Interacting livestock and fire may both threaten and increase viability of a fire-adapted Mediterranean carnivorous plant

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Summary

1. Quantifying interactive effects of environmental drivers on population dynamics can be critical for a robust analysis of population viability. Fire regimes, among the most widespread disturbances driving population dynamics, are increasingly modified by and interact with human activities. However, viability of fire-adapted species is typically assessed overlooking disturbance interactions, potentially resulting in suboptimal management actions.

2. We investigated whether increasing human disturbances in fire-prone ecosystems may pose a threat or an opportunity to improve population viability, using demographic data of the carnivorous, post-fire recruiting plant *Drosophyllum lusitanicum,* endemic to heathlands in the southwestern Mediterranean Basin. We built integral projection models and simulated population dynamics under different combinations of two key disturbance types affecting populations: fire and livestock browsing and trampling. We used perturbation analyses to determine potential long-term consequences of maintaining fundamentally different disturbance types.

3. Despite most populations inhabiting browsed habitats, simulations showed a greater extinction risk in populations under high livestock pressure compared with ones under low or moderate pressures. Extinction risk decreased when fire return intervals shortened in populations under low or moderate livestock pressure; however, the opposite pattern emerged in heavily browsed populations, where short intervals between fires increased extinction.

4. Elasticity analyses showed that decreases in viability under frequent disturbance interactions (heavy browsing and frequent fire) may be explained by selection against seed dormancy in populations with frequent browsing and trampling. This may potentially cause populations to collapse when fires kill above-ground plants without populations being able to recover from a seed bank.

5. *Synthesis and applications.* Incorporating disturbance interactions can result in a different assessment of viability of a fire-adapted species than considering fire regimes alone. In Mediterranean ecosystems, fire management may be more effective when integrating moderate human activities. However, replacing fires by human disturbances, a currently widespread strategy in many fire-prone ecosystems, is not recommended since it may fundamentally alter population dynamics and selection pressures and decrease viability of fire-adapted species.

Key-words: Bayesian integral projection models, disturbance interactions, *Drosophyllum lusitanicum*, elasticities, environmental drivers, fire, livestock disturbance, quasi-extinction, stochastic population growth rate (log λ_s)

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Introduction

Natural disturbances are key drivers of population dynamics (Tuljapurkar 1990; Boyce, Haridas & Lee 2006; Turner 2010). Among the various disturbance regimes to which natural populations are exposed, fires are the most widespread, regularly affecting ~40% of the Earth's terrestrial habitats (Bond & Keeley 2005; Bond, Woodward & Midgley 2005). In turn, many plant species in fire-prone habitats evolved strategies that link critical life cycle transitions to fire, e.g. post-fire recruitment from persistent seed banks (Bond & Keeley 2005). However, human activities increasingly interact with natural fire regimes (Lawson *et al.* 2010; Keeley *et al.* 2012). Beyond merely changing fire regimes through fire suppression policies or changes to land management (Valdecantos, Baeza & Vallejo 2008; Steel, Safford & Viers 2015), humans have introduced small-scale disturbances, typically involving vegetation removal, harvesting of plant parts, or intense livestock browsing, that co-occur with fires and affect an increasing number of fire-adapted species (e.g. Lawson *et al.* 2010; Mandle, Ticktin & Zuidema 2015; Tye *et al.* 2016). Yet, the demographic consequences of multiple, potentially interacting disturbance regimes remain poorly understood in many fire-prone ecosystems (Ehrlén *et al.* 2016; Tye *et al.* 2016).

Population dynamics of fire-adapted species may not necessarily be negatively affected by human disturbances. For example, when post-fire regeneration is triggered by indirect cues such as increased light levels or removal of allelopathic compounds (Renne *et al.* 2014), disturbances that mimic the effect of fire of removing vegetation may allow for continuing recruitment even as fire return intervals increase (Bond & Keeley 2005; Quintana-Ascencio, Weekley & Menges 2007). In addition, human disturbances may decrease competition between plants and therefore increase survival and growth (Sánchez-Velásquez *et al.* 2002; Tye *et al.* 2016).

However, small-scale, chronic human disturbances are fundamentally different from rare fire events and can lead to lasting changes in population structure and dynamics of fire-adapted species (Quintana-Ascencio, Weekley & Menges 2007; Lawson *et al.* 2010). For example, by significantly increasing plant longevity or fecundity, disturbances such as repeated vegetation removal exert novel selection pressures on organisms (Palkovacs *et al.* 2012), and their interaction with periodic high-intensity fires may severely destabilize populations and result in extinction (Mandle, Ticktin & Zuidema 2015; Darabant *et al.* 2016). For conservation management, quantifying both the potential long-term changes in population dynamics under human disturbances and the demographic effects of disturbance interactions in fire-prone ecosystems will be critical to assess the viability of fire-adapted species under increasing human pressures (Ashley *et al.* 2003; González-Varo *et al.* 2015).

Here, we use *Drosophyllum lusitanicum* (L.), Link (Drosophyllaceae) (*Drosophyllum* hereafter) to investigate the effects of interacting disturbances on population dynamics of a fire-adapted plant species. This rare carnivorous subshrub is associated with fire-prone, highly biodiverse heathlands in the SW Iberian Peninsula and N Morocco (Garrido *et al.* 2003). In natural heathlands, *Drosophyllum* has a life cycle typical of a short-lived seeder species (e.g. Menges & Quintana-Ascencio 2004; Fig. 1a), germinating from a persistent seed bank after fire (Paniw *et al.* 2016). Seed germination is triggered by both heat and removal of surrounding vegetation (Paniw, Salguero-Gómez & Ojeda 2015). However, with prevailing fire suppression policies across the species' range (Turco *et al.* 2016), most populations persist in habitats where chronic human disturbances – shrub slashing or browsing and trampling by livestock and game – mimic the removal of shrub canopy by fire (Garrido *et al.* 2003). Populations exposed to human disturbances show a markedly different population structure (longer above-ground survival of adult plants and annual recruitment; Paniw, Salguero-Gómez & Ojeda 2015) than fire-disturbed heathland populations but experience fire occasionally (Plan INFOCA – Incedios forestales 2012; Fig. 1). With increasing local extinctions across the species' range (Garrido *et al.* 2003), assessing population viability under different combinations of disturbances is not only important for conservation of heathland biodiversity but may also shed light on the potential fate of fire-adapted seeder species in Mediterranean ecosystems.

We quantified the dynamics of *Drosophyllum* populations exposed to variable time since last fire and two levels of browsing/trampling pressure by domestic ungulates (Fig. 1b). We asked (i) under what conditions disturbance interactions may cause population extinction vs. persistence. As population dynamics in human-disturbed habitats may differ from ones in natural heathlands (Paniw, Salguero-Gómez & Ojeda 2015; Paniw *et al.* 2016), we also asked (ii) how chronic disturbances may change selection pressures and what consequences such changes may have for management of this species. To answer the questions, we parameterized integral projection models (IPMs) and evaluated the effect of interactions between the two disturbance types on the stochastic population growth rate (log λ_s) and the probability of quasi-extinction ($P_q(t)$). The latter described the probability of population sizes decreasing below an extinction threshold by time t. We obtained both quantities by simultaneously simulating stochastic dynamics while assessing parameter uncertainty with Bayesian methods. Finally, we used prospective perturbations of vital rates to investigate selection pressures imposed by various regimes of interacting disturbances. We provide fully commented *R* scripts of our analyses, which can be adapted to quantify population-level effects of multiple disturbances in a wide range of systems.
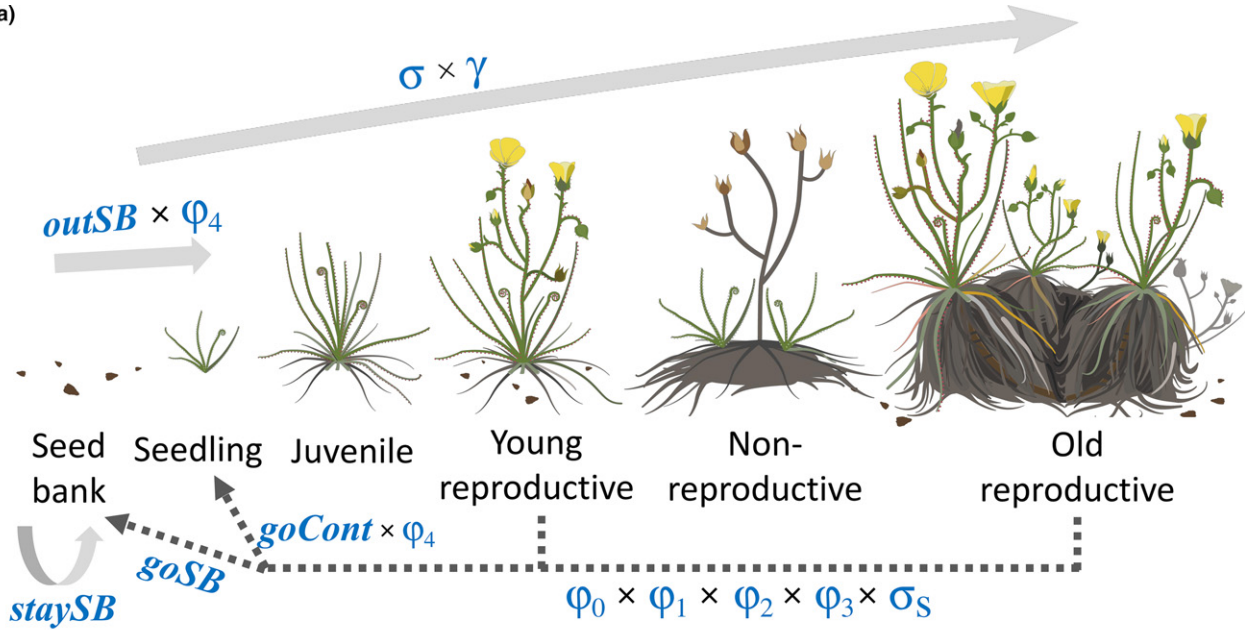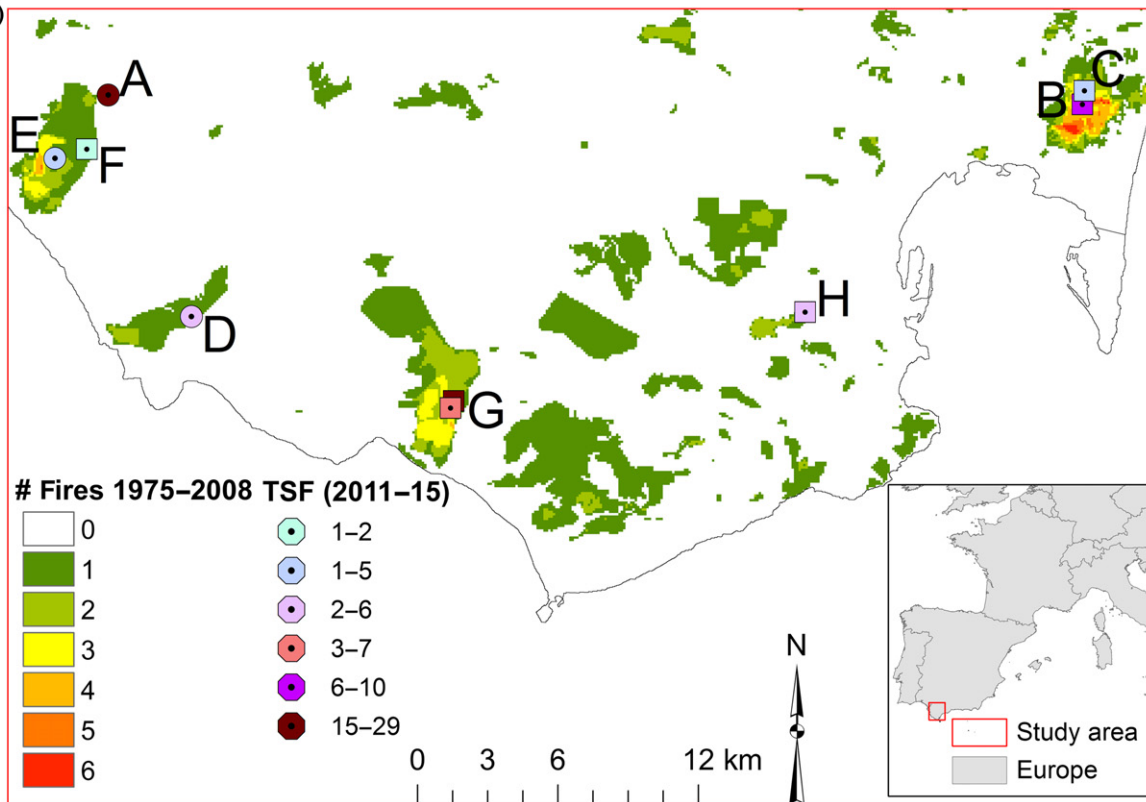
Fig. 1. The carnivorous subshrub *Drosophyllum lusitanicum* shows life cycle adaptations to recurrent fires and occurs in a fire-prone Mediterranean biodiversity hotspot. (a) In the integral projection models, life cycle transitions (here simplified to stages) were represented by 12 vital rates (blue); Solid and dashed arrows represent transitions of survival [above-ground (σ) or seed bank (*staySB*, *outSB*)]/ growth [above-ground (γ) or seedling size (φ_4)] and fecundity [flowering probability (φ_0), # stalks (φ_1), # flowers/stalk (φ_2), # seeds/flower (φ_3), immediate germination (*goCont*), and seed-bank ingression (*goSB*) or egression (*outSB*)], respectively; σ_S – above-ground seed survival. (b) The study sites (different letters) in which demographic data were collected all had burned at least once since 1975 and differed in time-since-fire (TSF) and livestock pressure, populations exposed to either high (squares) or low (circles) browsing and trampling of vegetation by domestic ungulates. Two populations with different TSF were pooled in site G. [Colour figure can be viewed at wileyonlinelibrary.com]

Materials and methods

STUDY SITES AND DEMOGRAPHIC DATA

To quantify vital-rate transitions in *Drosophyllum*, we parameterized IPMs (Easterling, Ellner & Dixon 2000) with census and experimental field and laboratory data. We estimated vital rates of individuals with above-ground biomass from five annual censuses (every April 2011–2015) of a total of 2378 individuals in eight populations (Fig. 1b). The populations differed with respect to (i) livestock pressure (*LS*) from browsing/trampling, experiencing either high (*HLS*) or low (*LLS*) pressure; and (ii) time-since-fire (*TSF* hereafter), between 1 and >26 years (Fig. 1b; Table S1.1 in Appendix S1, Supporting Information). As Mediterranean heathland habitats do not change significantly in species composition and structure >3 years after fire (Ojeda, Marañón & Arroyo 1996), we transformed TSF into a categorical variable consisting of 1, 2, 3, or >3 years since fire.

The above-ground vital rates obtained from the census data included survival (σ), growth (γ), probability of flowering (φ_0), number of flowering stalks (φ_1), number of flowers per stalk (φ_2), number of seeds per flower (φ_3) and seedling size distribution the next year (φ_4) (Fig. 1a). We used plant *size* = log(# of leaves × length of longest leaf (cm)), after model selection for σ, γ, φ_0 and φ_1, as the continuous state variable in all IPMs (see below). We also quantified above-ground seed survival from the demographic census data as $\sigma_S = 1 -$ flower damage (Appendix S1). We then used this parameter to modify vital rates describing seed production (φ_0, φ_1, φ_2, φ_3 and φ_4).

We performed two field seed-burial experiments and a greenhouse germination trial to quantify seed fates and thereby the discrete, size-independent component of IPMs (Table 1). Overall, >5100 seeds were used in the experiments (Fig. 1a; details in Appendix S1). Both field experiments were designed to ensure that seed-bank dynamics were measured at the same time-scale as the rest of the species' life cycle modelled (Paniw *et al.* 2016). We buried seeds in open (recently burned) and vegetated (long unburned) heathlands and estimated seed survival in the soil, i.e. seed-bank stasis (*staySB*), and seedling establishment, i.e. the probability of establishment in the spring following seed dispersal (*goCont*) and the probability of egression from the seed bank at least two springs after dispersal (*outSB*) (Fig. 1a). We defined the proportion of seeds entering the seed bank (*goSB*) as $1 - goCont - \omega_S$, where ω_S = seedling mortality prior to the census (Appendix S1). In greenhouse trials, we exposed seeds to heat and smoke treatments and quantified germination, which we used as a proxy for seed-bank egression after fires (*outSB* in TSF_0). For TSF_0 and TSF_1, *staySB* was estimated from an examination of *Drosophyllum* seeds in soil samples from recently burned patches (Appendix S1).

MODEL PARAMETERIZATION

We fit all vital-rate models in a Bayesian framework (as in Paniw *et al.* 2016), using normal ($\mu = 0$; $1/\theta^2 = 1 \times 10^{-6}$) or uniform uninformative priors (Appendix S1). We used Markov chain Monte Carlo (MCMC) sampling to estimate the distributions of 206 model parameters quantifying vital rates. The MCMC

Table 1. Parameterization of the models used to describe vital rates of *Drosophyllum lusitanicum*. The models shown described the data best among several candidate models. Parameter superscripts indicate parameter names in the R scripts (Appendix S2). TSF, time-since-fire; LS, livestock pressure; PFS, post-fire habitat state. The parameters modelled were: α_0 – intercept; α_j, $\alpha_k\alpha_p$ – mean response at each TSF level j, LS level k, or PFS level p compared with α_0; – TSF × LS interaction; β_c – slope for size; β_{jc}, β_{kc} – TSF × size and LS × size interaction, respectively; α_s, α_b – random effect on α_0 for each site s or block b. Distributions B, $\aleph$, and NB – Bernoulli, normal and negative binomial distribution, respectively. ΔDIC indicates the difference in values between the chosen model and the second-best model with fewer parameters, indicated by superscript letters a–j (Appendix S1)

Vital rate	Parameters	Link function	Likelihood distribution	ΔDIC
Survival (σ)	$\mu^{surv} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ (\beta_c + \beta_{jc}[TSF] + \beta_{kc}[LS]) \times size + \alpha_s[site]$	logit(σ)	$\sigma \sim B(\mu^{surv})$	-82.0^f
Growth (γ)	$\mu^{gr} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ (\beta_c + \beta_{jc}[TSF] + \beta_{kc}[LS]) \times size + \alpha_s[site]$	Identity	$\gamma \sim \aleph(\mu^{gr}, \tau^{gr})$	-25.0^f
	$\log(\tau^{gr}) = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$			-112.0^j
Probability of flowering (φ_0)	$\mu^{fl} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ (\beta_c + \beta_{jc}[TSF] + \beta_{kc}[LS]) \times size + \alpha_s[site]$	logit(φ_0)	$\varphi_0 \sim B(\mu^{fl})$	-90.0^f
Number of flowering stalks (φ_1)	$\mu^{fs} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ (\beta_c + \beta_{jc}[TSF] + \beta_{kc}[LS]) \times size + \alpha_S[site]$	log(φ_1)	$\varphi_1 \sim NB(\rho^{fs}, \mu^{fs})$	-5.0^f
Number of flowers per stalk (φ_2)	$\mu^{fps} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ \beta_c \times size + \alpha_s[site]$	log(φ_2)	$\varphi_2 \sim NB(\rho^{fps}, \mu^{fps})$	-7.0^c
Seedling size (φ_4)	$\mu^{sds} = \alpha_0 + \alpha_j[TSF] + \alpha_k[LS] + \alpha_{jk}[TSF \times LS]$ $+ \alpha_s[site]$	Identity	$\varphi_4 \sim \aleph(\mu^{sds}, \tau^{sds})$	-5.0^d
	$\log(\tau^{sds}) = \alpha_0 + \alpha_j[TSF]$			-48.0^h
Immediate germination (*goCont*)	$\mu^{goCont} = \alpha_0 + \alpha_p[PFS] + \alpha_b[block]$	logit(*goCont*)	$goCont \sim B(\mu^{goCont})$	-38.2^a
Stasis is seed bank (*staySB*)	$\mu^{staySB} = \alpha_0 + \alpha_p[PFS] + \alpha_b[block]$	logit(*staySB*)	$staySB \sim B(\mu^{staySB})$	-6.8^a
Egression from seed bank (*outSB*)	$\mu^{outSB} = \alpha_0 + \alpha_p[PFS] + \alpha_b[block]$	logit(*outSB*)	$utSB \sim B(\mu^{outSB})$	-206.0^a

sampling was run for 2 100 000 steps using three chains, and the parameter distributions were obtained from the last 100 000 MCMC samples, subsampling every 500th value (see `vitalRateModels.R` in Appendix S2). Convergence after the burn-in of 2 000 000 steps was assessed visually and with posterior predictive checks.

We modelled the above-ground vital rates as functions of the continuous predictor *size* using generalized linear mixed models. We accounted for environmental variability in all the models by including TSF and LS as fixed effects, and used *site* as a random effect (Table 1). Using DIC criteria, we chose the most plausible model for each vital rate (Table 1; see Appendix S1 for all candidate models), testing interactions between size, TSF and LS. We also described the variance (τ) of the predicted distributions of mean growth (γ) and seedling size (φ_4) as functions of TSF and LS, which provided a better model fit than assuming homoscedasticity of variance (Table 1). The number of seeds per flower (φ_3) did not differ significantly between populations, and we treated it as a constant = 9·8 in all models.

Vital rates describing immediate germination (*goCont*) or seed-bank dynamics (*staySB*, *outSB*) were defined as binomial functions, i.e. proportions of total seed number in open and vegetated experimental patches using *block* as random effect (Table 1). We then associated predictions obtained for the seed-bank models with TSF categories in each LS state, assuming that estimates from open and vegetated patches represented seed-bank dynamics under HLS and LLS, respectively (Table S1.2).

IPM CONSTRUCTION

In order to associate environmental states with vital rates in stochastic simulations (see below), we built IPMs from the 600 posterior estimates of vital rates for each combination of the five TSF, two LS, and eight site-effect estimates (see `makeIPM.R` in Appendix S2). The IPMs consisted of two coupled equations integrated over $L = 0$ and $U = 9.6$ sizes x at t to give a vector of sizes y at $t + 1$. The lower and upper integration limits corresponded to the minimum observed size and $1.1 \times$ maximum observed size, respectively. The first of the two equations describes seed-bank dynamics (S) at $t + 1$ through the contribution of seeds produced by above-ground individuals (*goSB*) and seeds remaining in the seed bank (*staySB*) at t:

$$S(t+1) = S(t)staySB + \int_L^U \varphi_0(x)\varphi_1(x)\varphi_2(x)\varphi_3\sigma_{SgoSBn}(x,t)dx$$

eqn 1

The second equation describes the dynamics of above-ground individuals through establishment of seedlings from the seed bank, survival of established individuals, and contributions of seedlings by reproductive individuals at t:

$$n(y,t+1) = S(t)outSB\varphi_3(y) + \int_L^U [\sigma(x)\gamma(y,x)$$
$$+ \int_L^U \varphi_0(x)\varphi_1(x)\varphi_2(x)\varphi_3\sigma_{SgoCont}\varphi_4(y)]n(x,t)dx$$

eqn 2

IPMs for TSF_0 (burning) consisted of stasis in and germination from the seed bank, with 0 transition probabilities elsewhere, reflecting the death of above-ground individuals by fire.

STOCHASTIC SIMULATIONS

We investigated the effects of disturbance interactions on viability and selection pressures of *Drosophyllum* by simulating population dynamics from the IPMs. Environmental variability in the simulations consisted of stochastic transitions between TSF and LS states. We simulated stochastic TSF transitions as a Markov chain process with states corresponding to TSF categories: 0, 1, 2, 3 and >3 years after fire, and transitions corresponding to probability of fire (ρ) = 1/fire return interval (Fig. 2). We used 10 fire return intervals, from 10 to 100 years at 10-year increments (Fig. 2), which characterize the fire-frequency range in the study region (Ojeda 2009).

Stochastic transitions between HLS and LLS were based on different scenarios of heathland conservation. First, we explored the differences in the effect of fire regimes on dynamics of populations where HLS is maintained (no conservation) compared with dynamics in populations under low livestock pressure (LLS —optimum conservation). We therefore modelled populations fixed in their respective LS state. Here, fires could occur in each LS state independently, and stochastic simulations varied for TSF transitions only (Fig. 2a; `sLambdafixedLS.R` in Appendix S2).

Second, we explored the effects on population dynamics when livestock pressure, in addition to fire, varied in a given population, representing variable conservation efforts (Paniw, Salguero-Gómez & Ojeda 2015). We therefore considered transitions between LS states and integrated TSF and LS into one Markov chain with states determined by each combination of TSF and LS (Fig. 2; `sLambdaStochLS.R` in Appendix S2). LS transitions were defined by three probabilities (c_1) of a population experiencing HLS at t and remaining in HLS at $t + 1$, depicting low to high conservation of natural heathlands: 0·99 (high Pr (HLS)), 0·5 (moderate Pr(HLS)) or 0·2 (low Pr(HLS)) (Fig. 2b). Accordingly, populations transitioned from HLS to LLS with probabilities = 1−Pr(HLS). In turn, populations experiencing LLS at t could face HLS at $t + 1$ with probabilities c_2: 0·5, 0·3, or 0·1 in $TSF_{>3}$. The latter probabilities were derived from estimates of rates of human disturbance (% of habitat loss in the last 20 years) in mature heathlands across the range of *Drosophyllum*: in Portugal where habitat degradation is largest (0·5), in Morocco where degradation is moderate (0·3), and in Southern Spain where the proportion of natural heathland habitats is largest (0·1) (Paniw, Salguero-Gómez & Ojeda 2015). In TSF_3, populations under LLS transitioned to HLS with probabilities arbitrarily fixed at 0·1 to mimic low herbivory pressure in natural habitats.

For each scenario of heathland conservation, we ran 100 simulations, each for 4500 years (Fig. 2). We included parameter uncertainty by running the 100 simulations for each of the 600 MCMC samples of parameters (Table 1; see also Paniw *et al.* 2016). At each of the 4500 iterations during a simulation, an environmental state (combination of TSF and LS) was picked based on the state transition probabilities given by the Markov chain. That state was represented by one of eight IPMs, corresponding to each of the eight estimates of the random site effect at a given TSF × LS combination (Fig. 2). For each simulation,

600 posterior parameter samples from vital-rate models

↓

100 stochastic simulations of **fire** and **livestock** disturbances modeled as

↓

(a)

Fire stochastic:
→ States: TSF_0, TSF_1, TSF_2, TSF_3, $TSF_{>3}$

→ Transition probability ρ: 1/10, 1/20, 1/30, 1/40, 1/50, ..., 1/100

Livestock fixed:
→ States: HLS, LLS
→ Transition probability c: 0

Environmental transition matrix

Time t

Time $t+1$	0	1	2	3	>3
0	ρ	ρ	ρ	ρ	ρ
1	1−ρ	0	0	0	0
2	0	1−ρ	0	0	0
3	0	0	1−ρ	0	0
>3	0	0	0	1−ρ	1−ρ

Example simulation $t = 1$ to n:

HLS: IPM_{0s1t}, IPM_{1s1t+1}, ..., $IPM_{>3s4n}$

LLS: IPM_{0s4t}, IPM_{1s2t+1}, ..., IPM_{3s8n}

(b)

Fire and **livestock** stochastic:
→ States: 0HLS, 1HLS, 2HLS, 3HLS, >3HLS, 0LLS, 1LLS, 2LLS, 3LLS, >3LLS
→ Transition probability ρ: 1/10, 1/20, 1/30, 1/40, 1/50, ..., 1/100
→ Transition probability c_1: 0·99, 0·5, 0·2
→ Transition probability c_2: 0·5, 0·3, 0·1

Environmental transition matrix

Time t

Time $t+1$	0HLS	0LLS	1HLS	1LLS	2HLS	2LLS	3HLS	3LLS	>3HLS	>3LLS
0HLS	ρc_1	$0{\cdot}1\rho$	ρc_1	$0{\cdot}1\rho$	ρc_1	$0{\cdot}1\rho$	ρc_1	$0{\cdot}1\rho$	ρc_1	$0{\cdot}1\rho$
0LLS	$\rho(1-c_{1j})$	$0{\cdot}9\rho$	$\rho(1-c_{1j})$	$0{\cdot}9\rho$	$\rho(1-c_{1j})$	$0{\cdot}9\rho$	$\rho(1-c_{1j})$	$0{\cdot}9\rho$	$\rho(1-c_{1j})$	$0{\cdot}9\rho$
1HLS	$(1-\rho)c_1$	$0{\cdot}1(1-\rho)$	0	0	0	0	0	0	0	0
1LLS	$(1-\rho)(1-c_{1j})$	$0{\cdot}9(1-\rho)$	0	0	0	0	0	0	0	0
2HLS	0	0	$(1-\rho)c_1$	$0{\cdot}1(1-\rho)$	0	0	0	0	0	0
2LLS	0	0	$(1-\rho)(1-c_{1j})$	$0{\cdot}9(1-\rho)$	0	0	0	0	0	0
3HLS	0	0	0	0	$(1-\rho)c_1$	$0{\cdot}1\rho$	0	0	0	0
3LLS	0	0	0	0	$(1-\rho)(1-c_{1j})$	$0{\cdot}9\rho$	0	0	0	0
>3HLS	0	0	0	0	0	0	$(1-\rho)c_1$	$0{\cdot}1\rho$	$(1-\rho)c_1$	$(1-\rho)c_2$
>3LLS	0	0	0	0	0	0	$(1-\rho)(1-c_{1j})$	$0{\cdot}9\rho$	$(1-\rho)(1-c_{1j})$	$(1-\rho)(1-c_2)$

Example simulation $t = 1$ to n:

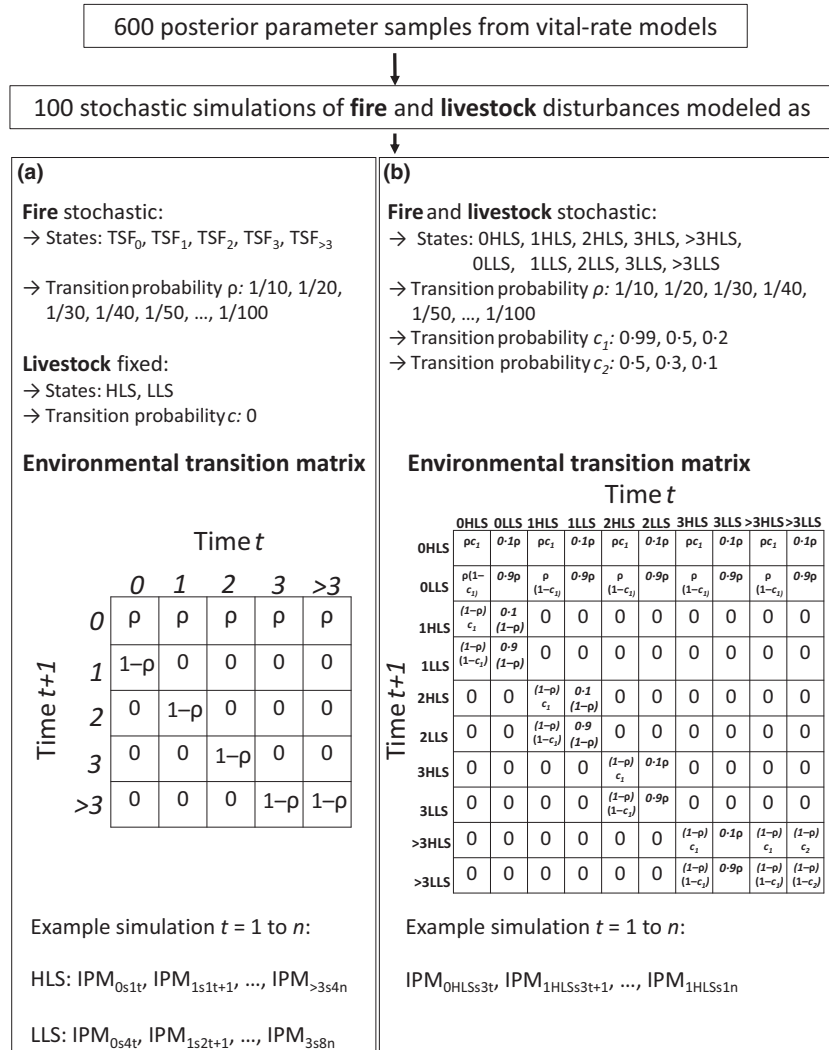$IPM_{0HLSs3t}$, $IPM_{1HLSs3t+1}$, ..., $IPM_{1HLSs1n}$

Fig. 2. Description of stochastic simulations used to model the effects of fire and livestock browsing/trampling on the population dynamics of *Drosophyllum lusitanicum*. We performed 100 simulations for each of 600 posterior parameter samples, by considering (a) only stochastic transitions, with probability ρ, in fire states but assuming fixed livestock-pressure states, and (b) stochastic transitions in fire and livestock-pressure states (with transition probabilities defined by c_1 and c_2). The resulting environmental transition matrices produced different sequences of IPMs representing a combination (identified by subscripts) of: 0, 1, 2, 3 or >3 years of time since fire (TSF); HLS (high) or LLS (low) livestock pressure; and $s(1–8)$ – random site; for each $t = 1$ to n projection.

we calculated the stochastic population growth rate, log λ_s, discarding the first 500 years (Caswell 2001, eqn 14.61). We also obtained the probability of quasi-extinction by $t = 150$ years, $P_q(150$ years), across simulations, where populations were considered extinct when the total number of individuals (including seeds in the seed bank) $N < 100$.

To infer differences in selection pressures on life-history strategies of populations exposed to different combinations of fire and livestock disturbances, we perturbed each vital rate used to compose the IPMs by its mean, μ, and standard deviation, σ, across all environmental states (Haridas & Tuljapurkar 2005; see Appendix S3 for details and *R* scripts in Appendix S2 for examples). We then used the chain rule to calculate (i) how these perturbations affected the IPM kernels, and (ii) how the latter in turn affected log λ_s. These calculations provided us with elasticities, E_a^μ and E_a^σ, of $a = $ log λ_s to changes in the mean and variance of vital rates, respectively. These two measures quantify the strength of selection pressures on life-history traits in stochastic environments (Haridas & Tuljapurkar 2005). Here, we used a subset of four fire return intervals and excluded parameter uncertainty for simplicity and computational efficiency. We calculated average (±95% nonparametric CI) E_a^μ and E_a^σ across the 100 stochastic simulations.

Results

DISTURBANCE INTERACTIONS AND POPULATION VIABILITY

Our simulations of the stochastic population growth rate, log λ_s, showed significant interactive effects between fire regimes and livestock pressure on *Drosophyllum* populations. In populations maintained under LLS but experiencing varying fire regimes, mean log λ_s (across simulations and parameters) decreased and mean probability of quasi-extinction $P_q(150$ years) increased monotonically as the fire return interval *shortened* (Fig. 3a,b). However, populations maintained under high browsing (HLS) showed the opposite trend with mean log λ_s increasing and mean $P_q(150$ years) decreasing monotonically with *extended* fire return interval (Fig. 3a,b). In populations maintained under HLS, lowest $P_q(150$ years) $\approx 0{\cdot}5$, remaining high even at a fire return interval of 100 years. When livestock pressure, in addition to fire, was assumed to vary through time in a given population, log λ_s and $P_q(150$ years) patterns in populations under high and low/moderate Pr(HLS) were very similar to ones in
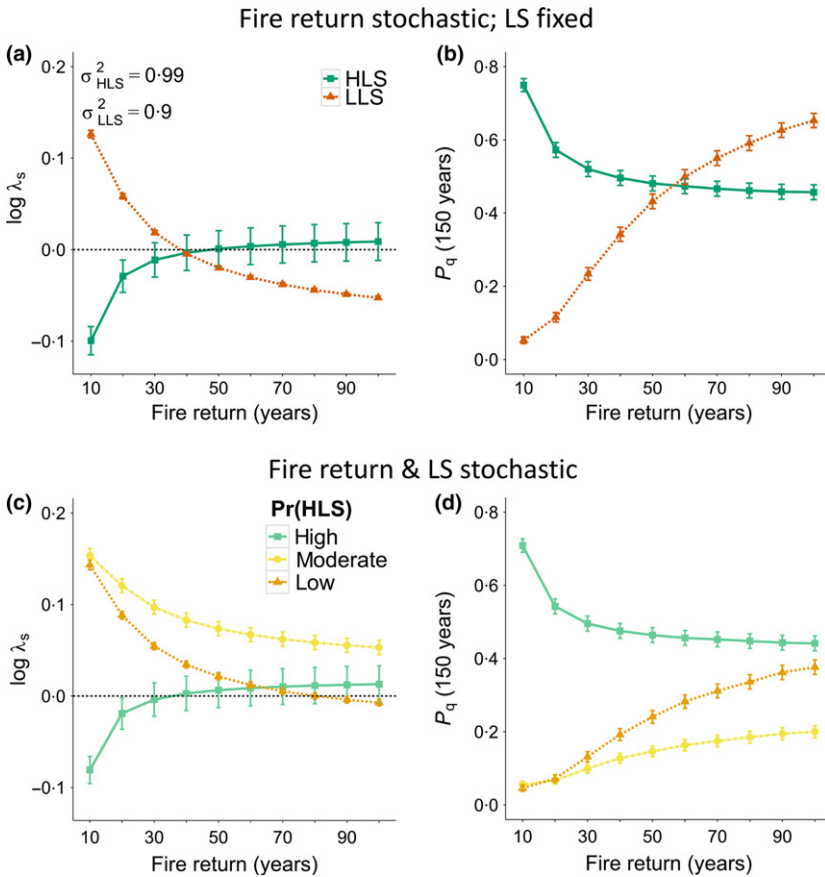
Fig. 3. Stochastic population growth rate, log λ_s (a, c) and probability of quasi-extinction after 150 years, $P_q(150$ years) (b, d), across stochastic simulations of interactions of 10 fire return intervals and livestock (LS) pressure, high (HLS) or low (LLS). For each fire return interval, LS states were either fixed (a, b) or fluctuated stochastically (c, d). In the latter, probabilities to change LS states were determined by high, intermediate and low probability of HLS in time t. Values at each fire return × LS combination depict mean of 60 000 log λ_s from 600 samples of the posterior parameter distributions and 100 stochastic simulations of log λ_s obtained for each parameter value. Error bars depict variance attributed to parameter uncertainty. σ^2 = proportion of log λ_s variance explained by parameter uncertainty for simulations using HLS and LLS. Bars of log λ_s crossing horizontal dotted line correspond to constant population sizes through time. [Colour figure can be viewed at wileyonlinelibrary.com]

populations maintained under HLS and LLS, respectively (Fig. 3c,d). However, populations under moderate browsing, or moderate Pr(HLS), had highest log λ_s across all fire return intervals, ranging from 0·15 (10-year return interval) to 0·05 (100-year interval) – much higher compared with populations maintained under LLS, ranging from 0·13 (10-year interval) to −0·05 (100-year interval) (Fig. 3a,c). Consequently, $P_q(150$ years) were lowest (<0·10) under moderate browsing at a fire return interval of 10 years.

A great deal of variation, largely due to vital-rate parameter uncertainty, was associated with log λ_s estimates (Fig. 3a,c; Fig. S3.1a,c in Appendix S3). High parameter uncertainty resulted in the 95% CI of log λ_s estimates always including 0 values, implying little certainty in effect of both disturbances on long-term stochastic dynamics (Fig. S3.1a,c in Appendix S3). However, parameter uncertainty did not change the general trend in the response of log λ_s and $P_q(150$ years) to varying fire and livestock disturbances.

SELECTION OF LIFE-HISTORY STRATEGIES UNDER DIFFERENT DISTURBANCE REGIMES

Selection pressures, quantified by elasticities E_a^μ and E_a^σ, differed starkly in populations maintained under HLS compared to ones exposed to LLS and largely disturbed by fire. Whereas under LLS, mean increases in seed-bank stasis (*staySB*) and egression (*outSB*) were critical in

increasing log λ_s, vital rates describing survival (σ), growth (γ), flowering (φ_0) and immediate germination (*goCont*) were under much stronger selection relative to other vital rates under HLS (Fig. 4). The importance of σ, γ, φ_0 as well as *goCont* and *outSB* increased with extending fire return interval in populations maintained under HLS (Fig. 4a). The same occurred for *staySB* and *outSB* in populations under LLS.

Our simulations showed that vital-rate variation was largely selected for and against in populations under HLS and LLS, respectively. In HLS populations, increases in the standard deviation of above-ground vital rates were favoured across fire return intervals, although E_a^σ were small compared to LLS populations (Fig. 4b). In LLS populations, variability in above-ground vital rates (Table 1) as well as *staySB* and *outSB* would potentially threaten populations, while variability in the remaining vital rates had negligible effects log λ_s (Fig. 4b; Appendix S3).

E_a^μ and E_a^σ for vital rates in populations exposed to varying livestock pressures under high probability of HLS were similar to the ones maintained under HLS while those with low probability of HLS were similar to ones maintained under LLS. When probabilities of changing from LS states were intermediate, increases in above-ground vital rates and seed-bank stasis resulted in high E_a^μ and E_a^σ with increasing fire return interval (Fig. S3.3).
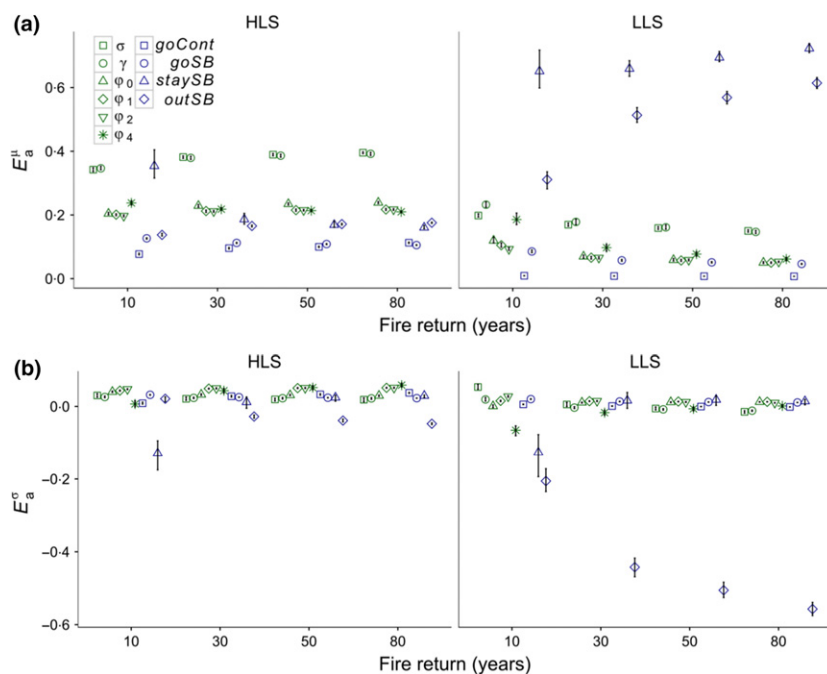
Fig. 4. Elasticities of log λ_s to changes in (a) the average (E_a^μ) and (b) standard deviation (E_a^σ) of 10 vital rates obtained from stochastic simulations of four fire return intervals using vital rates from populations exposed to high (HLS) and low (LLS) livestock pressure. See Appendix S3 for details on calculations. Vital rates represent above-ground processes [survival (σ), growth (γ, φ_4) and reproduction (φ_0, φ_1, φ_2)] and seed fates [immediate germination (*goCont*) and seed-bank ingression (*goSB*), stasis (*staySB*) and egression (*outSB*)]. Error bars show a 95% nonparametric CI calculated from 100 simulations at each fire return. [Colour figure can be viewed at wileyonlinelibrary.com]

Discussion

In Mediterranean and other fire-prone ecosystems, which occupy ~40% of terrestrial habitats world-wide (Bond, Woodward & Midgley 2005), human disturbances have been increasingly replacing or interacting with natural fire disturbances in the last century (Turner 2010; Duwyn & MacDougall 2015; Tye *et al.* 2016). Our study suggests a more effective conservation management of fire-adapted seeder species by combining different disturbance regimes, rather than substituting human disturbances for fire (Fuhlendorf *et al.* 2009; Fernandes *et al.* 2013). Fire management aimed at chronic removal of potential fuel to decrease the probability of burning (Valdecantos, Baeza & Vallejo 2008) may compromise the viability of species and may therefore decrease local biodiversity. This is in part because chronic small-scale disturbances may select against life-history adaptations to severe disturbance events and compromise populations when such disturbances inevitably occur.

Due to the high parameter uncertainty associated with vital-rate estimates in our analyses, which has been demonstrated in stochastic population models for other fire-adapted species (Evans, Holsinger & Menges 2010; Elderd & Miller 2016), we cannot reliably predict the exact long-term fates of our studied populations. However, by comparing potential selection pressures and population dynamics under different combinations of disturbance regimes, we highlight emerging issues for the management of species increasingly exposed to human pressures (Bonebrake *et al.* 2014) and provide tools to address such issues.

HUMAN–FIRE INTERACTIONS ARE AN OPPORTUNITY AND A THREAT TO CONSERVATION

Many species with flexible strategies to buffer environmental variability may have the potential to adapt to human disturbances (Hendry, Farrugia & Kinnison 2008). Some species even show higher growth rates in human-disturbed habitats compared to naturally disturbed ones (e.g., Tye *et al.* 2016; Vieira-Neto, Vasconcelos & Bruna 2016). Our simulations showed that growth rates were consistently higher and risk of extinction lower in *Drosophyllum* populations under varying livestock pressures compared with ones maintained under low pressures. The positive effects of browsing may be explained by the fact that for a large number of species, including *Drosophyllum*, moderate levels of livestock browsing and trampling may be typical of prehistoric conditions where ungulates were abundant and created open space for periodic recruitment in between large-scale disturbance events (Pykälä 2000; Velle *et al.* 2014). Such periodic recruitment and subsequent seed input into the seed bank has been shown to ensure population viability under a wide range of natural disturbance regimes for threatened (Pardini, Vickstrom & Knight 2015) and invasive (Renne & Tracy 2007) species alike. In the southwestern Mediterranean Basin, where fire suppression remains a management goal (Andrés & Ojeda 2002; Valdecantos, Baeza & Vallejo 2008), our results can be used to design novel management strategies that combine recurrent fires with browsing to conserve heathland biodiversity (Baeza *et al.* 2007; Fernandes *et al.* 2013).

Despite human activities potentially playing a positive role in the conservation of fire-adapted species, our simulations suggest that fire suppression policies, enforced by substituting human disturbances for fires, may compromise population viability. For *Drosophyllum*, populations maintained under high browsing pressure showed consistently high P_q(150 years) $\approx 0{\cdot}5$, even when fire return intervals are extended (Fig. 3). When also burned frequently, as is likely to occur despite fire suppression

(Syphard *et al.* 2009), such populations are not viable (Fig. 3). Frequent disturbance interactions have been shown to reduce population viability of a number of species (e.g., Lawson *et al.* 2010; Darabant *et al.* 2016). In this sense, the apparent persistence of *Drosophyllum* populations in human-disturbed habitats may constitute an extinction debt by which true extinction inevitably follows a time-lag inversely proportional to rates of population turnover – in our case slowed by the seed bank (Tilman *et al.* 1994; González-Varo *et al.* 2015).

UNDERSTANDING SELECTION PRESSURES UNDER DIFFERENT DISTURBANCES TO IMPROVE MANAGEMENT

In this study, we aimed to understand the demographic processes that may lead to population collapse under frequent human and fire disturbances. Elasticity analyses showed that human disturbance (HLS) favoured survival and growth of established *Drosophyllum* individuals and yearly germination over seed-bank stasis, which was selected for in fire-disturbed populations under LLS. As immediate germination vs. ingression into the seed bank constitutes a direct trade-off (Cohen 1966), a depleted soil seed bank may be expected in human-disturbed populations. In such populations, higher fitness (and viability) may be achieved through increases in survival of reproductive individuals, which may confer more tolerance to year-to-year environmental variation and high seedling mortality caused by the nature of human disturbances (Morris *et al.* 2008). The fact that elasticities of log λ_s to increases in vital-rate variability are almost negligible for critical above-ground vital rates (Fig. 4b) may indicate that increased longevity in human-disturbed populations is buffering against variability in vital rates (Morris *et al.* 2008). At the same time, high levels of browsing/trampling may increase damage to reproductive structures and mortality of plants, either directly or indirectly via exposure to adverse microhabitat conditions (e.g. solar radiation or wind; Smit *et al.* 2007). Therefore, when human disturbances occur frequently or co-occur with fires, the increased environmental variability leads to higher mortality of above-ground individuals, which cannot be compensated by germination from a diminished seed bank. This phenomenon may explain the frequent population collapse in human-disturbed habitats of *Drosophyllum* (Garrido *et al.* 2003) as well as other fire-dependent species (Quintana-Ascencio, Weekley & Menges 2007), and highlight the need for management that avoids frequent disturbance interactions (Vilà & Terradas 1995).

It is alarming then that a large number of fire-adapted species, including most populations of *Drosophyllum*, are found in human-disturbed habitats (González-Varo *et al.* 2015; Paniw, Salguero-Gómez & Ojeda 2015; Tye *et al.* 2016). Our results indicate that conservation efforts in human-disturbed habitats may need a different approach from ones in natural habitats, where moderate browsing may benefit populations. For *Drosophyllum* and other fire-adapted seed species (e.g., Quintana-Ascencio, Weekley & Menges 2007), protection of large above-ground individuals may be prioritized in heavily human-disturbed populations, while a seed bank may have to be re-established in such populations before fire management can be introduced. We argue that considering selection pressures exerted by different disturbance types is crucial for a successful management of populations. At the same time, a full analysis of life-history evolution and its application to management – beyond the scope of this study – would likely need to consider vital-rate trade-offs. In human-disturbed populations of *Drosophyllum*, where several above-ground vital rates are under strong selection (Fig. 4), such trade-offs and plant physiology will likely constrain potential adaptations and population dynamics in the absence of fires (Benton, Plaistow & Coulson 2006).

Our analyses emphasize the need for detailed analyses of various environmental drivers as human activities increasingly affect natural ecosystems (Turner 2010). We encourage ecologists and provide tools to explore interactions of environmental drivers while assessing uncertainty in analyses, which allows for more robust interpretations of patterns.

Authors' contributions

Acknowledgements

Data accessibility

Study design and model parameterization: uploaded as online supporting information.

R scripts and Demographic census data of *Drosophyllum lusitanicum* and posterior samples of vital-rate parameters. Dryad Digital Repository https://doi.org/10.5061/dryad.40qt2 (Paniw *et al.* 2017).

Additional modelling results: uploaded as online supporting information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Study design and vital-rate model parameterization.

Appendix S2. Overview of R code.

Appendix S3. Overview of elasticity calculations and additional modelling results.