had similar extinction probabilities to small isolated patches, while large isolated patches were more similar to large aggregated patches.

4 | DISCUSSION

The integration of landscape-level environmental drivers and detailed demographic data yields a powerful tool for understanding species abundances, distributions and dynamics at larger scales. This study, using an unusually detailed, spatially expansive, long-term dataset, shows the possibility of unravelling complex interactions between landscape patterns and ecological disturbances affecting a species' distribution and demography. We took advantage of a long-term dataset to decouple effects of disturbance from population and year effects. Understanding drivers of demographic change (Ehrlén et al., 2016) may improve our ability to predict population changes (Crone et al., 2013). Scaling up predictions from populations to landscapes allows the evaluation of species responses to changing drivers, such as climate change (Opdam & Wascher, 2004).

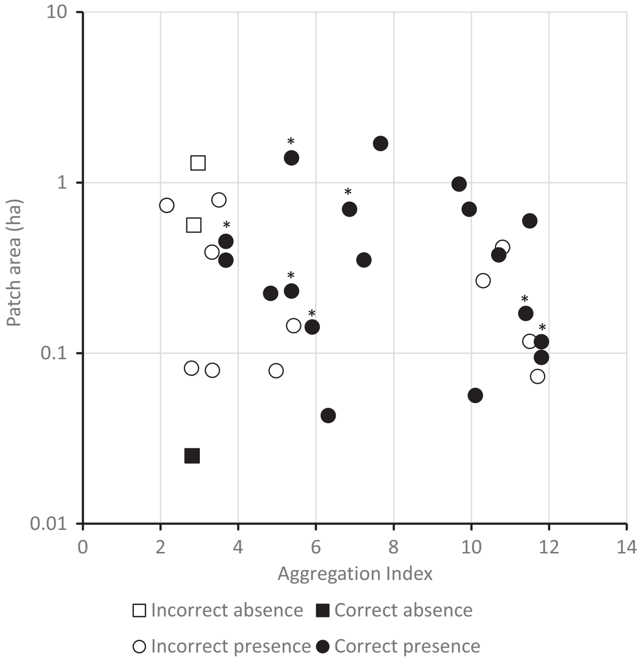

FIGURE 6 Model patch occupancy in 2016 predicted by aggregation and patch area. Correct predictions are indicated with filled symbols: correctly predicted presences (filled circles) and correctly predicted absences (filled squares). Incorrect predictions are indicated by open symbols: incorrectly predicted presences (open circles) and incorrectly predicted absences (open squares). Filled circles with an asterisk were populations with poor abundance predictions

In this paper, we use integral projection models parameterized with long-term census data that varied in response to landscape variables to analyse the demography of a habitat specialist. Similar to our previous work (Quintana-Ascencio et al., 2003), we show that *H. cumulicola* vital rates were strongly related to fire, the predominant ecological disturbance. Yet, in the present study, we provide further evidence that vital rates were also affected by small scale landscape patterns such as elevation that alter the distance to the water-table (e.g. survival in recently burned patches was higher at lower relative elevations) and larger scale patterns of patches in the landscape such as patch aggregation (e.g. survival was higher in large aggregated patches). Size-dependent patterns in vital rates were shifted depending on the ecological context. For example, the survival of smaller plants was more sensitive than larger plants to time-since-fire, but mainly at lower elevations. Reproduction in this species started earlier at higher relative elevations and larger patches.

Population growth was greater at higher elevations. These locations are farther to the water-table and soils are more prone to drying (Weekley, Gagnon, Menges, Quintana-Ascencio, & Saha, 2007). However, these elevations have lower shrub cover and larger gaps (Dee & Menges, 2014; Menges, Wally, Salo, Zinthefer, & Weekley,

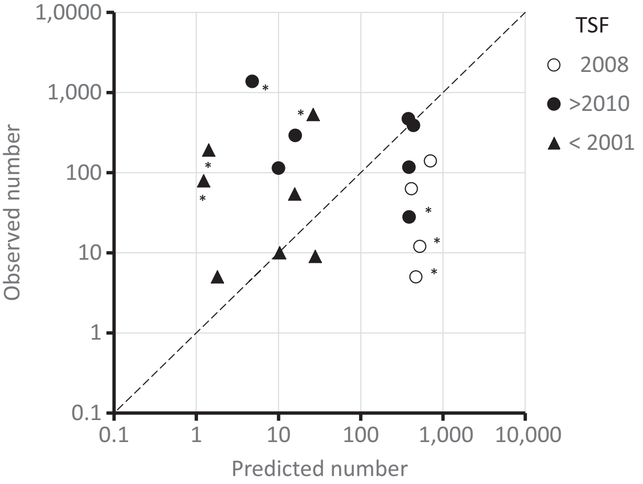

FIGURE 7 Observed vs. predicted number of reproductive adults. Each point represents the number of predicted and observed plants in an occupied habitat patch in 2016. The dotted line is the 1:1 line. Symbols with asterisk were populations with intermediate patch area and aggregation shown in Figure 6. Symbols indicate the year of the last fire

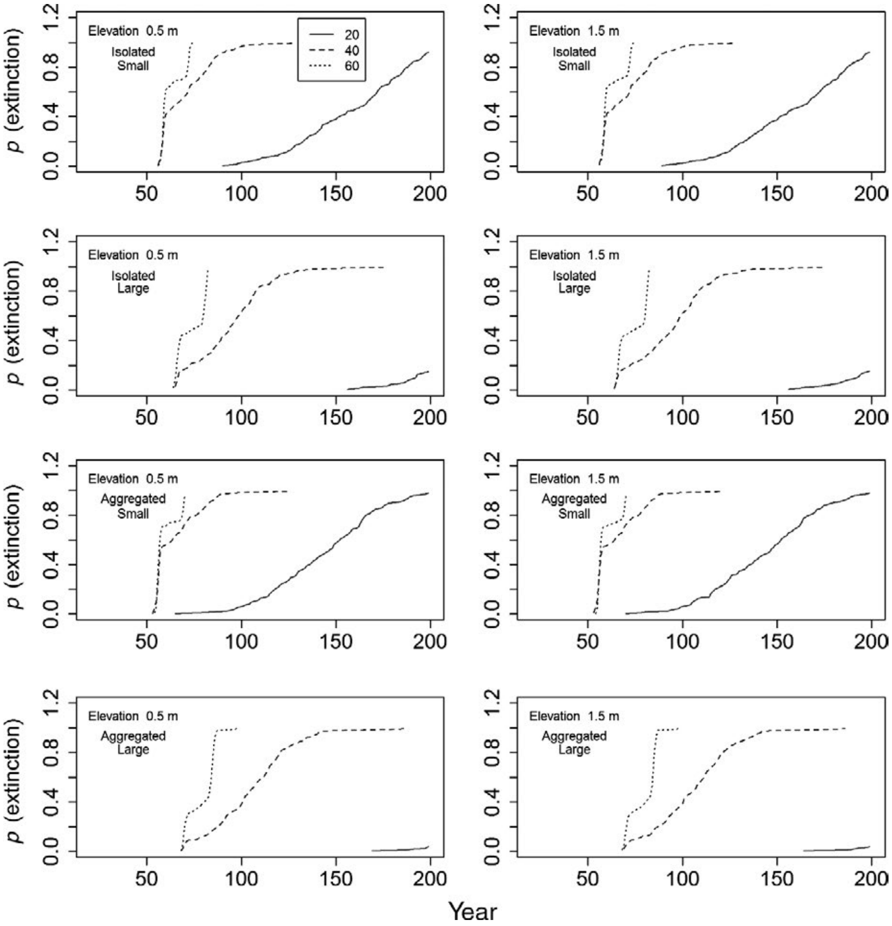

FIGURE 8 Cumulative probability of extinction ($N < 1$) as a function of projected year, fire frequency (20, 40 and 60 years; in legend), relative elevation (0.5 and 1.5 m), patch size (small = 0.08 ha and large = 1.0 ha) and patch aggregation (isolated = 5 and aggregated = 10)

2008), suggesting lower interspecific competition. *H. cumulicola* is a microhabitat (gap) specialist, favouring microsites with low shrub and litter cover (Quintana-Ascencio & Morales Hernández, 1997) and being rarely found in smaller gaps (<4 m^2; Menges, Crate, et al., 2017). The combination of large open gaps and higher elevations supports higher population growth, especially in recently burned areas.

Overall, these data indicate the importance of metapopulation dynamics. *Hypericum cumulicola* occupancy and population growth predictions were highest in large, aggregated habitat patches, consistent with patterns found in analyses of metapopulation structure (Quintana-Ascencio & Menges, 1996) and observed extinctions and colonizations (Miller et al., 2012). Large habitat patches may have several advantages for metapopulation dynamics, including a larger target for rescues, greater diversity of microhabitats, and the ability to support larger populations less prone to demographic or environmental stochasticity (Hanski, Moilanen, & Gyllenberg, 1996; Wolf, Brodmann, & Harrison, 1999). Larger habitat patches may also be more likely to support larger populations of the dominant shrub Florida rosemary, which may act as a foundation species for *H. cumulicola* and other herbaceous plants that are vulnerable to competition from resprouting shrubs (Menges, 2007). However, previous assessments of occupancy based on landscape configuration of patch aggregation and patch size (Miller et al., 2012; Quintana-Ascencio & Menges, 1996) better predicted *H. cumulicola* patch presence and absence than this analysis, where we predicted that the majority of patches will be occupied. Model predictions of abundance were most reliable for patches with the extremes of patch area or aggregation. Otherwise, abundances in patches with intermediate patch area or aggregation were overpredicted in long-unburned patches and underpredicted in patches with more recent fires. In this study, predictions of occupancy and abundance were weaker for habitat patches with small and intermediate size and aggregation. We have previously documented that unoccupied patches can be suitable habitat for *H. cumulicola* (Quintana-Ascencio et al., 1998). These results indicate that limited dispersal and unfavourable matrix habitats can synergistically contribute to colonization failure (Angert, Bayly, Sheth, & Paul, 2018). Few studies have integrated population models and landscape-level environmental drivers to characterize species distributions, although this approach has great promise for assessing the consequences of environmental changes (Ehrlén & Morris, 2015).

Drivers predicting vital rates were not always the same as drivers associated with occurrence. For example, *H. cumulicola* occupancy peaked at higher elevations but many vital rates peaked at lower elevations. This may reflect lags in demography (demographic inertia; Garcia & Zamora, 2003) such as the role of seed banks in allowing populations to persist between disturbances (Eriksson, 1996). Better understanding of the spatial and temporal dynamics of seed dormancy and dispersal and the role of environmental factors on their variation will greatly benefit our understanding of regional plant population persistence. In the Florida scrub, we have documented the disappearance of *H. cumulicola* and *Eryngium cuneifolium* populations (a co-occurring gap specialist) between fires, and their genetic and demographic recovery after fire (Dolan, Quintana-Ascencio, & Menges, 2008; Menges & Quintana-Ascencio, 2004). In addition, landscape changes in extreme microsites (e.g. the largest open patches) may lag behind other landscape patterns. These persisting critical microsites may allow populations in some patches to continue for many years (Oostermeijer, Van't Veer, & Den Nijs, 1994). Short-term or limited studies in areas with these persisting patches may be biased, as patches where all plants have died cannot be a source of data. This demographic ghost of mortality past may explain unexpected demographic patterns in chronosequence studies.

As well as unravelling the interacting effects of fire, local and broad landscape patterns on demography, our analyses have important implications for land management of Florida scrub and other ecosystems with spatially and temporally variable fire regimes. Fires can occur less frequently at higher elevations than lower elevations and still maintain metapopulation viability. Fires need to occur more often for small and isolated habitat patches, to promote demographically healthy populations of *H. cumulicola*. Because lower elevation areas have greater and more continuous vegetative cover, fires may be more complete than at higher elevations, supporting useful spatial variation in the fire regime (Menges, Main, et al., 2017). Intermediate fire frequencies and modest spatial patchiness in fires may minimize extinction of obligate seeding species in many pyrogenic ecosystems (Bradstock, Bedward, Scott, & Keith, 1996; Ooi, Whelan, & Auld, 2006).

Many critiques of demographic modelling have pointed out that models do a poor job of predicting beyond more than a few years (Crone et al., 2013; Menges, 2000). By incorporating the use of common drivers, such as weather, habitat suitability, disturbances, landscape patterns and land management, we can improve our understanding of temporal and spatial variability in demography (Ehrlén & Morris, 2015; Menges, 2007). Weaknesses of population models can be attributed to their frequent dependence on short spans of data (Menges, 2000) and on their frequent blindness to underlying drivers (Ehrlén & Morris, 2015). The scaling up of local demography to landscapes, accomplished by a combination of approaches, can lead to more effective management for ecological diversity.

ACKNOWLEDGEMENTS

We thank many Archbold research assistants and interns and UCF students that helped to collect and organize these data. R. Lavoy, M. Morales-Hernández, A. Z. Quintana-Morales, E. M. Quintana-Morales and C. W. Weekley provided extraordinary support. F. López-Borghesi helped with simulations. This work was partially funded by NSF-DEB 1347247 and NSF-DEB 0812753. Computer simulations were facilitated by the UCF Advanced Research Computing Center (Stokes).

AUTHORS' CONTRIBUTIONS

P.F.Q.-A. and E.S.M. designed this study and collaborated with S.M.K. and S.A.S. organizing and implementing field work and curating the data. V.L.S. gathered and prepared the G.I.S. data and produced the maps. P.F.Q.-A. and A.S.D. developed the model. P.F.Q.-A. and E.S.M. wrote the initial version of the manuscript and all the authors edited the manuscript.

DATA ACCESSIBILITY

Data available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/fb8661cc0af964a4c5caace85b72b036 (Quintana-Ascencio & Menges, 2018).

ORCID

Pedro F. Quintana-Ascencio http://orcid.org/0000-0001-7587-8166

Eric S. Menges http://orcid.org/0000-0002-9486-4189

REFERENCES

Abrahamson, W., Johnson, A., Layne, J., & Peroni, P. (1984). Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales ridge. *Florida Scientist*, *47*, 209–250.

Angert, A. L., Bayly, M., Sheth, S. N., & Paul, J. R. (2018). Testing range-limit hypotheses using range-wide habitat suitability and occupancy for the Scarlet Monkeyflower (*Erythranthe cardinalis*). *The American Naturalist*, *191*, E76–E89. https://doi.org/10.5061/695984

Bond, W. J., & Keeley, J. E. (2005). Fire as a global "herbivore": The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*, 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bradley, B. A., & Mustard, J. F. (2006). Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, *16*, 1132–1147. https://doi.org/10.1890/1051-0761(2006)016[1132:CTLDOA]2.0.CO;2

Bradstock, R. A., Bedward, M., Scott, J., & Keith, D. A. (1996). Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. *Conservation Biology*, *10*, 776–784. https://doi.org/10.1046/j.1523-1739.1996.10030776.x

Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J., & Sears, M. W. (2010). Can mechanism inform species' distribution models? *Ecology Letters*, *13*, 1041–1054.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and inference: A practical information-theoretic approach*. New York, NY: Springer.

Christman, S. P., & Judd, W. S. (1990). Notes on plants endemic to Florida Scrub. *Florida Scientist*, *53*, 52–73.

Coile, N. C., & Garland, M. A. (2003). *Notes on Florida's endangered and threatened plants* (4th ed., 127 p.). Gainesville, FL: Florida Department of Agriculture and Consumer Services/Division of Plant Industry.

Crone, E. E., Ellis, M. M., Morris, W. F., Stanley, A., Bell, T., Bierzychudek, P., … Menges, E. S.(2013). Ability of matrix models to explain the past and predict the future of plant populations. *Conservation Biology*, *27*, 968–978. https://doi.org/10.1111/cobi.12049

Crone, E. E., Menges, E. S., Ellis, M. M., Bell, T., Bierzychudek, P., Ehrlén, J., … Williams, J. L. (2011). How do plant ecologist use matrix population models? *Ecology Letters*, *14*, 1–8. https://doi.org/10.1111/j.1461-0248.2010.01540.x

Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., … Buckley, Y. M. (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, *20*, 969–980. https://doi.org/10.1111/ele.12794

Dee, J. R., & Menges, E. S. (2014). Gap ecology in Florida scrubby flatwoods: Effects of time-since-fire, gap size, gap aggregation, and microhabitat on species occurrence and composition. *Journal of Vegetation Science*, *25*, 1235–1246. https://doi.org/10.1111/jvs.12170

Dolan, R. W., Quintana-Ascencio, P. F., & Menges, E. S. (2008). Genetic change following fire in populations of a seed-banking perennial plant. *Oecologia*, *158*, 355–360. https://doi.org/10.1007/s00442-008-1151-6

Dolan, R. W., Yahr, R., Menges, E. S., & Halfhill, M. D. (1999). Conservation implications of genetic variation in three rare species endemic to Florida rosemary scrub. *American Journal of Botany*, *86*, 1556–1562. https://doi.org/10.2307/2656793

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, *81*, 694–708. https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Ehrlén, J., & Morris, W. F. (2015). Prediction changes in the distribution and abundance of species under environmental change. *Ecology Letters*, *18*, 303–314. https://doi.org/10.1111/ele.12410

Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmental explicit structured population models of plants. *Journal of Ecology*, *104*, 292–305. https://doi.org/10.1111/1365-2745.12523

Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations: A practical guide to the integral projection model*. Cham, Switzerland: Springer Publishing. https://doi.org/10.1007/978-3-319-28893-2

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *The American Naturalist*, *167*, 410–428. https://doi.org/10.1086/499438

Eriksson, O. (1996). Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos*, *77*, 248–258. https://doi.org/10.2307/3546063

Estill, J. C., & Cruzan, M. B. (2001). Phytogeography of rare plant species endemic to the southeastern United States. *Castanea*, *1*, 3–23.

Evans, M. E. K., Menges, E. S., & Gordon, D. R. (2003). Reproductive biology of three sympatric plants endemic to Florida scrub. *Biological Conservation*, *111*, 235–246. https://doi.org/10.1016/S0006-3207(02)00293-8

Garcia, D., & Zamora, R. (2003). Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *Journal of Vegetation Science*, *14*, 921–926. https://doi.org/10.1111/j.1654-1103.2003.tb02227.x

Gibson, D. J., & Menges, E. S. (1994). Population structure and spatial patterns in the dioecious shrub *Ceratiola ericoides*. *Journal of Vegetation Science*, *5*, 337–346. https://doi.org/10.2307/3235857

Goodman, L. A. (1969). The analysis of population growth when the birth and death rates depend upon several factors. *Biometrics*, *25*, 659–681. https://doi.org/10.2307/2528566

Gurevitch, J., Fox, G. A., Fowler, N. L., & Graham, C. H. (2016). Landscape demography: Population change and its drivers across spatial scales. *Quarterly Review of Biology*, *91*, 459–485. https://doi.org/10.1086/689560

Hanski, I., Moilanen, A., & Gyllenberg, M. (1996). Minimum viable metapopulation size. *The American Naturalist*, *147*, 527–541. https://doi.org/10.1086/285864

Hanski, I., & Thomas, C. D. (1994). Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. *Biological Conservation*, *68*, 167–180. https://doi.org/10.1016/0006-3207(94)90348-4

Hoffman, W. A. (1999). Fire and population dynamics of woody plants in a neotropical savanna: Matrix model projections. *Ecology*, *80*, 1354–1369. https://doi.org/10.1890/0012-9658(1999)080[1354:FAPDOW]2.0.CO;2

Johnson, A. F., & Abrahamson, W. G. (1990). A note on the fire response of species in rosemary scrubs on the southern Lake Wales Ridge. *Florida Scientist*, *2*, 138–143.

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*, 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Mande, L., Ticktin, T., & Zuidema, P. A. (2015). Resilience of palm populations to disturbances by interactive effects of fire, herbivory and harvest. *Journal of Ecology*, *103*, 1032–1043. https://doi.org/10.1111/1365-2745.12420

Menges, E. S. (1999). Ecology and conservation of Florida scrub. In R. C. Anderson, J. S. Fralish, & J. M. Baskin (Eds.), *The savanna, barren, and rock outcrop communities of North America* (pp. 7–22). New York, NY: Cambridge University Press. https://doi.org/10.1017/CBO9780511574627

Menges, E. S. (2000). Population viability analyses in plants: Challenges and opportunities. *Trends in Ecology and Evolution*, *15*, 51–56. https://doi.org/10.1016/S0169-5347(99)01763-2

Menges, E. S. (2007). Integrating demography and fire management: An example from Florida scrub. *Australian Journal of Botany*, *55*, 261–272. https://doi.org/10.1071/BT06020

Menges, E. S., Crate, S. J. H., & Quintana-Ascencio, P. F. (2017). Dynamics of gaps, vegetation, and plant species with and without fire. *American Journal of Botany*, *104*, 1825–1836. https://doi.org/10.3732/ajb.1700175

Menges, E. S., & Hawkes, C. V. (1998). Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecological Applications*, *8*, 935–946. https://doi.org/10.1890/1051-0761(1998)008[0935:IEOFAM]2.0.CO;2

Menges, E. S., & Kohfeldt, N. M. (1995). Life history strategies of Florida scrub plants in relation to fire. *Bulletin of the Torrey Bot Club*, *122*, 282–297. https://doi.org/10.2307/2996320

Menges, E. S., Main, K. N., Pickert, R. L., & Ewing, K. (2017). Evaluation of a fire management plan for fire regime goals in a Florida landscape. *Natural Areas Journal*, *37*, 212–227. https://doi.org/10.3375/043.037.0210

Menges, E. S., & Quintana-Ascencio, P. F. (2004). Population viability with fire in *Eryngium cuneifolium*: Deciphering a decade of demographic data. *Ecological Monographs*, *74*, 79–99. https://doi.org/10.1890/03-4029

Menges, E. S., Wally, A., Salo, J., Zinthefer, R., & Weekley, C. W. (2008). Gap ecology in Florida scrub: Species occurrence, diversity, and gap properties. *Journal of Vegetation Science*, *19*, 503–514. https://doi.org/10.3170/2008-8-18399

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., … McMahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. *Methods in Ecology and Evolution*, *5*, 99–110. https://doi.org/10.1111/2041-210X.12146

Miller, T., Quintana-Ascencio, P. F., Maliakal-Witt, S., & Menges, E. S. (2012). Metacommunity dynamics over 16 years in a pyrogenic shrubland. *Conservation Biology*, *26*, 357–366. https://doi.org/10.1111/j.1523-1739.2011.01807.x

National Center for Airborne Laser Mapping. (2005). Airborne Laser Swath Mapping Project: Precise Topography for Biological Study, Archbold Biological Station. NFS sponsored, flown April 11 and 21, 2005.

Ooi, M. K. J., Whelan, R. J., & Auld, T. D. (2006). Persistence of obligate-seeding species at the population scale: Effects of fire intensity, fire patchiness and long fire-free intervals. *International Journal of Wildland Fire*, *15*, 261–269. https://doi.org/10.1071/WF05024

Oostermeijer, J. G. B., Van't Veer, R., & Den Nijs, J. C. M. (1994). Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology 31*, 428–438. https://doi.org/10.2307/2404440

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, *117*, 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In G. E. Likens (Ed.), *Long-term studies in ecology; approaches and alternatives* (pp. 110–135). New York, NY: Springer-Verlag. https://doi.org/10.1007/978-1-4615-7358-6

Quintana-Ascencio, P. F., Dolan, R. W., & Menges, E. S. (1998). *Hypericum cumulicola* demography in unoccupied and occupied Florida scrub patches with different time-since-fire. *Journal of Ecology*, *86*, 640–651. https://doi.org/10.1046/j.1365-2745.1998.00285.x

Quintana-Ascencio, P. F., & Menges, E. S. (1996). Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. *Conservation Biology*, *10*, 1210–1219. https://doi.org/10.1046/j.1523-1739.1996.10041210.x

Quintana-Ascencio, P. F., & Menges, E. S. (2000). Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *American Journal of Botany*, *87*, 690–699. https://doi.org/10.2307/2656855

Quintana-Ascencio, P. F., & Menges, E. S. (2018). Demographic measures of *Hypericum cumulicola* (Hypericaceae) in 15 populations in Florida Rosemary Scrub patches with different time-since-fire, at Archbold Biological Station, Highlands County, Florida from 1994-2015. *Environmental Data Initiative*, https://doi.org/10.6073/pasta/fb8661cc0af964a4c5caace85b72b036

Quintana-Ascencio, P. F., Menges, E. S., & Weekley, C. W. (2003). A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Conservation Biology*, *17*, 433–449. https://doi.org/10.1046/j.1523-1739.2003.01431.x

Quintana-Ascencio, P. F., & Morales Hernández, M. (1997). Fire-mediated effects of shrubs, lichens and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. *Oecologia*, *112*, 267–271.

Quintana-Ascencio, P. F., Weekley, C. W., & Menges, E. S. (2007). Comparative demography of a rare species in Florida scrub and road habitats. *Biological Conservation*, *137*, 263–270. https://doi.org/10.1016/j.biocon.2007.02.009

Revelle, W. (2017). *Procedures for psychological, psychometric, and personality research*. http://personality-project.org/r/psych. Downloaded 01/206/2018

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., ... Buhr, H. (2015). The COMPADRE plant matrix database: An open online repository for plant demography. *Journal of Ecology*, *103*, 202–218. https://doi.org/10.1111/1365-2745.12334

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*, 2833–2849. https://doi.org/10.1890/10-0097.1

Turner, M. G., & Romme, W. H. (1994). Landscape dynamics in crown fire ecosystems. *Landscape Ecology*, *9*, 59–77. https://doi.org/10.1007/BF00135079

Tye, M. R., Menges, E. S., Weekley, C. W., Quintana-Ascencio, P. F., & Salguero-Gómez, R. (2016). A demographic ménage à trois: Interactions between disturbances both amplify and dampen population dynamics of an endemic plant. *Journal of Ecology*, *104*, 1778–1788. https://doi.org/10.1111/1365-2745.12642

Ulrey, C., Quintana-Ascencio, P. F., Kauffman, G., Smith, A. B., & Menges, E. S. (2016). Life at the top: Long-term demography, microclimatic refugia, and responses to climate change for a high-elevation southern Appalachian endemic plant. *Biological Conservation*, *200*, 80–92. https://doi.org/10.1016/j.biocon.2016.05.028

US Fish and Wildlife Service. (1999). *Multi-species recovery plan for the threatened and endangered species of South Florida*. Vero Beach, FL: US Fish and Wildlife Service.

Weekley, C. W., Gagnon, D., Menges, E. S., Quintana-Ascencio, P. F., & Saha, S. (2007). Variation in soil moisture in relation to rainfall, vegetation, gaps, and time-since-fire in Florida scrub. *Ecoscience*, *14*, 377–386. https://doi.org/10.2980/1195-6860(2007)14[377:VISMIR]2.0.CO;2

Wolf, A., Brodmann, P. A., & Harrison, S. (1999). Distribution of the rare serpentine sunflower, *Helianthus exilis*, (Asteraceae): The roles of habitat availability, dispersal limitation, and species interactions. *Oikos*, *84*, 69–76. https://doi.org/10.2307/3546867

Wood, S. N., Pya, N., & Saefken, B. (2016). Smoothing parameter and model selection for general smooth models. *Journal of the American Statistical Association*, *111*, 1548–1563. https://doi.org/10.1080/01621459.2016.1180986

Young, C. C., & Menges, E. S. (1999). Gap-phase dynamics and microhabitat specialization: Post-fire regeneration of scrubby flatwoods communities on the Lake Wales Ridge. *Florida Scientist*, *62*, 1–10.

Yule, G. U. (1912). On the methods of measuring association between two attributes. *Journal of the Royal Statistical Society*, *75*, 579–652. https://doi.org/10.2307/2340126

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Quintana-Ascencio PF, Koontz SM, Smith SA, Sclater VL, David AS, Menges ES. Predicting landscape-level distribution and abundance: Integrating demography, fire, elevation and landscape habitat configuration. *J Ecol*. 2018;00:1–14. https://doi.org/10.1111/1365-2745.12985