Biological Conservation 168 (2013) 90–98

Contents lists available at ScienceDirect

Biological Conservation

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

Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime

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ARTICLE INFO

Article history:
Received 23 August 2013
Accepted 12 September 2013

Keywords:
Disturbance
Fire
Functional response
Mediterranean
Reptiles
Repeated-fire regimes

ABSTRACT

Wildfires are common disturbances that have a major impact on ecosystems. Recent decades have seen an increase in fire frequency and extension due to the combined effects of climate change and land-use history. We studied the taxonomic and functional response of a reptile assemblage to repeated fires in southern France to understand shifts in dominant species and diversity, as well as the mechanisms that underlie responses according to functional traits of species. In the spring of 2010, we sampled reptiles in areas with three types of fire regime: unburned, burned once (2003) and burned 4–5 times (last fire in 2003) along a fire history of 51-years period. With this field sampling design, we examined the intermediate disturbance hypothesis and the habitat accommodation model of succession as methods to predict reptile responses to natural fire regimes. We also compared habitat structure at the study area between 1944 and 2006 to certify that repeated-fire regimes have modified the habitat for reptiles. The comparison of the habitat structure between both periods demonstrated that repeated-fire regimes modified the landscape from a homogeneous sparse forest to a contrasted heterogeneous mixture of scrubland and dense forest. We found a loss of reptile diversity after one and multiple fires, a result that contradicts the intermediate disturbance hypothesis. Reptile composition differed among the three fire regimes: there was a shift in dominant species and a reduction of beta diversity related to an increase in the number of fires. We also observed a functional response to repeated fires, with an increased frequency of insectivorous reptiles, which live in open areas, are specialists in their ecological niche, and have a short lifespan. These results suggest that reptile replacement according to fire regime accounts for a habitat accommodation model following particular traits of species. Our study indicated that areas subjected to repeated fires have a more strictly Mediterranean reptile assemblage than unburned areas, due to the ability of Mediterranean species to survive thermal environments in open (burned) areas. At a regional scale, changes in dominant species between unburned and repeatedly burned areas might be an argument for maintaining a patchwork of areas burned at variable intervals. However, the increase in fire frequency and extension suggests a future scenario of extinction for species negatively impacted by fire, such as the endangered Hermann's tortoise *Testudo hermanni*, for which the study area is home to one of the last native populations in the western Mediterranean.

1. Introduction

Understanding the response of species to environmental change is a major goal in predicting its effects on biodiversity (Hooper et al., 2005). Wildfires are considered among the disturbances that have a major impact on ecosystem functioning and composition in many areas of the world (Bond et al., 2005). Fire act as an environmental filter selecting these species better adapted to the narrow post-fire environmental conditions (Pausas and Verdú, 2008), and consistently, species may be adapted to this natural disturbance in prone-fire regions. Thus, it is possible to build a model to predict animal responses to fire as a function of particular habitat requirements (Nimmo et al., 2012). Empirical studies show that the response of organisms to fire is complex, often resulting in species-specific responses within a single taxonomic group [e.g. ants (Rodrigo and Retana, 2006), amphibians (Pilliod et al., 2003), reptiles (Driscoll and Henderson, 2008; Lindenmayer et al., 2008; Santos and Poquet, 2010), and arthropods (Moretti et al., 2004, Moretti et al., 2006)]. These inconsistent results suggest that response to fire can vary greatly according to intrinsic factors of

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0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.09.008

organisms (e.g. functional traits, Moretti et al., 2009), as well as extrinsic factors such as fire regime (Moreira and Russo, 2007) and severity (Pausas et al., 2002), environmental gradients (Arnan et al., 2006), climatic region (Moretti et al., 2009), pre-fire habitat type (Rodrigo et al., 2004, 2008), and post-fire management (Castro et al., 2010).

The intermediate disturbance hypothesis and the habitat accommodation model of succession have been examined as methods to predict biotic responses to natural fire regimes (Driscoll and Henderson, 2008; Lindenmayer et al., 2008). The first states that biodiversity increases at localities subjected to intermediate rates of disturbance (Connell, 1978), and the second suggests that communities recover following disturbance linked to the recovery of habitat structure (Fox, 1982). In fire-adapted regions such as the Mediterranean, biota and ecosystems are highly dynamic and resilient (Blondel et al., 2010), then expecting empirical support of biotic responses to the intermediate disturbance hypothesis and the habitat accommodation model of succession. However, resilience varies according to the nature and the complexity of the habitat (Westman and O'Leary, 1986; Jacquet, 2006), and an increase in fire frequency prevents mature ecosystems from returning to their pre-fire state, maintaining it in earlier successional stages (Mouillot et al., 2003). Thus, the interval between consecutive fires plays a major role in the Mediterranean community's resilience capacity (Keeley, 1986; Eugenio et al., 2006). In the region's plant communities, several authors have reported resprouting difficulties (Eugenio and Lloret, 2004) and decreasing resilience patterns (Díaz-Delgado et al., 2002; Vilà-Cabrera et al., 2008) following recurrent wildfires. As wildfires promote scrubland and herbaceous expansion to the detriment of forests (Pausas and Vallejo, 1999; Vilà-Cabrera et al., 2008), this may result in a parallel shift in animal groups, a pattern that could be more intense after repeated fires. Given the strong association between plant and animal responses in fire-disturbed areas (Moretti and Legg, 2009), we would expect repeated fires to generate profound shifts in species composition in parallel with changes in vegetation structure.

We examined the response of a reptile assemblage of a locality with a repeated fire regime in southern France assessing reptile abundances in unburnt, once burnt and repeated burnt transects. Fire usually improves the habitat for reptiles (Bury, 2004); as a consequence, several species take advantage of post-fire conditions and colonize new suitable thermal environments (Huey, 1991). This *a priori* positive response, however, is not homogeneous within a reptile assemblage, as habitat attributes and other environmental factors vary across the post-fire succession, favoring or harming species depending on their requirements (Rugiero and Luiselli 2006; Valentine and Schwarzkopf, 2008; Santos and Poquet, 2010), and promoting species-specific responses in reptiles within a single community (Driscoll and Henderson, 2008; Santos and Poquet, 2010).

In the context of a repeated fire regime, first we tested the intermediate disturbance hypothesis expecting higher reptile species richness in once burnt sites, and the most contrasted faunas between unburned and repeated burned transects. Response to fire has been extensively studied at a taxonomic level (e.g. in the Mediterranean basin by Moreira et al., 2001; Herrando et al., 2003; Brotons et al., 2008; Santos et al., 2009). More recently, several studies have examined the taxonomic response in parallel to the functional response of biota (Moretti and Legg, 2009; Mateos et al., 2011). This double approach provides information about taxonomic differences between burned and unburned areas and also about the mechanisms that drive community responses to environmental changes such as fire (Moretti et al., 2009). If repeated fires reduce plant diversity and increase abundance of xerophitic species (Pausas and Vallejo, 1999), we could expect a similar functional response in animal communities. If repeated fires favor plant species capable of rapid population recovery (Mouillot et al., 2003; Eugenio et al., 2006; Vilà-Cabrera et al., 2008), we could expect similar functional responses of animal species, favoring those with a short lifespan and a rapid population turnover. In this scenario, we have examined reptile functional responses to one and multiple fires according to their life-history traits as a partial approach to test the habitat accommodation model that predicts biotic positive responses according to specific habitat requirements.

2. Materials and methods

2.1. Study area and fire history

The study area was the Massif des Maures (Var, Provence region, southern France, 4°5′E /43°16′N; Fig. 1A). This is a vast coastal mountain chain with a surface area of around 1350 km^2 limited by the Mediterranean Sea (to the south), an agricultural plateau (to the north) and two rivers (to the east and west). The lithology of the massif is magmatic with a substrate composed of granite, gneiss and schist layers, in contrast to the calcareous layer of the rest of the region. The relief is abrupt, with several low-altitude chains (maximum altitude 780 m) oriented in a west–southwest to east–northeast direction along 60 km and crossed by permanent streams.

The study area has suffered very few disturbances apart from fire, in contrast to other nearby coastal areas that have been severely modified by humans. The vegetation consists of native forests, with oaks (*Quercus suber*, *Q. ilex*, *Q. pubescens*) and pines (*Pinus pinea*, *P. pinaster*, *P. halepensis*) making up the dominant tree species. Valleys around streams are occupied by deciduous forests (e.g. *Alnus glutinosa*, *Salix* spp., *Populus nigra*, *Fraxinus oxyphylla*). The most thermophilous sites are Mediterranean scrublands dominated by *Cistus* spp. *Arbustus unedo*, *Erica arborea* and *Myrtus communis*. The climate is Mediterranean, with an annual rainfall between 600 mm (on the coast) and 1200 mm (in the massif), annual sun exposure of 2880 h per year, and mild temperatures (mean minimum in January between 2 and 6 °C, mean maximum in July between 27 and 31 °C). The massif is partially protected by the French National Forest Office.

The study area is characterized by a high frequency of forest fires. We had access to fire-history mapping performed since 1958 by the *Direction Départementale de l'Agriculture et de la Forêt* (DDAF: Departmental Office of Agriculture and Forests) and the *Office National des Forêts* (ONF: French National Forest Office) in the Department of Var. During this 51-year period, 62.5% of the study area has burned at least once, 22.2% twice, and 13.5% three or more times. The spatial distribution of fires during this period was very heterogeneous: several zones in the center of the massif never burned, whereas others in the western and eastern parts burned up to six times with a fire frequency between consecutive fires averaging 10 years. Thus, the study area is a complex mosaic in terms of the number of fires, the frequency between consecutive fires, and the time elapsed since the last fire that occurred. This spatial distribution makes the Massif des Maures a natural laboratory to test the response of organisms to repeated fires.

2.2. Transect selection and sampling method

From April to June 2010, we sampled reptiles in 87 linear transects during sampling periods of 1 h per transect. Transects were carried out on sunny days during periods of maximum reptile activity. Each transect was sampled by one person walking slowly at a constant speed (average length per transect was 1.7 ± 0.05 km) and registering all visual reptile encounters. Given the transect length, this method allowed us to sample the habitat heterogeneity