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 $\lambda_s$)

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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 & Viets 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 (Palkova 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 – Incendios 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 λs) and the probability of quasi-extinction (Ps(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.

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 \([\sigma]\) or seed bank \([\text{staySB, outSB}]\)/ growth \([\gamma]\) or seedling size \(\phi_4\) and fecundity \([\text{flowering probability } \phi_0, \# \text{ stalks } \phi_1, \# \text{ flowers/stalk } \phi_2, \# \text{ seeds/flower } \phi_3, \text{ immediate germination } \text{goCont}, \text{ and seed-bank ingestion } \text{goSB} \text{ or egression } \text{outSB}], \text{ respectively; } \sigma_S = \text{above-ground seed survival.} \) (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 (φ₀), number of flowering stalks (φ₁), number of flowers per stalk (φ₂), number of seeds per flower (φ₃) and seedling size distribution the next year (φ₄) (Fig. 1a). We used plant size = log(# of leaves × length of longest leaf) (cm), after model selection for σ, γ, φ₀ and φ₁, as the continuous state variable in all IPMs (see below). We also quantified above-ground seed survival from the demographic habitat data as σₛ = 1−flower damage (Appendix S1). We then used this parameter to modify vital rates describing seed production (φ₀, φ₁, φ₂, φ₃) and φ₄).

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: φ₀ – intercept; φ₁, φ₂, φ₃ – mean response at each TSF level j, LS level k, or PFS level p compared with φ₀; TSF × LS interaction; φ₁ – slope for size; LS × TSF × size and LS × size interaction, respectively; φ₂, φ₃ – random effect on φ₀ for each site s or block b. Distributions B, N, and NB – Bernoulli, normal and negative binomial distribution, respectively. ADIC 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).

We performed two field seed-burial experiments and a greenhouse germination trial to quantify seed rates 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−goSB, where φ₀ = 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 TSF₀). For TSF₀ and TSF₁, 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 (µ = 0; 1/σ² = 1 × 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
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 size 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 (\(\tau\)) of the predicted distributions of mean growth (\(\gamma\)) and seedling size (\(\phi_k\)) 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 (\(\phi_f\)) 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 x 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 \(t\):

\[
S(t + 1) = S(t)\text{staySB} + \int_{L}^{U} \phi_0(x)\phi_f(x)\phi_2(x)\phi_5\sigma_{goSB}(x,t)dx
\]

\[
eqn 1
\]

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 \(t\):

\[
n(y,t+1) = S(t)\text{outSB}\phi_0(y) + \int_{L}^{U} \sigma(x)y(y,x)
\]

\[
+ \int_{L}^{U} \phi_0(x)\phi_1(x)\phi_2(x)\phi_5\sigma_{goCont}(y)\pi(x,t)dx
\]

\[
eqn 2
\]

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 \(\geq\)3 years after fire, and transitions corresponding to probability of fire (\(p\)) = 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; `s.LambdafixedLS.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; `s.LambdafixedStochLS.R` in Appendix S2). LS transitions were defined by three probabilities \(c_i\) 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\(_2\). 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 I; 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 x LS combination (Fig. 2). For each simulation,
we calculated the stochastic population growth rate, \( \log \lambda_s \), discounting the first 500 years (Caswell 2001, eqn 14.61). We also obtained the probability of quasi-extinction by \( t = 150 \) years, \( P_q(150) \), 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, \( \mu \), and standard deviation, \( \sigma \), 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 \( \lambda_s \). These calculations provided us with elasticities, \( E^s_\mu \) and \( E^s_\sigma \), of \( \alpha = \log \lambda_s \) 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) \( E^s_\mu \) and \( E^s_\sigma \) across the 100 stochastic simulations.

**Results**

**DISTURBANCE INTERACTIONS AND POPULATION VIABILITY**

Our simulations of the stochastic population growth rate, \( \log \lambda_s \), showed significant interactive effects between fire regimes and livestock pressure on *Drosophyllum* populations. In populations maintained under LLS but experiencing varying fire regimes, mean \( \log \lambda_s \) (across simulations and parameters) decreased and mean probability of quasi-extinction \( P_q(150) \) increased monotonically as the fire return interval shortened (Fig. 3a,b). However, populations maintained under high browsing (HLS) showed the opposite trend with mean \( \log \lambda_s \) increasing and mean \( P_q(150) \) decreasing monotonically with extended fire return interval (Fig. 3a,b). In populations maintained under HLS, lowest \( P_q(150) \approx 0.5 \), 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 \( \lambda_s \) and \( P_q(150) \) patterns in populations under high and low/moderate Pr(HLS) were very similar to ones in...
populations maintained under HLS and LLS, respectively (Fig. 3c,d). However, populations under moderate browsing, or moderate Pr(HLS), had highest log $\lambda_s$ across all fire return intervals, ranging from $0/C1_{15}$ (10-year return interval) to $0/C1_{05}$ (100-year interval) – much higher compared with populations maintained under LLS, ranging from $0/C1_{13}$ (10-year interval) to $0/C0_{0}$ (100-year interval) (Fig. 3a,c). Consequently, $P_q(150\text{ years})$ were lowest ($<0/C1_{10}$) 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 $\lambda_s$ estimates (Fig. 3a,c; Fig. S3.1a,c in Appendix S3). High parameter uncertainty resulted in the 95% CI of log $\lambda_s$ 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 $\lambda_s$ and $P_q(150\text{ years})$ to varying fire and livestock disturbances.

**SELECTION OF LIFE-HISTORY STRATEGIES UNDER DIFFERENT DISTURBANCE REGIMES**

Selection pressures, quantified by elasticities $E_{sl}$ and $E_{sr}$, 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 ($\text{staySB}$) and egression ($\text{outSB}$) were critical in increasing log $\lambda_s$, vital rates describing survival ($\sigma$), growth ($\gamma$), flowering ($\varphi_0$) and immediate germination ($\text{goCont}$) were under much stronger selection relative to other vital rates under HLS (Fig. 4). The importance of $\sigma$, $\gamma$, $\varphi_0$ as well as $\text{goCont}$ and $\text{outSB}$ increased with extending fire return interval in populations maintained under HLS (Fig. 4a). The same occurred for $\text{staySB}$ and $\text{outSB}$ 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 above-ground vital rates were favoured across fire return intervals, although $E_{sr}$ were small compared to LLS populations (Fig. 4b). In HLS populations, variability in above-ground vital rates (Table 1) as well as $\text{staySB}$ and $\text{outSB}$ increased with extending fire return interval in populations maintained under HLS (Fig. 4a). The same occurred for $\text{staySB}$ and $\text{outSB}$ 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 $E_{sr}$ were small compared to LLS populations (Fig. 4b). In HLS populations, variability in above-ground vital rates (Table 1) as well as $\text{staySB}$ and $\text{outSB}$ would potentially threaten populations, while variability in the remaining vital rates had negligible effects log $\lambda_s$ (Fig. 4b; Appendix S3).

$E_{sl}$ and $E_{sr}$ 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 $E_{sl}$ and $E_{sr}$ with increasing fire return interval (Fig. S3.3).
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 (Pykäälä 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 $P_e(150$ years) $\approx 0.5$, 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. ingestion 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 $\lambda_0$ 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

M.P., F.O., and R.S.G. conceived the ideas and designed methodology; M.P. and F.O. collected the data; M.P., P.Q.A., and R.S.G. analysed the data; M.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility


Additional modelling results: uploaded as online supporting information.

References


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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.