

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Using wildfires as a natural experiment to evaluate the effect of fire on southern California vernal pool plant communities



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ARTICLE INFO

Article history: Received 9 March 2016 Received in revised form 24 May 2016 Accepted 24 May 2016 Available online 14 June 2016

Keywords: Vernal pools Fire, natural experiment Global change Invasive species Messy data

ABSTRACT

Fires in Mediterranean-type ecosystems (MTEs) have been studied widely with emphasis on shrub and grassland vegetation types. Although vernal pools comprise a very small fraction of MTEs, they are important to regional biodiversity due to high local endemism. Fire frequency has been increasing in MTEs and while altered fire regimes have been shown to threaten native shrub communities, their effect on vernal pools is uncertain. Due to the number of at-risk species in this habitat, experiments with potentially harmful effects are problematic. Therefore, we initiated this study to take advantage of two anthropogenic but unplanned fire events. The analysis uses data collected from 2001 to 2009 on a site burned in 2000 and 2003. We analyzed the data in an exploratory framework and applied unadjusted and adjusted models using different parameterizations of the exposure variables. The results did not provide evidence that fire reduced the abundance of native vernal pool species in southern California. There is provisional evidence of a positive but temporary effect of fire on native vernal pool species. Our analysis demonstrates an exploratory analytical approach for use with problematic data sets that can arise when conservation objectives constrain opportunities for experimental studies.

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1. Introduction

Vernal pools, though comprising a very small fraction of the landscape, have a disproportionately high interest for research and conservation due to the specialized adaptations of their flora and fauna and consequent high local endemism (Zedler, 1987). While vernal pools exist within the larger fire-prone Mediterranean-type ecosystem (MTE), fire is not considered to have been important in the evolution of vernal pool species or maintenance of species assemblages. Native pool species offer little biomass to carry fire (Cox and Austin, 1990), however invasive species have increased flammable biomass in vernal pools (Marty, 2005; Davies and Nafus, 2013). While the widespread occurrence of fires in MTEs has led to abundant literature on the effects of burning on the dominant ecological communities (e.g. Keeley et al., 2012), there have been few studies of the effects of fire on vernal pool biota.

Abbreviations: MCAS, Marine Corps Air Station; RC, relative cover; RF, relative frequency.

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http://dx.doi.org/10.1016/j.gecco.2016.05.005

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Vernal pools are seasonal ponds whose resident species tolerate hydrologic extremes, from inundation in winter to desiccation in summer. In addition, they experience high year-to-year variability in hydrological factors and encompass a strong moisture gradient from dry pool edges to wet centers. As a result, life history strategies include a summer dormant period with underground storage structures and/or resting structures such as cysts or seeds that can persist for decades (Zedler, 1990; Wells et al., 1997; Dallman, 1998). Vernal pool plant communities contain species restricted to pools (obligates) and species that occur both in pools and adjacent uplands. They are largely comprised of annual plants with few perennial species (Holland and Jain, 1984).

Species invasions resulting in altered fire-fuel characteristics (Marty, 2005; Davies and Nafus, 2013) and increased frequency of fire in MTEs (Syphard et al., 2007) mean that fire may now threaten native vernal pool species, making understanding fire effects important for conservation management. While extreme hydrological conditions confer resistance to invasion by upland species (Collinge et al., 2011), these conditions vary within pools, among pools, and over time. This variation results in conditions that periodically provide suitable habitat for exotic upland annual grasses (Gerhardt and Collinge, 2007), increasing the continuity and quantity of fire-fuel loads (Brooks and Berry, 2006).

While invasion by exotic annual grasses may provide fuels that bring fire to habitats where it was previously rare (Brooks and Berry, 2006), fire characteristics are not necessarily the same due to fuels differences (Davies and Nafus, 2013). Even with annual grass invasion, vernal pools typically have lower and more variable fuel loads than surrounding grasslands due to strong abiotic and biotic gradients (Zedler, 1987; Bliss and Zedler, 1998). Fires can burn around pools or skip portions where the duration of inundation results in lower fuel loads, and fires can occur early in summer when upland vegetation has dried but pool vegetation retains enough moisture to resist burning (Cox and Austin, 1990). Cox and Austin (1990) reported 80% of pool edges but only 20% of pool centers burned in an experimental study of fire in vernal pools. In addition, they found lower fire intensity within the pools than in surrounding uplands. Still, the build-up of thatch from exotic upland annual grasses (Marty, 2005) can increase fuel continuity and quantity (Davies and Nafus, 2013), potentially resulting in hotter, more complete burns in vernal pools with high populations of these grasses. The greater fuel quantity and continuity provided by invasive grasses thus is a threat to plant species in vernal pools.

Fire effects on plant populations are highly variable, depending both on species characteristics (e.g. seed longevity, timing of seed dispersal and location of perennating buds), and fire characteristics (e.g. seasonal timing, intensity and duration) (Keeley et al., 2012). Because fire temperatures drop rapidly at and below the soil surface (Daubenmire, 1968; Busse et al., 2010), species with long-lived seedbanks and belowground perennating buds are buffered from fire effects. Fire may adversely affect species that hold seed in the canopy after senescence by killing the current seed crop (Cox and Austin, 1990), but long-lived soil seed banks may provide sufficient seed to maintain populations. Conversely, species with short-lived seed such as exotic annual grasses (Russi et al., 1992) are often temporarily reduced by fire, which can consume the current year's seed crop (D'Antonio et al., 2002).

We therefore expect that fire would have a larger adverse effect on exotic annual grasses in vernal pools than native species. The effect size should depend on the timing of fire with respect to seed dispersal, with larger effects from predispersal fires (Parsons and Stohlgren, 1989; DiTomaso et al., 2006). The effect should be short-lived, on the order of 1–2 years depending on the time required for seedbank replenishment (Meyer and Schiffman, 1999; D'Antonio et al., 2002; Klinger et al., 2006).

While a previous experimental study concluded that fire did not adversely affect native vernal pool species and appeared to have a positive effect by mitigating effects of drought (Cox and Austin, 1990), the study did not determine the length of effects and lacked data on ponding, casting doubt on whether these differences represent fire effects. The effects of fire on invasive species are unclear. Cox and Austin (1990) found lower invasive species cover in burned pools compared to unburned pools, while Gerhardt and Collinge (2003) found no difference in cover and an increase in invasive species richness. We used vegetation transect data in conjunction with partial data on basin ponding over nine years to evaluate fire effects that could be inferred when the effects of hydrology were factored out. Our data set over nine years allowed us to evaluate fires followed by both wet and dry periods and to evaluate the duration of effects.

Here, we examine whether fire adversely affects obligate native vernal pool species. We also evaluate the impacts of fire on two sets of functional groups based on life form (grasses and forbs) and origin (native and exotic species), and compare the relative effect of fire on pool species and upland species that occur in pool basins.

2. Methods

2.1. Study site

Marine Corps Air Station (MCAS) Miramar is approximately 4 miles inland from the coast within the San Diego metropolitan region $(32^{\circ}50'41''N, -117^{\circ}7'19''W)$. The soils on the site are classified as Redding gravelly loam, 2%–9% slopes (USDA SCS, 1973). Native annual species dominate the pool flora, with pool specialists accounting for 42% of native annuals. Non-native grassland with occasional native perennial grasses (*Stipa* spp.) and shrubs characterize the vegetation surrounding the vernal pools. The topography consists of mima mounds interspersed with vernal pools and elongated swales. Average annual precipitation is 25.2 cm, ranging from 7.6 to 66 cm over the period of record (Western Regional Climate Center, WRCC, 2012).

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