



DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

THE RESPONSE OF REPTILE COMMUNITIES TO WILDFIRES IN
THE SERRA DA ESTRELA NATURAL PARK



Tiago António Pinto Ferreira

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Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia, realizada sob a orientação científica da Professora Doutora Helena Freitas (Universidade de Coimbra) e do Doutor Bruno Moreira (Universidade de Coimbra).

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2015

Acknowledgements

The achievement of this thesis would not be possible without the participation, help and support of a number of people who spare some of their time to help me. I will thank to some of those persons never forgetting so many others that contributed to this work.

To Dr. Bruno Moreira, Dr. Xavier Santos and Dra. Helena Freitas that guided me since the beginning and helped me constructing this project from the beginning. For being part of my family, for making me believe in myself and in this project, for being there for me when I most needed, for teaching me a lot of what I now know, for suffering with me in the not so good days and laughing with me in the best ones. This thesis is mine as it is yours.

To the Centre for Functional Ecology, BIODESERTS and Life Science Department for providing me the chance to significantly contribute with some of my work and knowledge.

To my parents and my sister for all the support, for seeing me grow as a scientist, for believing in me and being sure that I still have much to give. I also want to thank to my sister for all the support on the good and bad moments and, despite the distance, thank you for being always present.

To my girlfriend Helena who has seen how much effort, dedication and passion I have putted in this project, for being always with me, for comforting me every time I

need, for saying that I will have a future brilliant career and that she will always be by my side along that way. For all the love and proud she deposited and keeps deposit in me.

To Ivo Mauricio for representing what he does for me, for being a true brother, and for accompanying me for so many years and for more years to come. I also thank him for knowing me as he do and for being exactly equal to me.

To my Quilhoados, Adega and Miguitos friend groups for all the moments, all the coffees, dinners, nights out and friendship. Without them I would not be the person I am today, and my walk until here would not be the same.

To my friends on post-graduation room in CFE. It is an honour to be part of the best room in all the University.

To The British Herpetological Society for supporting this project and giving me the chance to trace my path on the science world.

To Ana Gonçalves, José Carlos Brito, Fernando Martínez-Freiría, Miguel Carretero, Alex Salas, Diana Ferreira, Ana Martins, Marco Fernández, Anamarija Zagar, Marco Sannolo, Catarina Ferreira, Eva Erzar, Raquel Ponti, Marcos Peso, and José Conde for helping me in everything I needed inside, and outside this project. Without them I would not be able to complete this document.

To finish, I would like also to thank to all other people that I do not mention here, but are in my heart and, somehow, helped to improve this dissertation.

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Abbreviations

ANOSIM – Analysis of Similarity

AF – *Anguis fragilis*

BC – *Blanus cinereus*

CG – *Coronella girondica*

Ch sp. – *Chalcides sp.*

GLMM – Generalized Linear Mixed Model

HH – *Hemorrhois hippocrepis*

ICNF – Instituto da Conservação da Natureza e Floresta

Liz – Lizard

LS – *Lacerta shreiberi*

MDS – Multi-Dimensional Scale

MM- *Malpolon monspessulanus*

PC – *Podarcis carbonelli*

PG – *Podarcis guadarramae*

PNSE – Serra da Estrela Natural Park

PsA – *Psammodromus algirus*

PsH – *Psammodromus hispanicus*

RS – *Rhinechis scalaris*

Sn – Snake

SVL – Snout-vent length

TL – *Timon lepidus*

TSF – Time since fire

TT - Turtle

VL – *Vipera latastei*

WWF – World Wildlife Found

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Resumo

O fogo é um componente importante em muitos ecossistemas terrestres, essencial para entender a ecologia e diversidade de comunidades em regiões propensas ao fogo. O fogo produz impactos na fauna directamente, através de mortalidade, ou indirectamente, por mudanças na estrutura do habitat e disponibilidade de recursos (ex., alimento). Nas últimas décadas o aquecimento global, o abandono das terras e mudanças nas actividades tradicionais como agricultura, pastoreio ou gestão das florestas estão a mudar a frequência e a extensão dos fogos. Neste contexto, entender/conhecer a resposta de organismos ao fogo é uma prioridade para a sua conservação. Os répteis são um bom grupo modelo para examinar o fogo pois são ectotérmicos, sensíveis a modificações na estrutura da vegetação, têm baixa mobilidade e taxas de dispersão, e enfrentam grandes taxas de declínio de populações e extinção.

O objectivo deste estudo é avaliar os efeitos do fogo nas comunidades de répteis a duas escalas geográficas: a uma escala global, onde examinei os padrões das respostas dos répteis ao fogo, considerando o efeito do tempo desde o último incêndio (Capítulo 1); a uma escala local, onde avaliei o efeito dos fogos naturais nas comunidades de répteis do Parque Natural da Serra da Estrela, na riqueza de espécies e abundância de indivíduos (Capítulo 2) e examinei como é que a ecologia trófica e as interações intra-específicas variam com o fogo, usando a lagartixa *Psammodromus algirus* como espécie modelo (Capítulo 3). Para isto usei um conjunto de metodologias de maneira a recolher e analisar todos os dados necessários para realizar este estudo (recolha de artigos científicos para a análise global; transectos para a visualização de répteis seguidos da caracterização da vegetação e do habitat; análise de conteúdo fecal e redes ecológicas para a dieta das lagartixas). Os principais resultados deste trabalho demonstram que, a uma escala global, a diversidade de répteis (riqueza) mas não a

abundância, diminui imediatamente após o fogo (<1 ano),mas recupera rapidamente para níveis anteriores ao fogo, com aumento da abundância. Em relação às cobras, o número de espécies não é significativamente afectada pelo tempo desde o último incêndio, mas a abundância diminui nos estádios mais tardios da sucessão ecológica.

No Parque Natural da Serra da Estrela, a abundância de répteis diminui nos primeiros 5 anos após o fogo mas recupera entre os 5 e os 20 anos de sucessão ecológica. Também concluí que a abundância de *Psammodromus algirus* (a espécie mais abundante) está positivamente relacionada com a cobertura arbórea, e negativamente relacionada com a herbácea. A diversidade de plantas é também um parâmetro relevante para os répteis, já que a sua presença está positivamente relacionada com a diversidade de espécies de plantas.

Relativamente à dieta, as redes ecológicas para as lagartixas recolhidas nos habitats ardidos e não ardidos, demonstraram que *P. algirus* apresenta uma dieta mais selectiva nas zonas não ardidas do que as ardidas. Também encontrei diferenças na disponibilidade de presas entre zonas ardidas e não ardidas.

Os meus resultados sugerem que imediatamente após o fogo há um decréscimo da riqueza de espécies, mas as comunidades recuperam rapidamente e a abundância aumenta em estádios iniciais de sucessão ecológica (tanto a nível global, como no Parque Natural da Serra da Estrela). Embora os répteis representem uma relação próxima com a estrutura do habitat, parecem estar bem adaptados a áreas com diferente tempo desde o último incêndio e apresentam abundância estáveis ao longo da sucessão ecológica. Mais ainda, possuem variação da dieta e estão acostumados a consumir uma grande variedade de presas quando as condições não são as adequadas.

Palavras-chave: Fogo, répteis, tempo desde o último incêndio, estrutura do habitat, sucessão ecológica, dieta.

Abstract

There is an increasing recognition that fire is an important component of many ecosystems in the world, essential to understand the ecology and diversity of communities in fire-prone regions. It impacts fauna directly, through mortality, or indirectly by changing habitat structure and resources availability. In recent decades global warming, land abandonment and changes in traditional agricultural activities are driving changes in the frequency and extent of fires. In this context, to know the response of organisms to fire regimes is a conservation priority. Reptiles are a good model group to examine their responses to fire as they are ectothermic, sensible to modifications in habitat attributes such as vegetation structure and canopy closure, have low mobility and dispersal rates, and experience high rates of population declines and extinction.

The purpose of this study is to evaluate the effects of fire on reptile assemblages at two geographic scales: at a worldwide scale, where I examined patterns of reptile responses to fire considering the time since fire effect with a meta-analysis methodology (Chapter 1); at a local scale, where I evaluated the effect of wildfires on the reptile communities of the Serra da Estrela Natural Park, namely on the population densities, species richness (Chapters 2) and examined how the trophic ecology and interspecific interactions varied with fire using the *Psammodrome* lizard as a model species (Chapter 3). For this, I used a set of proper methodologies in order to collect and analyze all the data needed to perform this study (search scientific data for a meta-analysis; transects for reptile surveys followed by vegetation and habitat structure characterization; fecal pellets analysis and network metrics for lizard's diet).

At a worldwide scale, lizards' diversity (richness) but not abundance decreases immediately after fire (<1 year) but recovers quickly to pre-fire levels with increased

abundance. Regarding snakes, diversity is not significantly affected by time-since-fire but abundance decreases in the latter stages of the post-fire succession.

In Serra da Estrela Natural Park, reptile abundance decreases in the first 5 years of post-fire succession, but increases in the interval between 5-10 years. I also found that *Psammodromus algirus* is positively related with tree cover, and negatively related with herbaceous cover. Plant diversity is also a relevant parameter for reptiles, since its presence (abundance) is positively related with the diversity of plant species.

Relatively to the diet, metrics of the bipartite network for lizards collected in unburned and burned habitats demonstrated that *P. algirus* presents more selective behaviors in unburned habitats, than in burned ones. I have also found differences between burned and unburned areas as regards availability of prey, being the burned area the one presenting the richest arthropod communities.

My results suggest that immediately after fire there is a decrease in species richness but communities recover quickly and reptile abundance increases in early stages of post-fire succession (both globally, and also in Serra da Estrela Natural Park). Although reptiles present a close relation with habitat structure, they seem well adapted to areas with different time since fire and present stable abundances across the post-fire succession. Moreover, they have diet variation and are adapted to consume a large variety of preys when conditions are not suitable. In undisturbed areas, they may present a selective behavior.

Keywords: Fire, reptiles, time-since-fire, habitat structure, post-fire succession, diet.

General Introduction

General Introduction

Fire is an important driver of many terrestrial biomes such as grasslands, savannas, boreal forests or Mediterranean shrublands. Indeed, the distribution and ecological properties of these fire-prone formations is determined by fire regimes (Bond *et al.*, 2005, Bond & Keeley, 2005; Pausas & Keeley, 2009). The effects of fire are manifested through all trophic levels from plants to mammals (e.g. Barton *et al.*, 2014; Santos *et al.*, 2014). Fire properties such as severity and extent, as well as the fire return interval and seasonality can have different consequences on population dynamics and community structure (Pausas *et al.*, 2002; Pastro *et al.*, 2011). The time of fire occurrence might be of great importance, regarding the effects it has in the communities/ populations, particularly for species with seasonal patterns, since the occurrence of a fire during the reproductive period are likely to be more harmful than in other time frame (e.g. hibernation period; Friend, 1993). Species response to fire depends on their particular life-history traits, habitat preferences and ability to cope with biotic and abiotic changes caused by disturbances (Fischer *et al.*, 2005). Some species may show a positive, a negative or a neutral response to fire, depending on a variety of factors (e.g. dietary, foraging habit, type of habitat, species adaptability to disturbed habitats, etc.).

Reptiles are a good model taxon to track the impact of fire because they are constituted by narrow-ranging species, highly sensible to modifications in habitat attributes such as vegetation structure and canopy densities, and have low mobility and dispersal rates (Valentine & Schwarzkopf, 2008). Moreover, reptiles experience high rates of population declines and extinction (Gibbons *et al.* 2000) and thus need special attention in terms of conservation and biodiversity monitoring (Böhm *et al.*, 2013).

Fire can drive changes in reptile species at multiple levels: at community level (e. g. species composition), at population level (e. g. reptile abundances [e. g. Santos & Poquet, 2010], genetic and phenotypic characteristics [Schrey *et al.*, 2011]), and at individual level (e. g. thermoregulatory opportunities [Webb and Shine, 2008]).

These changes can be produced directly by fire (e.g., different mortality rates; Smith *et al.*, 2001) or indirectly through changes in habitat structure (affecting thermoregulatory opportunities, protection/ cover from predators, shelters, etc) or in the diversity and/ or abundance of insects (affecting diet) (Potts *et al.*, 2003).

Particular traits can help individuals to persist fire and/ or are beneficial in the post-fire conditions. Thus the frequency of such traits (e.g., short lifespan in reptiles; Santos & Cheylan, 2013) in disturbed (burned) areas is expected to increase, with consequences on species abundance (i.e., the abundance of species having that trait (or trait value) is also expected to increase). Changes in population densities and gene flow associated to fire, also produce changes at the genetic level on reptile populations (Schrey *et al.*, 2011). However the relationship between genetic diversity and fire history (e.g., time since fire) might not be the same in all areas, and may result from differences in of population densities and social structure (Smith *et al.*, 2014).

Reptiles are highly dependent on habitat structure and species with different requirements are expected to respond differently to fire. According to the accommodate-model of succession, reptile community follows a probable order of recovery, based on the recovery of the vegetation after fire (Letnic, *et al.*, 2004). However it has been shown that reptiles' response to this disturbance is not homogeneous within a single community with some species becoming more abundant after fire, and others only recovering after many years (Driscoll & Henderson, 2008).

General Introduction

Thermoregulation one of the characteristics that is expected to be strongly be affected by fire, since fire opens the canopy, inevitably affecting the number of hours that reptiles can achieve optimal temperature (Fredericksen *et al.*, 1999). Heliothermic species benefit with the increase of insolation resulting from disturbance (because they regulate their body temperature directly from sun light or other heat source), while thermal conformer species may be negatively influenced by the reduction of canopy cover (since they regulate their temperature based on environmental temperature), because of the increase in surface temperatures. These differences in thermoregulatory opportunities may modulate fitness, future growth and survival of some species, consequentially affecting the composition of the entire reptile community (Elzer *et al.* 2013).

Food (i.e., prey availability) may also be determinant for reptile species abundance in a fire disturbed environment, since fire can alter food resources availability. Arthropods (reptile's primary food source) have a positive relationship with plant recovery along post-fire succession (Kim & Holt, 2012) and their establishment in a burned area may be a strong reason to reptile's establishment as well.

Objective

The main goal of this study is to examine how reptiles are affected by fires. To achieve this goal I performed different studies at two geographic scales (global and local): in the global analysis I examine patterns of reptile responses to fire along a chronosequence; at a local scale I evaluated the effect of wildfires and other abiotic factors (related to habitat structure and prey availability) on the reptile community of the Serra da Estrela Natural Park, considering species richness and abundance as well as the trophic ecology and intraspecific interactions of reptiles.

General Introduction

The specific objectives and hypothesis of this study are divided in three chapters. The first chapter intends to analyze whether there is a general pattern of reptile community (species richness and abundance) change with time since fire at a global (worldwide) scale. Since reptiles are ectotherm organisms, I expect an increase in species richness and abundance in relation to time since fire (at short/ medium term), and a decrease in long unburned areas. However, because different species may respond differently to fire (early successional species, generalist species, late successional species; Driscoll & Henderson, 2008) reptiles richness and abundance may be weakly explained by the TSF.

The second chapter aims to understand how the reptile community (species richness and abundance) change with fire history (time since fire and number of fires) and habitat structure (tree cover, shrub cover, herbaceous cover and diversity of vegetation) at a local scale (Serra da Estrela Natural Park). Specifically, I expect 1) an increase in species richness and abundance in relation to time since fire (at short/ medium term) followed by a decrease of these community metrics in long unburned areas; 2) lower species richness and abundance in sites with high fire recurrence; 3) lower species richness and abundance in sites with higher canopy cover; 4) relative abundances of reptiles will be related to vegetation structure of the habitat; particularly, reptiles' presence will be positively related with the diversity of plant species and the complexity of vegetation structure at a local scale.

The third chapter of this study intends to examine the effects of fire on the trophic ecology (i. e. diet and intraspecific interactions) of reptiles, using *Psammodromus algirus* as a model species. I predict that, in undisturbed (unburned areas) lizards will be more specialized in particular trophic resources then reducing intraspecific competition and increasing network modularity, compared with disturbed (burned areas).

Furthermore I expect this prediction to be modulated by variation in prey availability in the respective areas (unburned/ burned areas).

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Chapter One

The Response of Reptiles to Fire – A Global Analysis

Introduction

Reptiles can generally be considered more resilient to the short-term effects of fire when compared to other taxonomical groups, since they rely primarily on external sources for body heat (ectothermy) and present strong seasonal activity patterns (Friend, 1993). Some of these characteristics may provide advantages to reptiles; e.g. ectothermy may represent an advantage in places with low canopy density, since it enables reptiles to quickly archive optimal temperatures for daily activities (Webb & Shine, 2008), thus providing access to food and shelters before other competitors. However, for reptiles that regulate their temperature based on the environment ones (thermal conformers), the increase of surface temperature may affect these animals in a negative way. In fact, positive responses to post-fire conditions have been observed in some reptile communities, especially in Australia and in the Mediterranean basin (e.g. Nimmo *et al.* 2012a; Pianka & Goodyear, 2012; Santos & Poquet, 2010). However negative (Cavitt, 2000) or null (Greenberg & Waldrop, 2008, Perry *et al.*, 2009) responses have also been found. Furthermore, even when a particular community response is observed (positive, negative or null), not all species in the community response in the same way and some species may have a different response.

Fire may affect reptiles at different temporal scales. The direct impact of fire on reptiles includes animal mortality caused by contact with the flames (Smith *et al.* 2001), exposure to lethal temperatures (Smith *et al.* 2012), and smoke inhalation (Durbian, 2006). The indirect impacts of fires to reptile communities are those manifested through habitat modification, changes in food supply, or changes in the competitors' abundance (Russell *et al.*, 1999). Recent studies have shown low support of reptiles to follow the accommodate-model of succession (e.g. Driscoll & Henderson 2008; Kelly *et al.* 2011;

Smith, et al. 2013), indicating that other factors, beyond habitat, may be involved in fire responses in animals (e.g. Banks et al. 2012; Smith et al. 2014). However, some studies demonstrated that the reptile community follows a probable order based on the recovery of the vegetation assembly after fire (Letnic *et al.*, 2004; Santos & Poquet, 2010; Figure 1) with some species becoming abundant just after fire, while others taking many years to recover. Thus, it has been described that the reptiles' response to fire is not homogeneous within a single community; that is, it might follow different succession trajectories for reptile species during the vegetation structure recovery (Driscoll & Henderson, 2008). Reptiles' dependence on vegetation structure may trigger an enlarged movement activity (migration) to seek for shelter and appropriate areas to inhabit across different canopy densities, and availability of open spaces throughout the post-fire succession. This is expected to occur for late successional colonizers short time after a fire and for early successional colonizers when the vegetation becomes too dense (Driscoll *et al.*, 2012). This heterogeneous response to a given fire regime, based on the recovery of the vegetation, may place late-successional specialists at risk of local extinction, since a single fire can burn an entire area, removing any long-unburned habitat (Woinarski *et al.* 2004). However, the same might happen with fire suppression in areas with early-successional specialists (Driscoll & Henderson, 2008). Differences in the response of reptiles to fire may also be ecosystem-dependent. For instance, in grasslands, the recovery of vegetation (i.e., grasses) to pre-fire conditions can be rather fast; accordingly, reptile communities may show little or none response to fire in these habitats (Rochester *et al.*, 2010). On the contrary, in scrublands and forests the recovery of vegetation is slower and so, reptile communities may show disparate responses to fire (Ashton & Knipps, 2008).

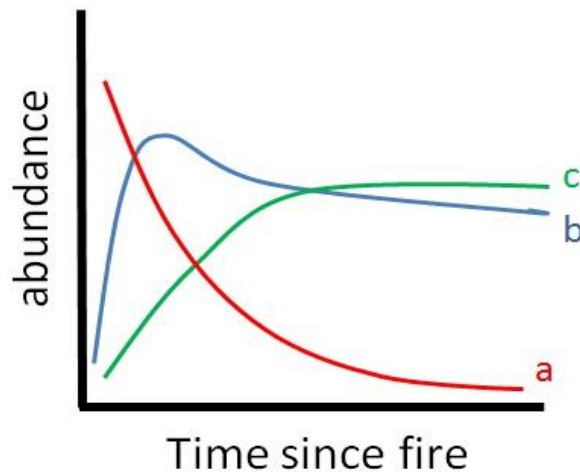


Figure 1 – Examples of reptile succession trajectories after a fire. (a) Early successional species that inhabit open areas are most abundant after a fire, and then decline. (b) Generalist species decline after a fire but have a quick recover. (c) Late successional species may take many years to recover (modified from Driscoll & Henderson, 2008).

Objectives

The objective of the study presented in this chapter is to search for a general pattern of how reptile communities (richness and abundance) change with time since fire at a global (worldwide) scale. Being reptiles ectotherm organisms, I expect that immediately after fire species richness and abundance decreases mainly because of direct mortality, low canopy cover and low availability of prey. At short/ medium term I expect an increase in species richness and abundance along with the increase on the vegetation cover and availability of prey, followed then by a decrease in long unburned areas because of habitats' complexity and lack of places for reptiles to thermoregulate.

Materials and Methods

Literature Searches

I performed a literature search on the Web of Science and Google Scholar, considering all publications up to January 2015. A set of combinations using the following words was used: fire*, burn*, wildfire*, prescribed* and reptil*, lizard*, snake*, turtle*, herpeto*. This search returned a total of 1373 studies. Then all these studies were scanned and those that did not address the effect of fire on reptiles were excluded. This selection resulted in a total of 156 scientific papers that were then carefully examined to match criteria suitable for analysis.

To be included in the analysis, the scientific papers had to address the following criteria: 1) assess the effect of fires (wild-and/or prescribed fires) on reptiles along a certain time frame; 2) to have data on the abundance and richness of reptiles between different fire intervals, and 3) the time since the last fire using paired burned and unburned plots or data gathered before and after a fire event. In studies that combined the effects of fire with other disturbances (e.g., application of pesticide or clear-cut), I only used values referring to control and burned areas. Studies that did not have control areas (areas that have never burned, or burned long time ago), that presented different methodologies within each type of experiment (e.g. different number of pitfalls in the same treatment), and did not have sampling effort for some experiments either in burned and unburned plots were also excluded.

After this selection process I had 31 definitive papers to include in the analysis.

Variables

Available data from each study was classified according to: 1) treatment (control or fire), 2) fire type (wildfire or prescribed fire); 3) time since fire; 4) type of experiment (control-treatment plots or before-after-fire); and 5) species caught or observed in the study (including the Taxonomic Order of the animal, namely lizard, snake or turtle). Some studies addressed the time since fire by intervals, rather than specifying the exact TSF. For this reason this parameter was compiled in fire intervals for all studies (<1 year; 1 -5 years; 6-10 years; 11-25 years and 26-50 years).

From the 31 papers examined, sixteen studies were replicated (that is, had at least two control and two treatment areas, or a before-after design), and fifteen studies were unreplicated. Sixteen studies accessed the effects through prescribed fires, while thirteen explored the effects through wildfires. One study did not specify which type of fire was mentioned and other study accessed the effects of both prescribed and wildfires. Nine studies were located in Australia, five in Europe, fourteen in North America and three in South America (Figure 2) and all took place in eight ecoregions following the version of the World Wildlife Fund (WWF) global classification system (Olson *et al.* 2001) (Supplementary Materials I).

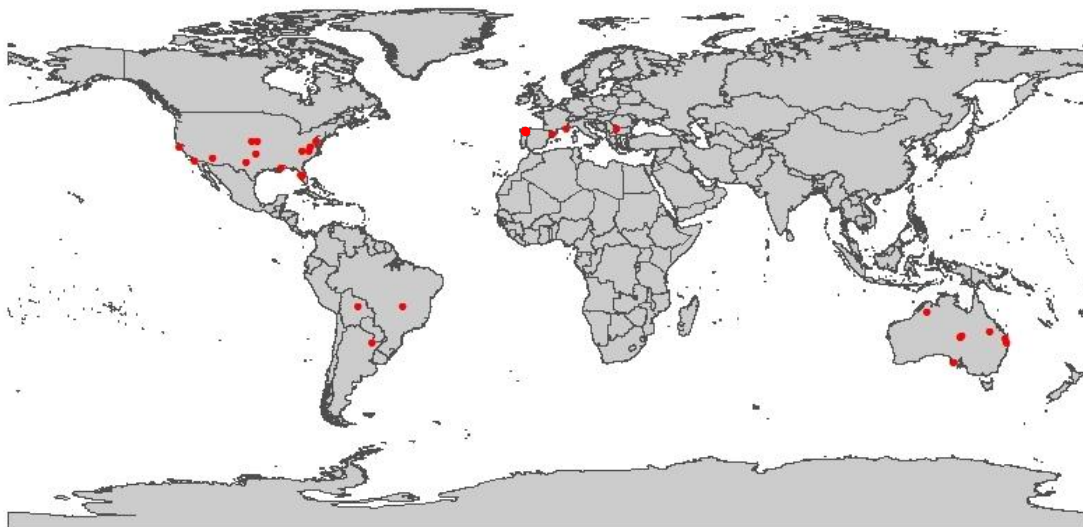


Figure 2 – The location of each of the studies included in the analysis.

Statistical Analysis

I have constructed a database that included the different categories mentioned above (e.g. Fire Type; Type of Experiment, etc.), as well as the abundances for each species, and the sampling effort according to each TSF interval for every study. This matrix was the basis for further analysis. The term “sampling effort” is used to quantify the number of trap-nights or travelled meters (for studies with pitfall traps and transects respectively) in the sampling method of each study. Due to the lack of information about the number of fires in the majority of the studies, I was not able to compile this; therefore the analysis was only done with TSF.

The effect of the time since fire on the dependent variables (species abundance and richness) was explored with a Generalized Linear Mixed Model (GLMM) with Poisson distribution and sampling effort (log transformed) as offset. This type of analysis is consistent with the data’s distribution and allowed to place variables such as “Study”, “Experiment Type (BA/CT)”, “Fire Type (PF/WF)” and “Species” as random effects. The statistical analysis was performed with “lme4” package (Bates *et al.*, 2008) on software R (R Development Core Team 2015).

Results

Species richness and number of individuals is significantly affected by time since fire (Figure 3A and B). Specifically, species richness is lower than in unburned areas (control) at the interval of < 1 year ($p < 0.001$; Figure 3A) while reptile abundance is higher than in unburned areas in the intervals between 1-5 years and 6-10 years after fire but lower in the interval 36-50 years (Figure 3B; Table I).

Table I – Output for the GLMM for both dependent variables according to the different fire intervals. Significant results in bold.

Species richness according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	935.47	947.46	-463.73	927.47		
Model (TSF)	10	929.90	959.87	-454.95	909.90	17.571	0.007
TSF	<u>Estimate</u>		<u>Std. Error</u>		<u>z value</u>		<u>p value</u>
1y	-0.303		0.101		-2.988		0.002
1-5y	0.088		0.071		1.242		0.214
6-10y	0.043		0.150		0.292		0.770
11-25y	0.077		0.186		0.414		0.679
36-50y	-0.564		0.338		-1.667		0.095
Reptile Abundance according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	16149.3	16161.3	-8070.7	16141.3		
Model (TSF)	10	5886.4	5916.3	-2933.2	5866.4	10275	<0.001
TSF	<u>Estimate</u>		<u>Std. Error</u>		<u>z value</u>		<u>p value</u>
<1y	-0.023		0.030		-0.775		0.438
1-5y	0.311		0.017		17.348		<0.001
6-10y	0.476		0.047		10.100		<0.001
11-25y	-0.016		0.038		-0.424		0.671
36-50y	-0.250		0.113		-2.202		0.027

Chapter One - Results

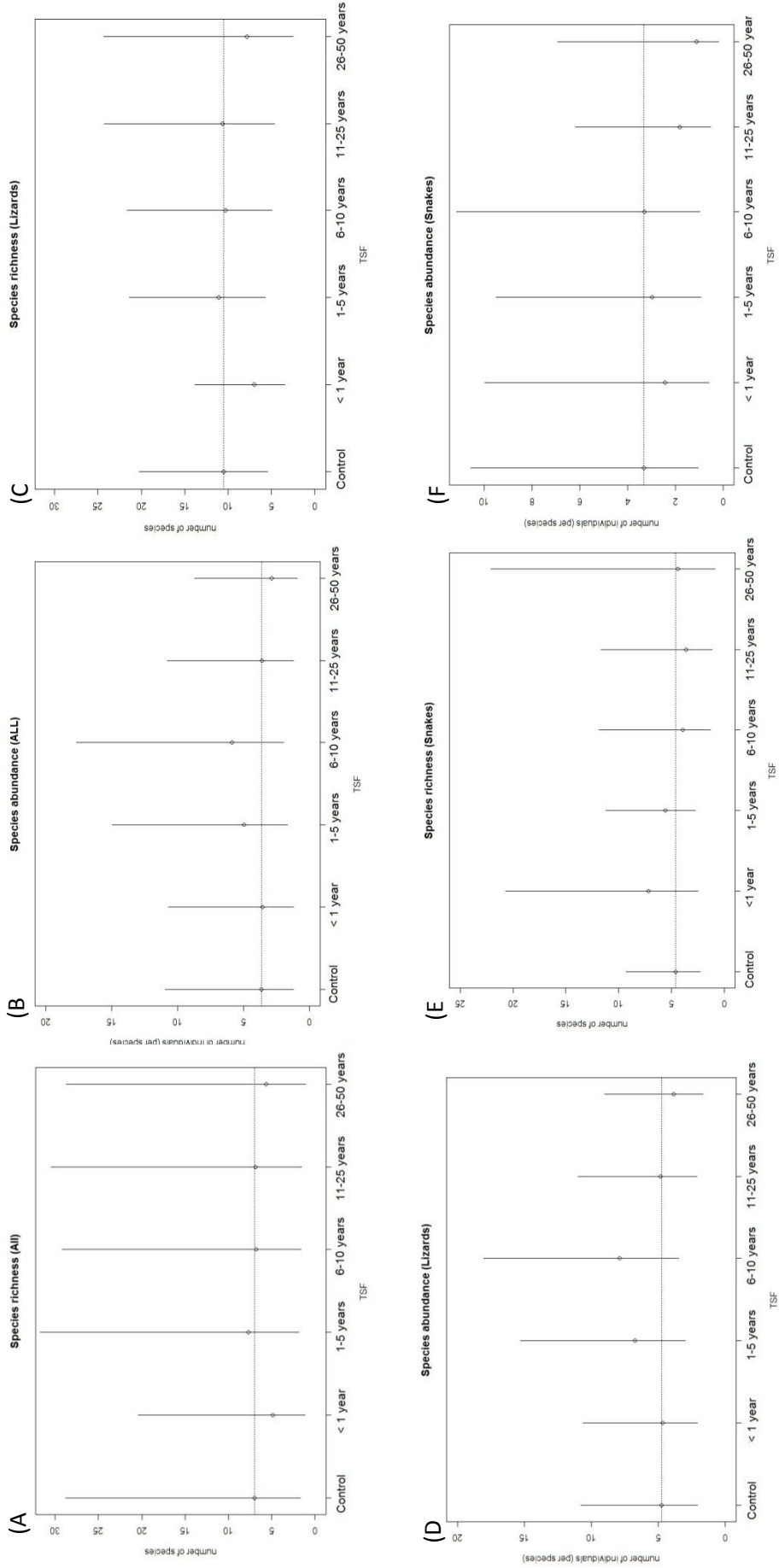


Figure 3 – Predicted reptile abundance and species richness (lizards (C; D) and snakes (E; F)) response according to TSF. Bars represent 95% confidence intervals; dotted horizontal line represents the control.

In order to understand if the responses varied in lizards and snakes separately, these two groups of reptiles were split and their response to fire were analysed (Tables II and III). There were statistical significant differences in lizard species richness in <1 year after fire ($p = 0.0008$) (Figure 3c; Table II) in comparison to control. In contrast, snake species richness is not altered along the post-fire stages (Figure 3e; Table III). However, for the abundance, snakes' number drops on the interval 11-25 years ($p=0.0075$) (Figure 3f; Table III), while lizards' abundance decrease in earlier stages (mainly between 1-5 years, and 6-10 years ($p<0.00001$) (Figure 3d; Table II).

Table II – Output for the GLMM for lizard richness and abundance according to the different fire intervals. Significant results in bold.

Lizard richness according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	549.92	560.05	-270.96	541.92		
Model (TSF)	9	545.20	567.99	-263.60	527.20	14.727	0.012
TSF	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>			
<1y	-0.3676	0.1097	-3.335	0.0008			
1-5y	0.0129	0.0862	0.149	0.881			
6-10y	-0.0082	0.1660	-0.050	0.960			
11-25y	0.0246	0.2343	0.105	0.917			
36-50y	-0.3676	0.4039	-1.555	0.119			
Lizard Abundance according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	4524.6	4537.8	-2258.3	4516.6		
Model (TSF)	9	3877.3	3900.1	-1929.7	3859.3	657.3	<0.001
TSF	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>			
<1y	-0.139	0.0303	-0.459	0.647			
1-5y	0.3527	0.0180	19.552	<0.001			
6-10y	0.5102	0.0477	10.688	<0.001			
11-25y	-0.0016	0.0381	-0.042	0.966			
36-50y	-0.2093	0.1150	-1.820	0.069			

Table III – Output for the GLMM for snake’s richness and abundance according to the different fire intervals. Significant results in bold.

Snake richness according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	287.34	295.37	-139.67	279.34		
Model (TSF)	9	293.10	311.17	-137.55	275.10	4.2375	0.516
TSF	<u>Estimate</u>		<u>Std. Error</u>		<u>z value</u>	<u>p value</u>	
<1y	0.08503		0.28237		0.301	0.763	
1-5y	0.21860		0.12485		1.751	0.080	
6-10y	0.17138		0.34797		0.493	0.622	
11-25y	0.12856		0.30512		0.421	0.674	
36-50y	-0.45444		0.61540		-0.738	0.460	
Snake Abundance according to TSF							
	<u>Df</u>	<u>AIC</u>	<u>BIC</u>	<u>logLik</u>	<u>deviance</u>	<u>X²</u>	<u>p</u>
Null Model	4	747.48	755.51	-369.74	739.48		
Model (TSF)	9	736.11	754.18	-359.06	718.11	21.38	<0.001
TSF	<u>Estimate</u>		<u>Std. Error</u>		<u>z value</u>	<u>p value</u>	
<1y	-0.30294		0.47103		-0.643	0.5201	
1-5y	-0.06945		0.05774		-1.203	0.2290	
6-10y	0.01417		0.20975		0.068	0.9461	
11-25y	-0.59057		0.22096		-2.673	0.0075	
36-50y	-1.07131		0.72697		-1.474	0.1406	

Discussion

Immediately after fire (less than 1 year) there is a significant decrease in species richness (particularly for lizards) but a quick recovery (after the first year). In addition to the mortality experienced by reptiles during the fire (Smith *et al.*, 2001), the elimination of the vegetation occurred immediately after the fire may induce post-fire migration of some species (late successional) from burned to unburned areas (Lyet *et al.*, 2009) which might be related with the decrease in species richness right after fire. Immigration is likely to occur more slowly (possibly takes months or longer) (Driscoll *et al.*, 2012) while the recently burned habitat would not have the conditions for immediate species establishment.

Species richness does not vary in the interval between 1-25 years; however within this interval I assume there is species turnover (substitution) according to changes in the habitat. The richness does not vary probably because of the unlikely coincidence of early and late colonizers (which would explain the uniformity of the number of species).

With respect to abundance, although reptiles may be affected by factors such as direct mortality through fire and vulnerability to predators, the thermal properties of microhabitats that ectotherms use for thermoregulation (Webb & Shine, 2008) probably mediates their fast recovery (Davis & Doherty, 2015). Indeed, some reptiles benefit with the post-fire habitat openness (Fredericksen *et al.*, 1999; Russel *et al.*, 1999) and thus their abundance increases after the first year of post-fire succession. This may be due to survival and/or colonization of habitats soon after fire for some reptiles, and only when the vegetation recovers to an appropriate stage for others (e.g. Pastro *et al.*, 2011). Reptile abundance peaks from the period 1-10 years after fire, and this is possibly

related to the quality of the habitat. The vegetation may attract potential prey items (Potts *et al.*, 2003; Kim and Holt, 2012) and provide shelter against predators, which can explain the increase in the abundance in the first ten years of post-fire succession. Moreover, the low vegetation cover (characteristic of the first years of post-fire succession) provides a continuous gradient of sun and shade, which enables thermoregulating animals to select their position (Carrascal & Díaz, 1989). This can ultimately enhance survival (by favouring optimal body temperatures and reducing predation pressure) and hence increase species abundance. After this period, reptile abundances decrease probably due canopy closure that affects negatively the necessary requirements for reptiles to thermoregulate.

Lizards follow the general pattern probably since they represent the main component of the reptile communities especially in terms of abundance. The decrease in lizards' species richness and abundance in long unburned areas (26-50 years) may also be a consequence of high vegetation densities and canopy closure which reduces the availability of open areas, and thus the places for reptiles to thermoregulate, consequentially decreasing reptiles' fitness (Elzer *et al.*, 2013). This might be particularly important in areas like in the Australasia or Palearctic and Nearctic ecogeographic realms (Olson *et al.*, 2001 Waldron *et al.*, 2008; Bailey *et al.*, 2012), where most reptile species need sun exposition. In contrast, this trend might not occur in tropics (e.g. in tropical rainforests) where reptiles are adapted to high canopy. In this region, a fast vegetation recovery would suggest a fast reptile recovery although this should be experimentally demonstrated in field-based studies in tropics, since this analysis only comprises three studies in this region.

Snake's species richness does not vary across the post-fire succession. However, it slightly increases within the first year following fire. This is probably associated with

the lack of vegetation that assures a better detection of these animals, since snakes are very secretive and difficult to observe in the field (Segura *et al.*, 2007), and not on a true increase in the number of species. The decrease in snake abundance can be related with this same scenario (canopy closure), or with the low detectability of snakes in dense vegetation areas. Other possible factors to explain low snake abundances in long unburned sites could be related with the lack of lizards as a prey since many snakes may include these reptiles in their diet. This would be more evident for non-adult snakes, since many species have ontogenetic shifts in diet from ectotherms to endotherms after sexual maturity (e. g. Saint-Girons, 1980).

This study provides a global and generalized view on how reptile communities respond to fire. Although a better look should be given to some particular species, especially the ones in danger of extinction, my study provides a general pattern of responses for whole communities. I do not discard that other possible factors may drive reptile responses to habitat changes. However, my study can give some guidelines in fire-prone regions in order to better draw fire-based habitat manipulations for the conservation of this taxon.

The small differences among the fire classes and the large variability within each fire class along the chronosequence may be consistent with the differences in responses between species. Because different species may have different habitat requirements and life-history traits which allows its presence in a certain fire class.

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Chapter Two

The Response of Reptiles to Wildfires in Serra da Estrela Natural Park

Introduction

Mediterranean ecosystems have been a target place to study biodiversity's responses to fire, since it is intrinsically linked to this region (Pausas, 2004; Pausas & Paula, 2012; Figure 4).

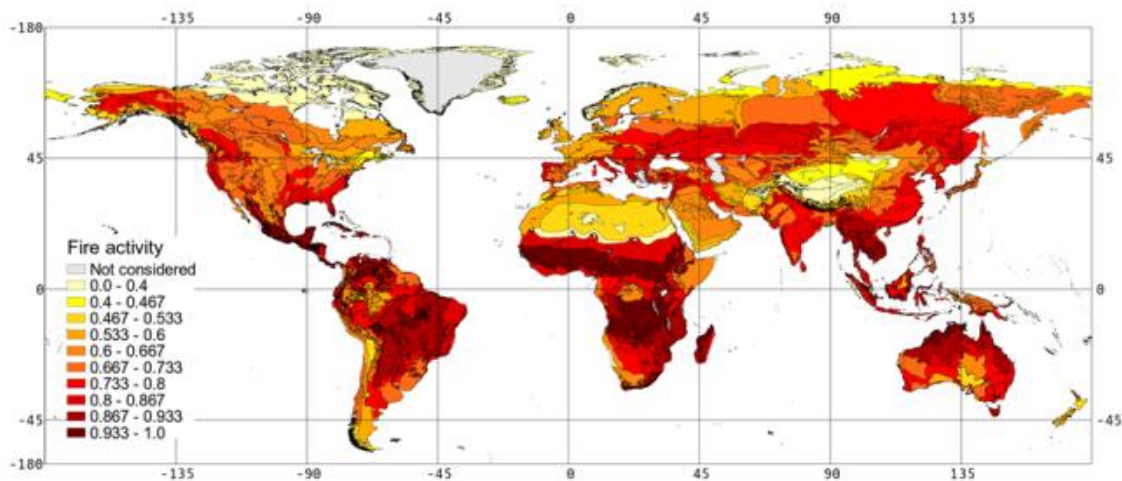


Figure 4 – Global fire activity, rescaled from 0 to 1 (Adapted from Pausas & Ribeiro, 2013) It is possible to see a higher fire incidence in the equatorial region, along with southwest Europe and Australia.

Mediterranean habitats are highly dynamic and resilient (Blondel *et al.* 2010) and many species bear adaptive traits that allow them to cope with the presence of fire in the ecosystem (Keeley *et al.* 2011; 2012). Portugal is one of the European countries with higher number of fires (Carvalho *et al.*, 2010; Figure 4).

Humans have been using fire routinely to assist on land management (e.g. removing undesired vegetation or creating suitable land for farming) (Moreira & Russo, 2007). Over the last century however, the increase of extensive agriculture, livestock grazing,

land abandonment and forestry is modifying fire regimes (Pausas, 2004; Moreira & Russo, 2007; Pausas & Ribeiro, 2013). Farmland abandonment increases the cover and continuity of early successional species (many of which with high flammability), consequentially increasing the fuel beds that are prone to burn. Moreover, many of these abandoned old fields are then transformed in extensive plantations (Pausas *et al.* 2008) homogenising landscapes and increasing fire risk. This land-use change is assumed to be the main driver for the increase of wildfires and burned area in recent decades (Pausas, 2004). Nowadays, most fire ignition sources have an anthropogenic origin and, together with land-use change and global warming, are driving changes in fire regimes resulting in increasing fire frequency and extension (Pausas, 2004; Bowman *et al.*, 2009; Pausas & Fernández-Muñoz, 2012).

Portuguese landscapes are recurrently affected by fires, especially in the northern part of the country (Figure 5). Portugal is well studied in terms of fire, particularly with studies focusing on causes of fire, and fire's spatial distribution (e.g. Carvalho *et al.*, 2010; Connor *et al.*, 2012; Lourenço *et al.*, 2012); however there is little information on the response of certain taxonomical groups to fire such as reptiles.

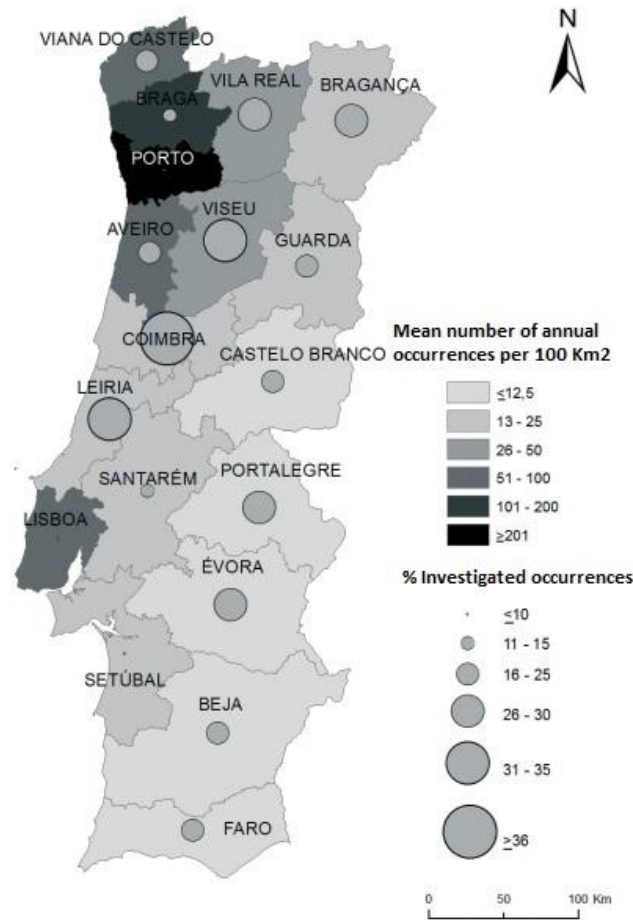


Figure 5 – Spatial distribution of the mean annual number of fire occurrences per 100 Km², and percentage of investigated occurrences (Modified from Lourenço *et al.*, 2012).

Objective

The objective of the study presented in this chapter is to understand how reptile communities (species richness and abundance) change with fire history and habitat structure at a local scale. At this scale is easier to control factors such as habitat structure, fire history (time since fire and number of fires). I conducted this study in an area of high interest in Portugal, Serra da Estrela Natural Park that is also affected by a deep fire history. I conducted field surveys in a number of sites selected according to a

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gradient of number of fires and time since fire periods. Specifically, I expect 1) an increase in species richness and reptile abundance in relation to time since fire (at short/medium term) followed by a decrease in long unburned areas; 2) a decrease in species richness and reptile abundance in sites with higher fire recurrence; 3) a decrease in species richness and reptile abundance with higher habitat canopy; 4) relative abundances of reptiles will be related to vegetation structure of the habitat; particularly, reptiles' presence will be positively related with the diversity of plant species and the complexity of vegetation structure at a local scale.

Material and Methods

Study area

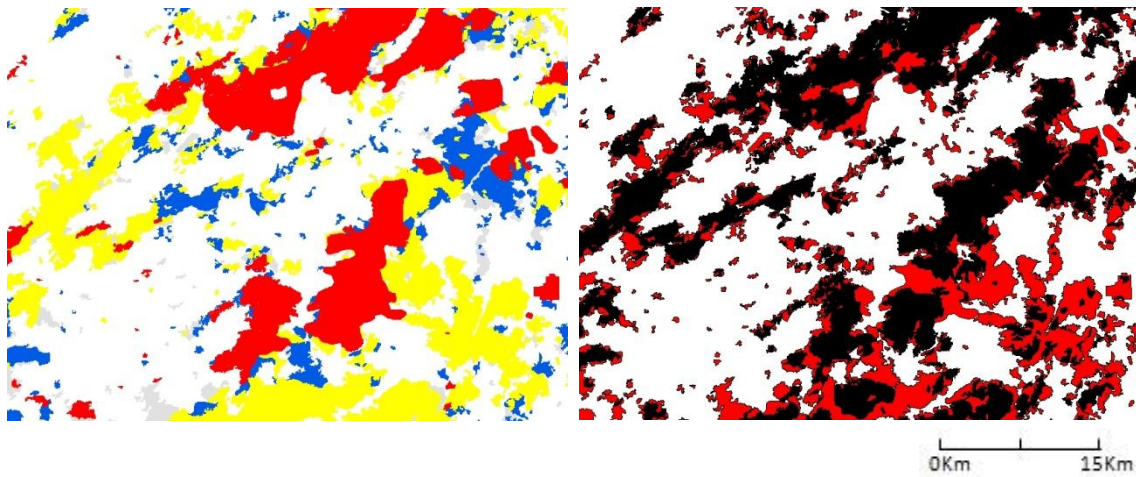
This study was performed in the Serra da Estrela Natural Park (PNSE). The PNSE is a Portuguese protected area that was created in 1979 and is located in the east of the Central region of Portugal (see Figure 8). It stretches 55 kilometers from Celorico da Beira in the north, down to Vide in the southwest, covering 88 850 hectares. The Serra da Estrela mountain is a huge granite-massif oriented southwest-northeast with a considerable altitudinal gradient (400-1993m), holding the highest summit of continental Portugal. Due to these characteristics, there are two contrasted climatic influences: Temperate (northern and western slopes and in the highest elevations) and Mediterranean (lower eastern slopes) (Jansen & Sequeira, 1999). The temperature is mainly controlled by global latitudinal position (Mediterranean macroclimate) and longitudinal position in respect to the Atlantic and the Iberian interior.

The mean annual rainfall is ca. 1800 mm in the summit and ca. 1000 mm in the plateaus (SNIRH). The average annual temperatures range from 4°C and 22°C, being January the coldest month and July the hottest month of the year. The park is a landscape mosaic with a wide range of habitats in part shaped by fire occurrence, including forested, shrubby and rocky areas. The PNSE has three distinct bioclimatic belts: 1) a meso-Mediterranean (below 900 m of altitude); 2) a supra-Mediterranean (between 900 and 1600 m); and 3) an oro-Mediterranean (above 1600 m). This study was performed within 250 and 1300 m (i.e., on the meso-Mediterranean and part of the supra-Mediterranean belts, Pinto da Silva & Teles, 1999). From the mountain foothills up to 900 m, the native vegetation that could be found included vast Mediterranean oak forests (*Quercus rotundifolia*; *Quercus suber*) at southeast and southwest slopes, and

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Quercus robur forest at the west north and northwest slopes. Extensive forests of ash trees (*Fraxinus angustifolia*) occurred associated with moist soils and, in the valleys along water lines, dense riparian patches of alders (*Alnus glutinosa*), willow (*Salix* sp.) and elms (*Ulmus minor*) would be present. Currently, most of these formations occupy small areas or have been replaced by meadows, pastures, croplands and forest stands due to human activities. Between the 900 m and the 1600 m, the potential autochthone vegetation would include Pyrenean oak forests (*Quercus pyrenaica*) and holm oak forest in the southeast and southwest slopes (characterized by Mediterranean climate), and Pyrenean oak forest in the western slopes (characterized by Atlantic climate). Groves of birch (*Betula alba*) and yew (*Taxus baccata*) are yet present in residual patches, mainly due to fires and agricultural practices. The ancient forests have therefore been replaced by shrublands mainly composed by *Erica* sp., *Calluna vulgaris*, *Cytisus* sp., *Genista* sp. and *Echinopartum* sp. (CISE, 2015).

Fire-history mapping from 1975 until 2013 (Figure 6) was obtained from Instituto da Conservação da Natureza e Florestas (ICNF). The spatial distribution of the fires is heterogeneous, with areas unburned since 1975, and other areas burned up to 12 times in the same period of time (Figure 6).



Time since the last fire:

- > 38 years
- 20 – 38 years
- 10 – 20 years
- 5 – 10 years
- < 5 years

Number of fires:

- 0
- 1
- ≥ 2

Figure 6 – Fire-history of the Serra da Estrela Natural Park with the time since the last fire and the number of fires.



Figure 7 – Photos from two transects in the Serra da Estrela Natural Park, showing the contrast between a recently burned area (~1 year, top) and a never burned area (>38 years, bottom).

Reptile communities of Serra da Estrela Natural Park

Twenty species of reptiles have been recorded in the park: 12 species of lizards and 8 species of snakes (Table IV; Lesparre & Crespo, 2008).

Table IV. Reptile species (lizards and snakes) occurring in the PNSE, and their area of occurrence. (adapted from Lesparre & Crespo, 2008).

Lizards	Area of Occurrence
<i>Anguis fragilis</i>	Farmlands; meadows; humid places, with canopy
<i>Blanus cinereus</i>	Dry sandy areas; beneath rocks
<i>Chalcides bedriagai</i>	Sandy and rocky areas
<i>Chalcides striatus</i>	Meadows; shrubby areas
<i>Iberolacerta monticola</i>	Rocky areas with low vegetation
<i>Lacerta schreiberi</i>	Dense vegetation near water spots
<i>Podarcis carbonelli</i>	Shrubby and rocky areas
<i>Podarcis guadarramae</i>	Distributed throughout the Park
<i>Psammodromus algirus</i>	Distributed throughout the Park
<i>Psammodromus hispanicus</i>	Sandy and low vegetation areas
<i>Tarentola mauritanica</i>	Farmlands; pinewoods
<i>Timon lepidus</i>	Rocky and shrubby areas
Snakes	
<i>Coronella austriaca</i>	Humid areas; rocky outcrops
<i>Coronella girondica</i>	Farmlands; meadows; exposed areas
<i>Hemorrhois hippocrepis</i>	Arid and rocky areas with low vegetation
<i>Malpolon monspessulanus</i>	Distributed throughout the Park (dense canopy areas and big rocks)
<i>Natrix maura</i>	Distributed throughout the Park (near water spots)
<i>Natrix natrix</i>	Distributed throughout the Park (near water spots)
<i>Rhinechis scalaris</i>	Dry and exposed areas; rocky areas; farmlands
<i>Vipera latastei</i>	Rocky outcrops with exposed areas

Transect selection and sampling method

I selected twenty one transects were using ArcGIS[®] and Google[™] Earth (Figure 6) according to different fire histories of each site. The criteria used to select the different transects were: 1) minimum length of 1 Km allowing a 45 minutes' walk; 2) the beginning of the transects close to a road, to facilitate in terms of time waste and logistics; 3) the most linear as possible to avoid the observation of the same reptile along the transect (Fig. 7). To address the questions in this work, transects were classified into seven different classes according to number of fires and time since fire (TSF):

Class 0F: unburned sites.

Class A: sites with a TSF between 20 to 38 years;

Class B: sites with a TSF between 10 to 20 years;

Class C1: sites with a TSF between 5 to 10 years and that have been burned only once;

Class C2: sites with a TSF between 5 to 10 years that burned two or more times;

Class D1: sites with a TSF of less than 5 years that have been burned only once;

Class D2: sites with a TSF of less than 5 years that have been burned two or more times.

Transects were located between the elevation of 250 m and 1300 m, because above this altitudinal range, there is reptile species substitution. For class, three replicated transects were selected. Replicates of the same class were spatially separated to avoid spatial autocorrelation (Figure 8). Moreover, transects were separated between them by a minimum distance of 300 m, to ensure independence among sampling and to avoid

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spatial autocorrelation (Heatwole and Taylor, 1987). Between May and September of 2014 and May and June of 2015 transects were surveyed for periods of 45 minutes each, visual survey method. This method has proved to be adequate to survey Mediterranean reptile communities (Santos & Cheylan, 2013). I visited each transect eight times, walking slowly at a constant speed. All transects were visited each time during approximately 4 days, and visits at each single transect were separated by at least one and a half week (Table V).

The search was carried out in sunny days, in order to sample reptiles during their active hours. All the reptiles observed were identified to species level, except the two skink species of *Chalcides* genus (*Chalcides striatus* and *Chalcides bedriagai*) that were joined into one group (*Chalcides* sp.), because of the similarities between them, and difficulty to observe on the field. All reptile sights were geo-referenced and the perpendicular distance to transect noted in order to access differences in reptile detectability (e.g. due to differences in vegetation cover). On the second period of observation (year 2014), one transect belonging to Class C2 had its vegetation cut (around ten meters on each side) and no reptiles were observed in 5 visits. For this reason this transect was excluded from the data analysis and the sampling periods occurring in 2015.

Table V - Date of each visit performed in PNSE.

Visit	Date
1	21-05-2014
2	01-06-2014
3	08-07-2014
4	28-07-2014
5	04-09-2014
6	11-05-2015
7	22-05-2015
8	02-06-2015

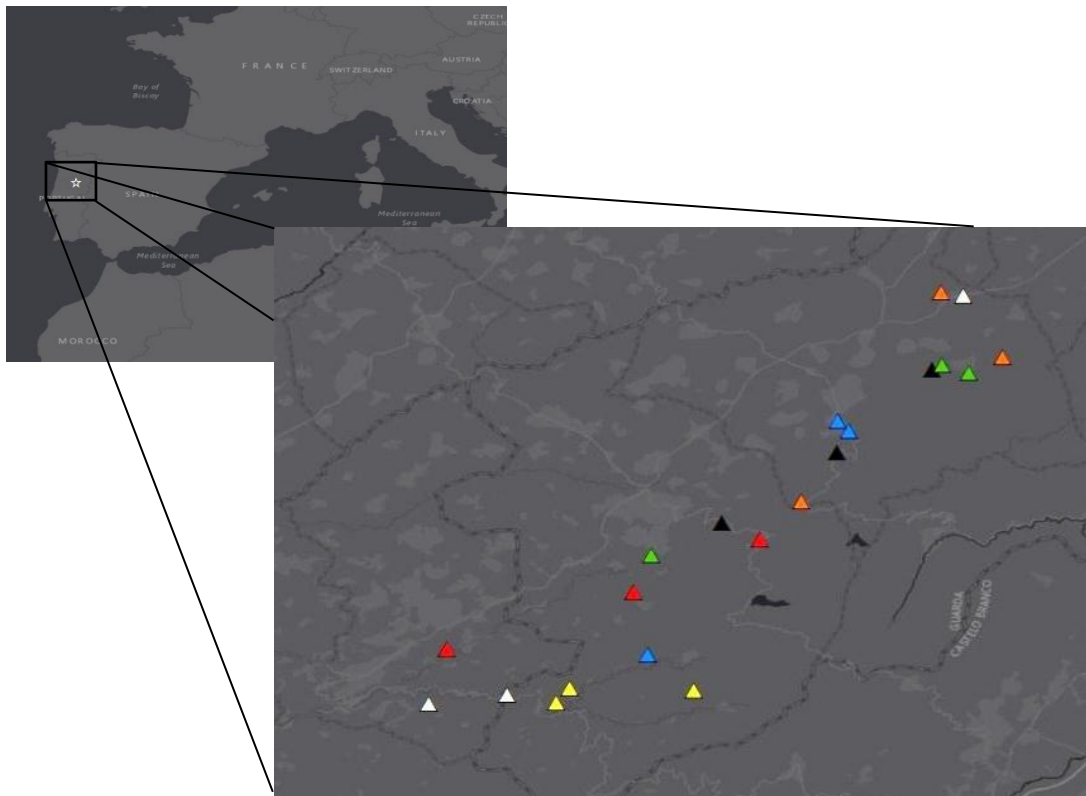


Figure 8 – Localization of the Serra da Estrela Natural Park on the west part of the Mediterranean basin; a zoom to the different study classes and their replicates (Green – Class 0F; White – Class A; Blue – Class B; Yellow – Class C1; Orange – Class C2; Red – Class D1; Black – Class D2).

Habitat measurements

Habitat structure and vegetation composition were characterized by sampling the vegetation along the entire transect length. For this, each transect was divided in sections of 20 m and vegetation of each side of the transect was characterized (1/ 2 m each side). Vegetation cover was classified according to strata (tree, shrub and herbaceous cover), and all the trees and shrubs were identified to species level. Because

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left and right sides of transects presented different vegetation types and percentages of cover, measurements were done independently for each side. With this data I constructed a matrix with the percentages of all the vegetation types for each transect, including the vegetation cover and number of species for each 20 m long patch. Vegetation structure and composition were overlapped with the reptiles' geo-referenced sights; then reptile abundance and diversity (richness) at each 20 m long patch was counted.

To access vegetation similarity among each 20 m long patch used for the vegetation cover sampling, I performed a multi-site similarity index (Baselga *et al.*, 2007). The greater this index value, the greater vegetation similarity among each patch. In order to test if reptile presence was related with number of plants, in each 20 m long patch, I counted the number of plant species and the number of reptiles recorded.

Statistical analysis

I used two community metrics to access the response of reptile communities to wildfires: species richness and abundance per transect. I also examined response for *Psammodromus algirus* because it was the only species of which I had sufficient data to analyze at species level. The effects of the explanatory variables (vegetation cover (trees, shrubs and herbaceous), TSF, number of fires and altitude) in my dependent variables were explored using Generalized Linear Mixed Models (GLMM) with Poisson distribution (count data). This type of analysis is consistent with the data's distribution and allowed to place "Visit" as random effect. For the microhabitat analysis I used a GLMM with binomial distribution (presence/ absence).

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I have also performed a linear regression with Tukey Contrasts to report if the detectability of reptiles was different facing different fire classes. All the analysis executed in this chapter was performed on software R (R Development Core Team, 2015) using the packages lme4, multcomp, lattice, mgcv and languageR (Bates *et al.*, 2008; Hothorn *et al.*, 2008; Sarkar, 2008; Wood & Wood, 2015; Baayen, 2011, respectively).

Results

Reptile Communities

Overall, considering the eight visits to each of the 20 transect I found 433 reptiles, belonging to 15 different species (of the 20 species present in the Natural Park, Table IV). Two of the six reptiles (*Iberolacerta monticola* and *Coronella austriaca*) that I did not detect are upland species (their altitudinal range habitats are higher than the ones I surveyed) and thus this was expectable. The other three species (*Natrix natrix*, *Natrix maura* and *Tarentola mauritanica*) were not found probably because the first two are usually characteristic of water spots (not consistent with my transects), and the third because has nocturnal habits. *Psammodromus algirus* was the most abundant species resulting in ca. 83% of all sights and detected in all the transects. *Podarcis guadarramae* was also detected in areas with different time since fire (ca. 6% of sights; detected in 55% of the transects).

The Linear Regression showed that the reptile detectability was not significant across all fire classes (Supplementary Materials III), suggesting that neither the different types of vegetation nor the transect width affect reptile surveys ($F = 2.228$; $DF = 426$; $p = 0.45$).

Significant differences were found in reptile abundance among transect types associated with the TSF ($p = 0.003$; Figure 9; Table VII). Reptile abundance is lower in recently burned areas (≤ 5 years) ($p = 0.009$), followed by an increase between 5 and 10 years of time since fire. The abundance reaches its peak between 11 and 20 years after fire, and finally decreases in long unburned areas (20-38 years) with respect to the unburned control transects ($p = 0.04$).

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Table VI – For each fire class, summary of reptile richness (Total and Mean \pm SE) and abundance (Mean \pm SE), plant richness (Mean \pm SE), tree cover (Mean \pm SE), shrub cover (Mean \pm SE), and herbaceous cover (Mean \pm SE) and the values of similarity index (Mean \pm SE). The codes represent: 0F – Areas that never burned; A – TSF 20-38 years; B – TSF 10-20 years; C1 – TSF 5-10 years, one fire; C2 – 10-20 years, \geq 2 fires; D1 – TSF < 5 years, 1 fire; D2 – TSF < 5 years, \geq 2 fires. AF – *Anguis fragilis*; BC – *Blanus cinereus*; Ch – *Chalcides sp.*; LS – *Lacerta shreiberi*; PC – *Podarcis carbonelli*; PsA – *Psammotromus algirus*; PsH – *Psammotromus hispanicus*; TL – *Timon lepidus*; CG – *Coronella girondica*; MM – *Malpolon monspessulanus*; HH – *Hemorrhois hippocrepis*; RS – *Rhinechis scalaris*; VL – *Vipera latastei*.

Class	Lizards											Snakes					Reptile Abundance
	AF	BC	Ch	LS	PC	PG	PsA	PsH	TL	CG	MM	HH	RS	VL	Reptile richness (Total)	Reptile richness	
0F	0	0	9	0	0	0	60	1	2	1	0	0	0	0	5	2.6 \pm 0.88	24.3 \pm 6.17
A	0	1	0	0	0	2	49	0	0	0	0	0	0	0	3	2 \pm 0.58	17.3 \pm 3.38
B	1	0	1	0	0	3	72	0	3	0	0	0	0	1	6	3 \pm 1.15	27 \pm 2.89
C1	0	0	0	0	0	7	70	1	1	0	0	1	0	1	6	3 \pm 1.15	27 \pm 1.53
C2	0	0	1	0	1	5	32	0	5	0	0	0	1	0	6	3 \pm 0.38	22.5 \pm 0
D1	0	0	2	4	0	5	31	0	1	1	1	0	1	0	8	4 \pm 0.58	15.3 \pm 1.86
D2	0	0	1	0	0	1	47	0	5	1	0	0	0	0	5	2.6 \pm 0.33	18.3 \pm 3.29

Class	Plant richness	Tree Cover	Shrub Cover	Herbaceous Cover	Similarity Index
0F	6.6 \pm 2.22	50.3 \pm 9.89	44.6 \pm 10.39	58.9 \pm 1.87	0,31 \pm 0.004
A	7 \pm 2.33	68.1 \pm 21.42	19.3 \pm 11.02	49 \pm 26.36	0,18 \pm 0.031
B	5.6 \pm 1.89	36.5 \pm 16.8	66.7 \pm 20.23	46.1 \pm 23.24	0,28 \pm 0.011
C1	5.6 \pm 1.89	26.3 \pm 21.3	56.6 \pm 7.93	39,6 \pm 13.16	0,35 \pm 0.069
C2	7 \pm 3.5	11.4 \pm 2.96	46.2 \pm 15.51	93.8 \pm 4.21	0,26 \pm 0.127
D1	5.3 \pm 1.78	22.3 \pm 19.23	43.6 \pm 5.3	74.1 \pm 5.97	0,21 \pm 0.042
D2	3 \pm 1	0,17 \pm 0.17	70.3 \pm 8.27	60,96 \pm 18.31	0,38 \pm 0.025

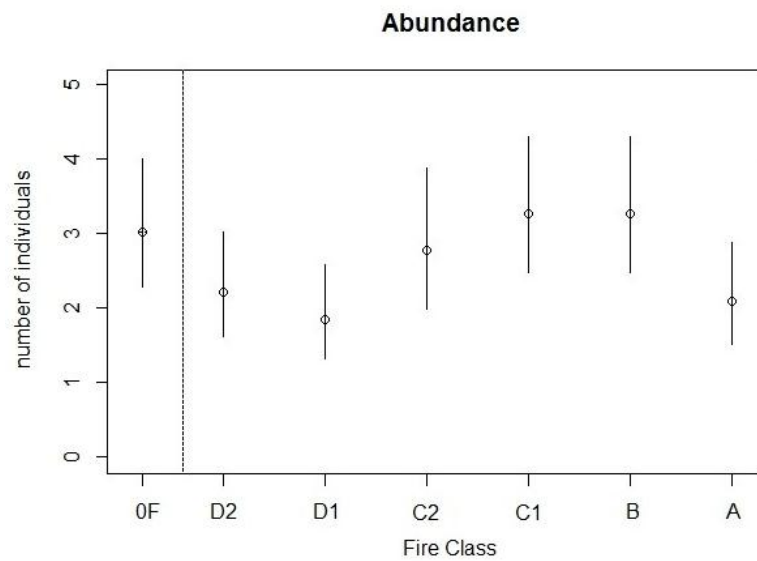


Figure 9 – Reptile abundance according to the different fire classes (D: ≤ 5 years; C: 5-10 years; B: 10-20 years; A: 20-38 years; 0F: ≥ 40 years) Bars represent 95% confidence intervals. Value on the left side of the dotted vertical line represents the control.

Although reptile abundance changes with time since fire, the same does not occur for reptile richness ($p = 0.6247$; Figure 10), although there is a slight increase in species richness < 5 years of post-fire succession (Table VI); nevertheless this is not statistically significant (Table VII).

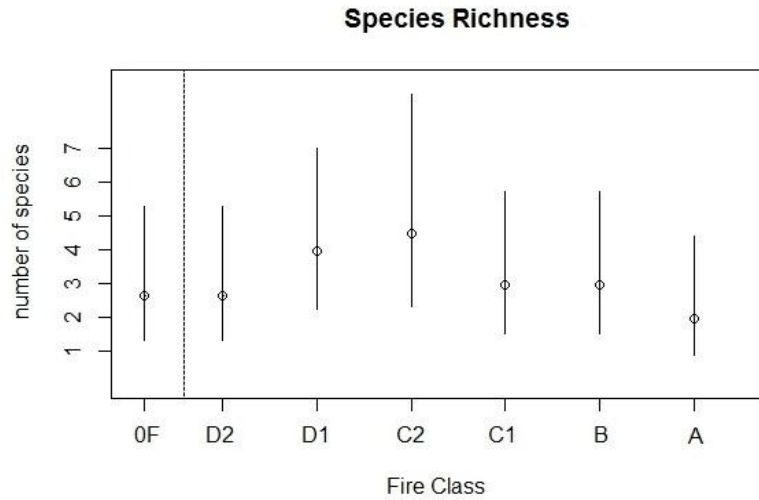


Figure 10 – Reptile species richness according to the different fire classes (D: ≤ 5 years; C: 5-10 years; B: 10-20 years; A: 20-38 years; 0F: ≥ 40 years) Bars represent 95% confidence intervals. Value on the left side of the dotted vertical line represents the control.

Fire recurrence did not significantly affect neither reptile richness nor abundance. Other environmental factors such as vegetation cover (tree, shrubs and herbs) did not influenced reptile abundance and species richness as well. The altitude also seems not to have a roll neither in species richness nor in reptile abundances with no differences found between the study areas (Table VII).

Table VII. Summary of the models tests against reptile’s species richness and reptile abundance.

	Species Richness		Reptile Abundance	
	Deviance	p value	Deviance	p value
TSF	4.39	0.625	19.52	0.003
Number of Fires	0.08	0.782	3.95	0.05
Tree Cover	2.26	0.132	2.35	0.125
Shrub Cover	0.06	0.812	1.34	0.248
Herbaceous Cover	3.26	0.071	3.16	0.076
Altitude	0.32	0.569	0.45	0.733

Habitat Structure

Despite some sampling areas present more plant species than others, when they were compared between them, no significant results were found when related with the dependent variables (reptile abundance and species richness).

Psammodromus algirus abundance

For *Psammodromus algirus*, abundance was positively related to the amount of tree cover ($p = 0.004$; Figure 11) and negatively related to herbaceous cover ($p = 0.0002$; Figure 12) present in an area.

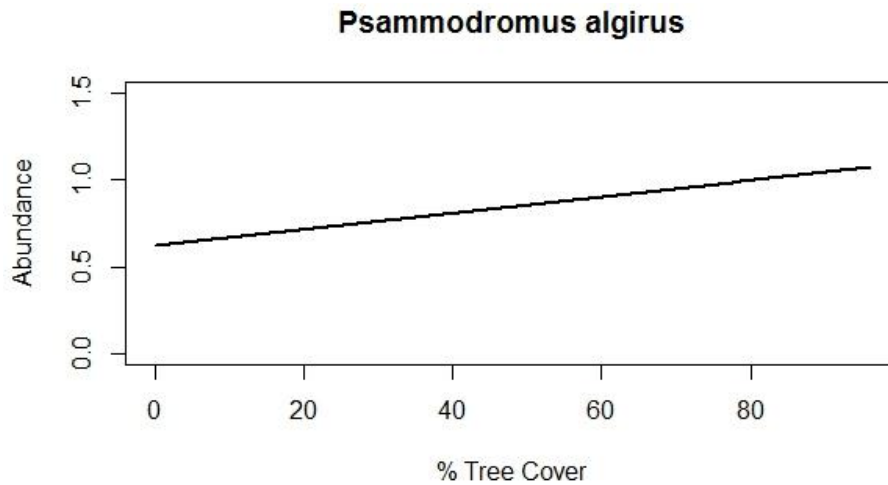


Figure 11 – Abundance of *Psammodromus algirus* in relation to the percentage of tree cover.

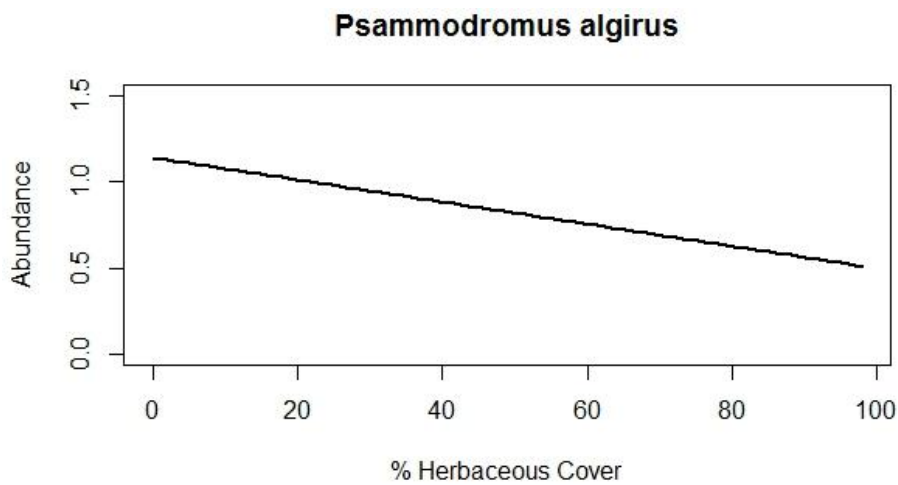


Figure 12 – Abundance of *Psammodromus algirus* in relation to the percentage of herbaceous cover.

The probability of reptile occurrence was positively related to plant species richness ($p = 0.003$) (Fig. 13).

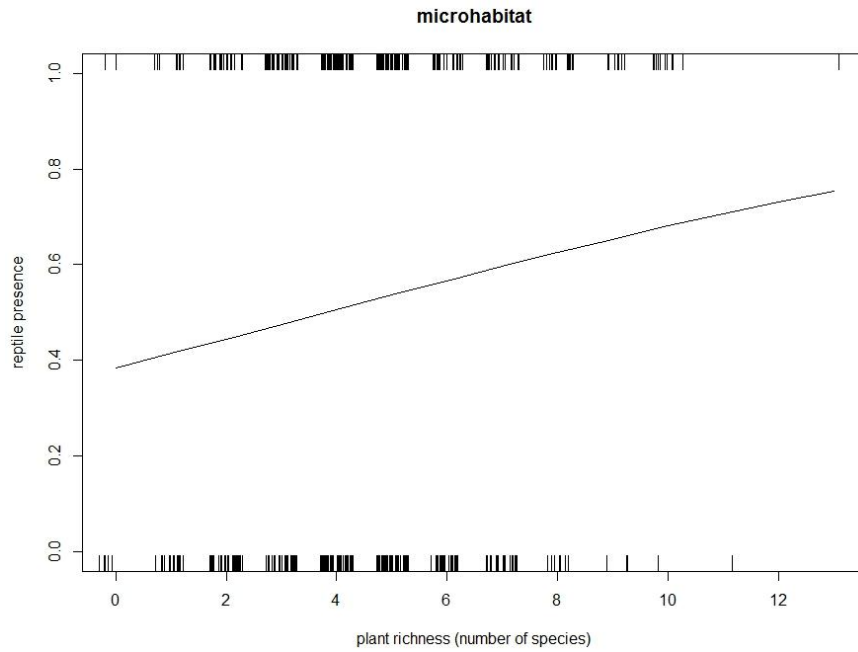


Figure 13 – Presence of reptiles in relation to plant richness. Upper ticks correspond to reptile presence and down ticks to reptile absence.

Discussion

Reptile abundance

Serra da Estrela Natural Park is known to have a fire return interval of ca. 19 years (Oliveira *et al.*, 2012), which suggests that reptile communities are well adapted to the fire regimes of the study area, since the peak on the abundance is around 5 to 20 years after the fire.

There is a weak effect of fire history and vegetation structure on reptile species richness and abundance at the Serra de Estrela. This result confirms that the Mediterranean reptile community studied can present diverse, complex and non-linear responses to fire. However, the statistical analyses detected some significant differences along the post-fire succession, and importantly, these differences in some cases mirror the general trends obtained in the analysis at worldwide scale.

For example, in the first 5 years after fire, reptile abundance was lower than in control transects although recovered in transects characterized by intervals between 5 and 20 years since fire. This lower abundances in Class D may be related with direct mortality (Smith *et al.*, 2001) caused by fire or to migration to areas that have not burned (Driscoll *et al.*, 2012), since conditions immediately after fire would not support reptiles for thermoregulatory and food resources reasons. The higher abundances in Class B can be characterized by a mixture of both scrubs and forest that provide different thermal and structural niches that can comprise higher abundances of reptiles. For Class C, the high abundances might be described with the amount of available prey in replicas composing this class. Agricultural areas present several species of plants, many of them annuals and perennials that produce flowers, thus attracting insects (Potts *et al.*, 2013) which are the main source of food for the majority of reptiles. The

continuous availability of this resource may provide the establishment of high number of reptiles. Reptile abundance was lower in transects with high TSF values (20-38 years without fire). Differences in reptile abundances between areas never burned and those burned 20-38 years ago were not expectable since the vegetation cover was likely recovered after a 20 or more years frame (Keeley et al. 2012). So, other factors are supposed to affect reptile abundances. I argue that the drop on reptile abundance in Class A can be related with the quality of the areas composing this fire class. The transects of this class were constituted by large extension of unnatural agricultural fields and pine plantations, with periodic management (vegetation cut) and this can be the origin on both low species richness and abundance of reptiles found in these areas. The impact of these land-use types has already been documented in other Mediterranean areas (Ribeiro *et al.*, 2009; Azor *et al.*, 2015). If areas belonging to Class A were not subject to high human intervention, this drop of reptile abundance would not be expected. In areas that have never burned (0F Class), reptile abundance is unexpectedly maintained as in the intermediate TSF stages. However, in these areas I have only observed *Chalcides* sp. and *Psammodromus algirus*. *Chalcides* sp. are known to be sensible to habitat modification (Pleguezuelos, *et al.*, 2009) and were practically only found in areas never burned or long unburned. Conversely, Santos & Poquet (2010) reported a decrease in both abundance and reptile diversity in long unburned areas in the Mediterranean habitat, while other studies have found the highest reptile diversity in unburned areas (Santos & Cheylan 2013; Mateus (2014). These differences can be attributed to the pre-fire habitat type, being a pine plantation in Santos and Poquet (2010) study site and natural forest in the latter. This fact suggests an interaction between time-since-fire and pre-fire habitat type for the response of reptile communities to fire.

Species Richness

Although the species richness does not vary across time since fire, the class D1 had the highest total number of species seen. However, for the eight observed species, I only had one casual observation for four of them, mostly snakes, known to be very secretive in habitat use and difficult to observe on the field (Segura *et al.*, 2007). For class C2, I also found high reptile richness, despite this class being constituted by only two replicates. This can be caused by the location of the areas that fall into agricultural lands. Despite the high modification that these areas might be subjected (even knowing my areas seem not to have changed much in approximately one year interval, duration of this study), they are composed by a great diversity of plant species and stone walls that provide shelter for many reptile species. Moreover, these transects also had patches of natural vegetation. At a regional scale, Cunha & Rego (2005) and Ribeiro *et al.* (2009) reported that agricultural areas had negative impact on reptile species richness, and identified them as one of the principal causes to reptile decline. Our results at a local scale suggest that some agriculture activities are compatible with high reptile species richness; for example, agriculture activities developed in a sustainable way, namely, the maintenance of heterogeneous landscapes with important relevance to the semi-natural habitat (Billeter, *et al.*, 2008).

Santos & Cheylan (2013) reported a loss of reptiles after multiple fires, but in PNSE we were not able to statistically identify this. Once again the reasons may be a consequence of the areas sorely modified by man, where repeatedly burned areas might have been farmed soon after fire. This would readily provide vegetation in the recently burned area, and could potentially be colonized sooner, which could explain the increase in abundance and species richness in such short time frame.

Vegetation Structure Effects on Reptile Metrics

Surprisingly, I did not find any effect of the habitat structure on the abundance of reptiles and species richness, in contrast of previous studies (e.g. Driscoll & Henderson, 2008; Santos & Poquet, 2010). However, measurements of habitat structure and the availability of open areas vary among transect classes. The recovery of reptile abundances in intermediate TSF stages can be associated with the openness of the habitat created by fire and with the increase of solar radiation, essential for reptile thermoregulation (Webb & Shine, 2008). I also argue that an increase of food items and shelters provided by low vegetation recovery in the first years after fire would be also responsible of changes in the reptile community. Although for the vegetation cover, no significant results were found for both reptile abundance and species richness, reptile presence (abundance) was positively related with the plant diversity at a local scale. Higher diversity of plant species is generally associated with more complex and stable habitats where a greater number of species can coexist (Bazzaz, 1975). Many of the shrub and herbaceous vegetation produce flowers that can attract pollinators, thus attracting reptiles that feed on them (Muñoz & Arroyo, 2004); moreover, many plants might also provide shelter from predators.

The landscape changes produced by fire with the subsequent increase of scrubland and open areas have been proved to be a major agent for expansion of low-mobility animal groups (e.g. reptiles, Santos and Poquet, 2010). Also, Cunha & Rego (2005) reported that reptiles shown preferences for areas constituted by open forests and scrublands. My results are consistent with these last authors, since the differences in reptile abundances across fire classes were noticeable, and the higher abundances were located in areas mainly composed by a mixture of both scrublands and sparse forests.

Psammodromus algirus

For *Psammodromus algirus*, the percentage of cover seems to be an important variable, since it is positively related with the percentage of tree cover, and negatively related with the percentage of herbaceous cover. This species is known to be associated with more scrub areas (Díaz & Carrascal, 1991), since scrubs generate a continuous sun/shade gradient along which the animals would be able to select their position (Carrascal & Díaz, 1989); however I could not find a relation between shrub cover and *P. algirus*. Nevertheless this species is considered generalist, i.e. it is able to thrive in a variety of different habitats and conditions, and can exploit a wide range of different resources. Moreover, it has been observed in all of the surveyed transects and in Serra da Estrela can be found anywhere in the Natural Park (Lesparre & Crespo, 2008).

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Chapter Three

Fire effects on the diet composition and intraspecific trophic interactions

Introduction

After the fire, many plant species may rapidly resprout or seed, because of the nutrients released from ashes, increasing the vegetative growth (conducting to an increase in the availability of resources), leading to a massive flush of flowering annuals and few perennials, characteristic in fire-prone areas (Bradshaw *et al.*, 2011). This regeneration of floral communities is closely matched by their principal pollinators' regeneration as well (Potts *et al.*, 2003). Indeed, the abundance and richness of herbivore insects has been shown to be positively related to plant recovery in the post-fire succession so, generalist and strong dispersers' insect species dominate early-successional sites and are later substituted by specialists and weaker dispersers along the post-fire succession (Kim & Holt, 2012). Similarly, as plant densities drop following diebacks, insect richness and abundance decreases as well (Kim & Holt, 2012).

The primary food items for most reptiles (except snakes) are invertebrates, mainly arthropods and many of these organisms are dependent feeders of plants. For this reasons, prey availability of reptiles is expected to vary between burned and unburned habitats. Food availability may determine reptile species success/ abundance in a disturbed environment, since fire can indirectly change food resources, leading to less abundance and/ or diversity, which can potentially increase the interspecific and intraspecific competition.

Variation in the trophic ecology of reptile species between burned and unburned sites has been scarcely examined. I have explored how diet vary in the lizard *Psammodromus algirus* in one burned and one unburned locality, and explored how lizards can compete for food by ecological network metrics. I also quantified prey availability in both areas.

Objective

The objective of the study presented in this chapter is to examine how the trophic ecology and interspecific interaction vary with fire using the *Psammodromus algirus* as a model species. Being this species a generalist feeder (Díaz & Carrascal, 1993; Salvador, 2015), I predict that lizards inhabiting unburned areas be more specialized in food resources to avoid intraspecific competition.

Material and Methods

Species description

Psammodromus algirus (Linnaeus, 1758) is a small ground-dwelling lacertid distributed across the Iberian Peninsula, south of France and northeast of Africa. In the Iberian Peninsula, it is an abundant species in most of its range, and presents sexual dimorphism, as well as geographic variation. This species is known to inhabit areas with low vegetation and scrubs, and pine forests, but tend to avoid zones with high densities of herbaceous vegetation (Martín & Lopez, 2002). It is mainly insectivorous, feeding especially on Araneae, Coleoptera and Diptera (Salvador, 2015); however, occasionally it can present cannibalism, if other prey items are scarce (Salvador, 2015).

Collecting pellets

I selected two areas (one never burned and another burned four times) that share the same altitudinal interval (unburned ~750 m a.s.l.; burned ~1000 m a.s.l.) and are relatively close to each other (~15 Km; Figure 14). Twenty-six individuals of the species *Psammodromus algirus* (the most common observed species) were captured in each area in the interval of two days at each area in June 2015. To collect the animals, groups of three to four researchers spread along the surrounding environment of the area (without reaching fire borders) and, with the help of panfish poles with nooses on the end, caught as many individuals as possible. Animals were collected under the permit N° 454 / 2015 / CAPT provided by ICNF. Lizards were measured (snout-vent-length, SVL, and tail length, TL), and sexed, and were then grouped in three categories, namely adult males, adult females and sub-adults, for further analyses. The abdomen of all lizards was gently massaged in order to collect a sample of feces (pellet) for further diet

description. Fecal analysis is an invasive method, with the advantage of not killing the animals; however, many of the soft bodied prey get lost in the digestive process, which can give a misleading perception of the real variety of consumed prey (Carretero, 2004). After these procedures individuals were released in the same areas where they were captured. Each pellet was stored in labeled Eppendorf vials containing ethanol (96%) and carried to the laboratory.

In the laboratory the fecal matter of each pellet was analyzed with a magnifying glass (Leica EZ4HD) and all the prey remains were identified to the Order level and quantified for each lizard, providing a matrix of prey items consumed in both areas.

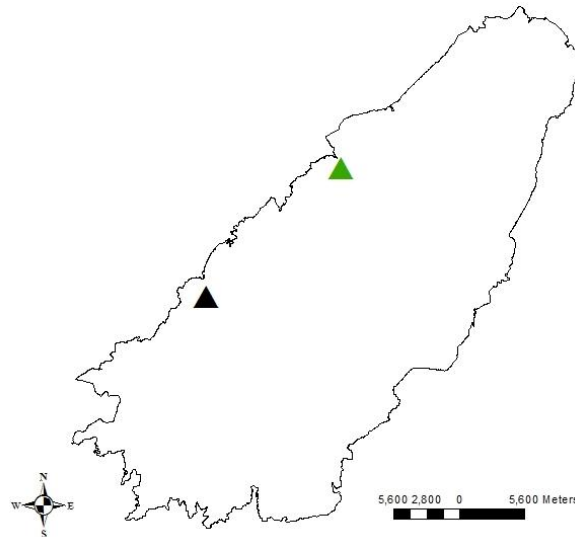


Figure 14 – Overview of the study areas in the Serra da Estrela Natural (green triangle represents the unburned area; the black triangle represents the burned area).

Prey (arthropod) availability

At each of the two sites selected previously, a set of pitfall traps were mounted in order to collect a representative sample of the present arthropod communities, since this is the main prey type for *P. algirus* (Díaz & Carrascal, 1993). Each set of pitfalls were constituted by four buckets (20 cl plastic cups) separated 2 to 3 meters of each

Chapter Three – Materials and Methods

other, placed on the ground with a plastic plate fixed above it, raised 3 to 4 cm of the ground to prevent rain water and other animals from entering in the pitfalls (Fig. 15). Each cup was filled with a liquid composed by one part water and one part coolant, to preserve the insects, and was checked twice after the installation (April and May 2015, respectively). When pitfalls were collected (on the second sampling), one belonging to the burned area was destroyed and was excluded from the analysis. The remaining (burned and unburned areas) were included in the present analysis.

Arthropods were taken from the pitfalls and placed in labeled tubes with alcohol (70%) and carried out to the laboratory. In the laboratory arthropods were identified to Order level and quantified.



Figure 15 – Assembling a pitfall trap in one of the study areas.

Statistical analysis

In order to examine the diet of *P. algirus*, two descriptors were calculated for every individual: prey abundance (minimum number of individual preys consumed, since many remains are lost in the digestive process) and prey richness (number of orders present). These were then compared between the burned and the unburned areas.

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So, a matrix of prey type abundances for each lizard was constructed. This matrix was the basis for further analysis. Differences in diet composition were calculated between pairs of lizards (using abundances of prey types) by the Bray-Curtis similarity index. From the similarity matrix, I performed an ANOSIM test (PRIMER-E, 2001), a non-parametric analysis to test differences between groups of samples that uses permutation/randomization methods on similarity matrix, which gives an R-value by comparing differences between lizards in the unburned and the burned sites. From the similarity matrix, I also ran a Multi-Dimensional Scaling analysis (MDS) in order to visualise the distribution of lizards according to their dietary differences. A similar procedure was also done for checking differences in prey availability between the unburned and the burned sites.

I also constructed a bipartite network to visualize and measure the trophic interaction between lizards. The network was constructed for the unburned and burned populations separately. This approach is an easy way to explore the trophic interactions (i.e. competition) between lizards within a population. In this network, lizards with the same prey type consumed were joined. To measure metrics of the trophic network, I used the software DIETA1 (Araújo *et al.*, 2008) to calculate the index E of interindividual variation (which measures the level of diet variation) and the weighted clustering coefficient C_{ws} (measures the diet clustering). If C_{ws} assumes a positive value between 0 and 1, the population is organized into clusters, which means that individuals have a discrete diet variation. If C_{ws} assumes negative values between 0 and -1, individuals' diets are overdispersed; this means individuals have a more continuous diet variation. E varies from 0 when diets are identical and there is no diet variation, towards 1 as diet variation increases. Then I compared the obtained results from E and C_{ws} with 999 theoretical (null) networks. Null networks are based on a set of randomizations of

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lizard-prey interactions. The software gives the proportion of theoretical networks with higher or lower values than the calculated value. If the null values of E are lower than the obtained values, the group presents high diet variation. The null values represent random diets between individuals within each population. If the null values of E are higher than the obtained values, the group present low diet variation. For the C_{ws} , if null values are higher than the obtained ones, it indicates clustering diet; and if they are lower than the obtained ones, it indicates overdispersion.

Linear regressions were also performed to relate the availability of prey items (data from pitfall traps) with the consumed ones (pellets) in both burned and unburned areas. The analysis was performed in software R (R Development Core Team 2015) with packages “bipartite”, “lme4” and “lattice” (Dormann *et al.*, 2008; Bates *et al.*, 2014; Sarkar, 2008, respectively).

Results

Diet

The data from both areas included fecal samples from 33 adults (16 males and 17 females) and 19 sub-adults. Specifically, in the unburned area I sampled 8 males, 9 females and 9 sub-adults, and in the burned area I sampled 8 males, 8 females and 10 sub-adults. In the unburned area 7 different Orders were detected, being Coleoptera the most predated prey type (54% of prey), whereas in the burned area I only identified 6 prey types, being Coleoptera and Hymenoptera the commonest prey types (23% and 27% respectively) (Table VIII).

Table VIII. Proportion of prey remains and its' respective Orders found in fecal pellets of the study sample of *Psammodromus algirus* in PNSE.

Orders	Abundance	
	Unburned	Burned
Araneae	0.09	0.1
Coleoptera	0.54	0.23
Hemiptera	0.16	0.16
Hymenoptera	0.12	0.27
Thysanoptera	0.01	0
Orthoptera	0.06	0.17
Diptera	0.01	0.06

There were no significant differences between pellets of lizards collected in the unburned and the burned areas neither on the abundance ($F = 0.6295$; $p = 0.4313$) nor on the richness ($F = 0.9961$; $p = 0.3231$). However, diets from lizards belonging to both areas are different ($R = 0.12$, $p = 0.006$). There was few overlap between diets of lizards collected in both areas (Figure 16). We found statistically significant differences on the abundance of consumed prey items by Order (results of the analysis $p = 0.0172$), since *P. algirus* inhabiting the unburned area consumed higher quantities of Coleoptera than the ones on the burned area (Table IX; Figure 17).

Table IX – Linear model output for the consumed prey items found in both study areas. Significant results in bold.

	<u>Estimate</u>	<u>Std. Error</u>	<u>t value</u>	<u>p value</u>
Araneae.B – Araneae.U	0.077	0.254	0.303	1.000
Coleoptera.B – Araneae.U	-0.807	0.254	-3.177	0.011
Diptera.B – Hemiptera.U	0.192	0.254	0.756	0.984
Hemiptera.B – Hemiptera.U	0.115	0.254	0.454	0.999
Hymenoptera.B - Hymenoptera.U	0.654	0.254	2.572	0.071
Orhoptera.B – Orthoptera.U	0.462	0.254	1.815	0.398
Thysanoptera.B – Thysanoptera.U	-0.038	0.254	-0.151	1.000

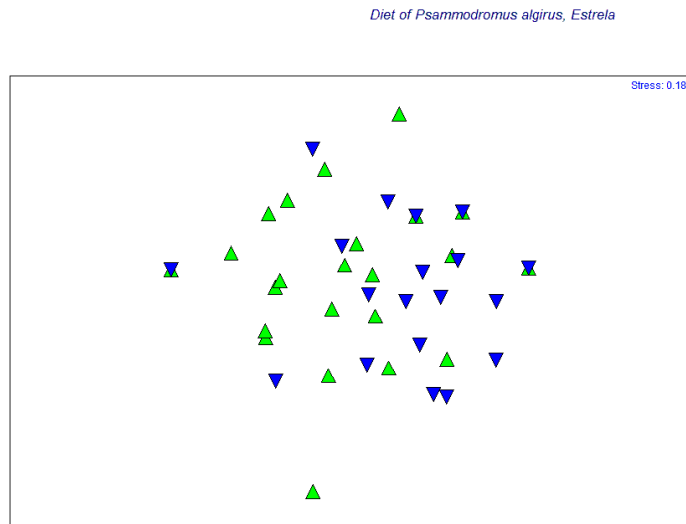


Figure 16 –Multi Dimensional Scale plot with the diets of lizards in burned and unburned areas (Green triangles = burned area; Blue triangles = unburned area).

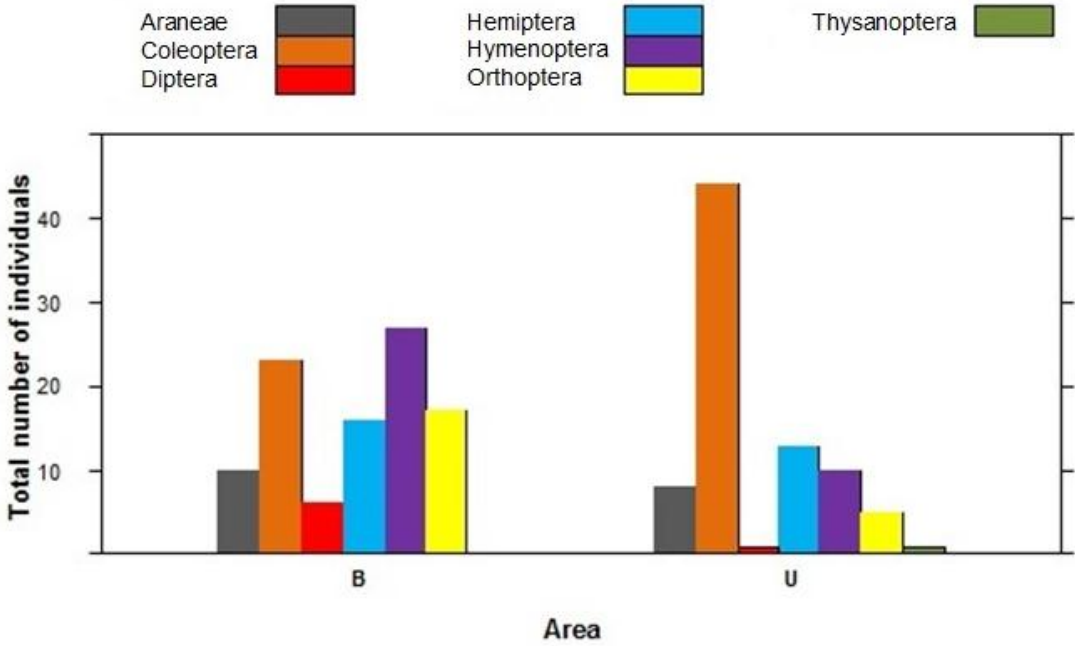


Figure 17 –Total number of individuals of insects (separated by orders) found on the pellets on both areas (B = burned area; U = unburned area).

Ecological networks and interactions predator-prey

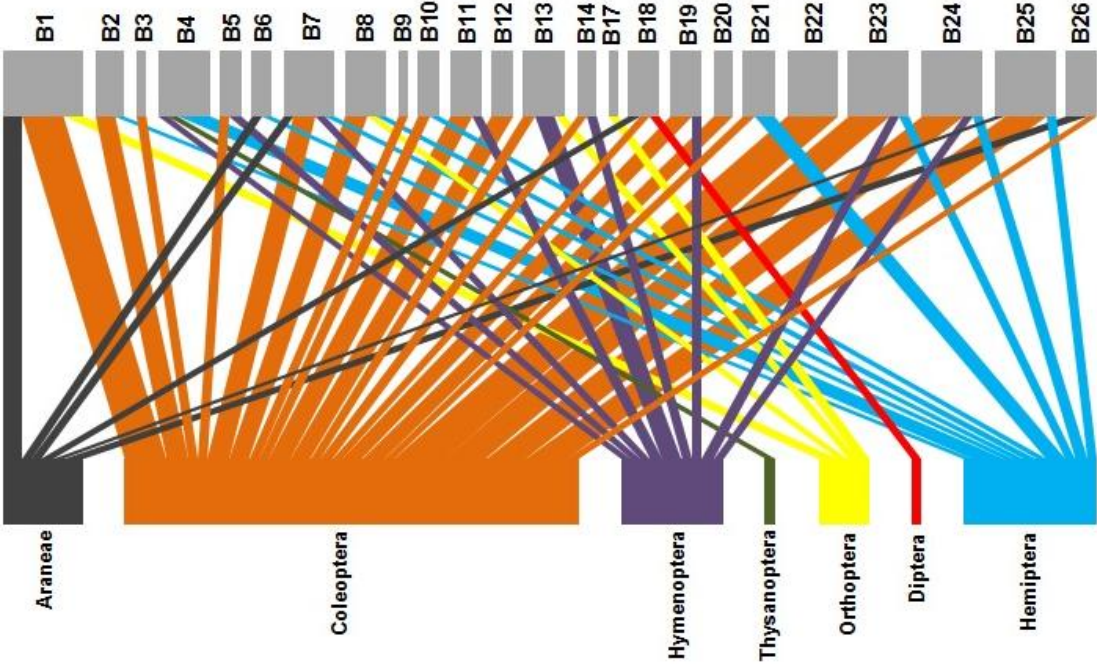


Figure 18 – Ecological network of the unburned area, with the distribution of consumed prey items per individual.

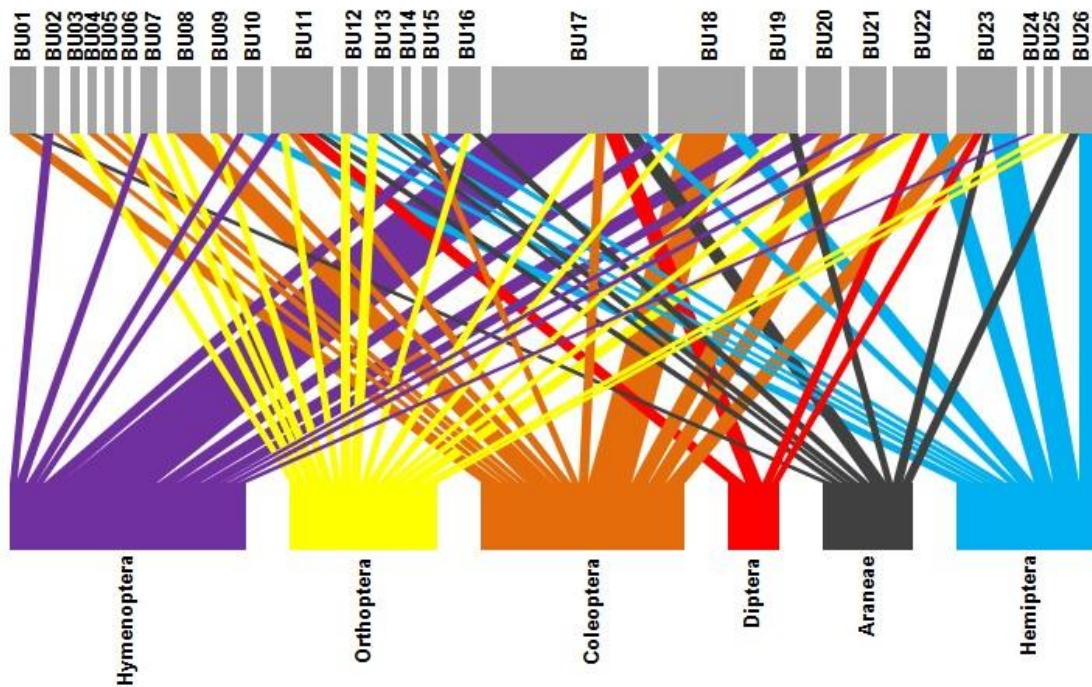


Figure 19 – Ecological network of the burned area, with the distribution of consumed prey items per individual.

The bipartite network on the unburned area (Figure 18) shows Coleoptera as a prey consumed by a high number of lizards, while on the bipartite network belonging to the burned area (Figure 19) individuals seem to be less selective, presenting no pattern in consumed prey. I found that the groups from both areas have high diet variations, although the unburned area present higher value ($E = 0.84$) than the burned area ($E = 0.63$). I also found that these two groups have diet clustering (unburned group $C_{ws} = 0.36$; burned group $C_{ws} = 0.21$). The null model analysis presented $P(E) = 0$ and $P(C_{ws}) = 0$ for the unburned area, and $P(E) = 0.01$ and $P(C_{ws}) = 0$ for the burned area.

9.2. Prey availability

In the pitfall traps, I collected 252 insects (mean insects collected per pitfall ~ 28.4; mean insects collected per sampling event ~ 113.5) belonging to 10 different orders in the unburned area, and 401 (mean insects collected per pitfall ~ 57.3; mean insects collected per sampling event ~ 200.5) belonging to 9 different orders in the burned area (Figure 21). In the unburned area the most common caught prey order was Coleoptera (~ 57%) and in the burned area Diptera (~ 30%) and Hymenoptera (~ 23%) represent more than the half of caught arthropods (Table X). Prey availability (relative abundances per taxon) between both areas was different ($R = 0.402$, $p = 0.001$). A visual confirmed these differences (Figure 20).

Table X. Proportion of collected arthropods and its' respective Orders found in pitfall traps in both unburned and burned areas.

<u>Orders</u>	Area	
	<u>Unburned</u>	<u>Burned</u>
Coleoptera	0.575	0.107
Diptera	0.115	0.307
Araneae	0.167	0.069
Hymenoptera	0.045	0.231
Hemiptera	0.004	0.009
Diplopoda	0.004	0
Lepidoptera (larvae)	0.016	0
Opiliones	0.004	0.002
Collembola	0.063	0.117
Acari	0.008	0.149
Orthoptera	0	0.005

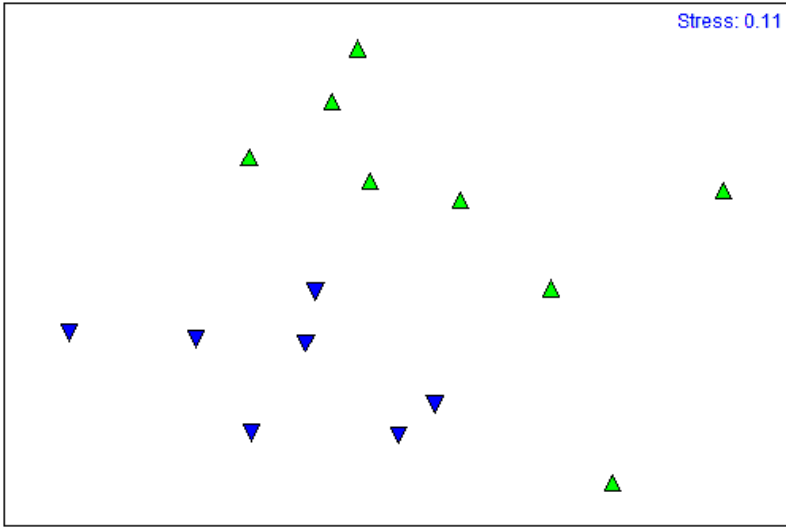


Figure 20 – Multi Dimensional Scale plot of the prey availability between the burned and the unburned areas (Blue triangles = burned area; Green triangles = unburned area).

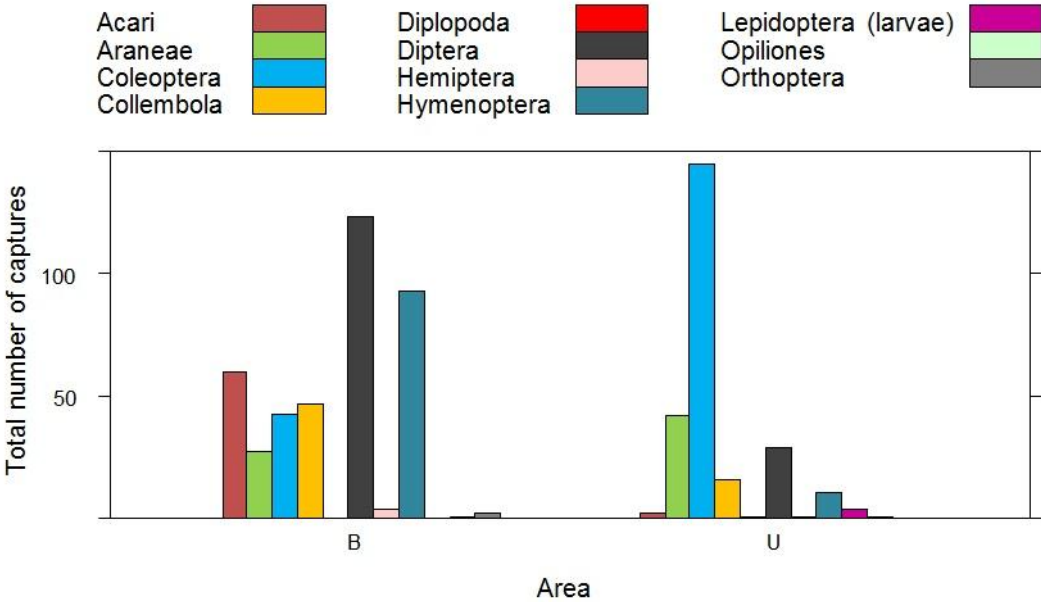


Figure 21 –Total number of individuals of insects (separated by orders) captured in pitfall traps on both areas (B = burned area; U = unburned area).

Comparison between diet and prey availability

There was an overall positive correlation between the abundances of prey types in pellets and in pitfall traps and a significant interaction between prey availability and area (burned vs. unburned) (Table XI) (Figure 22).

Table XI – Linear models between consumed and available preys in pitfalls.

Significant results in bolt.

	<u>Estimate</u>	<u>Std. Error</u>	<u>t value</u>	<u>p value</u>
(Intercept)	5.931	3.107	1.909	0.072
Pitfalls	0.069	0.059	1.158	0.261
Area unburned	-4.864	4.109	-1.184	0.250
Pitfalls:Area unburned	0.205	0.085	2.418	0.025

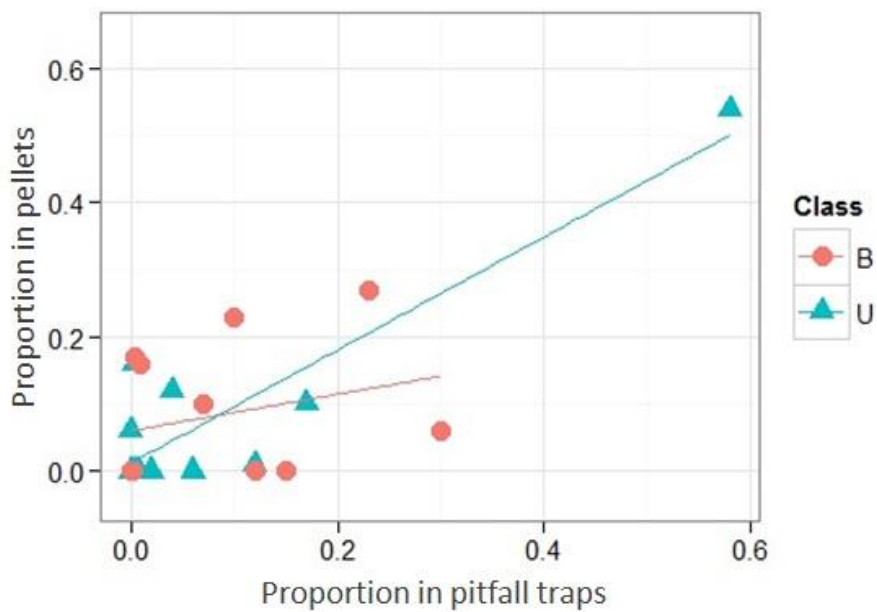


Figure 22 – Correlation between the proportion of consumed prey and the proportion of available prey items (B = burned area (red circles); U = unburned area (blue triangles)).

Discussion

Through the analysis of the data obtained from the fecal pellets and the pitfall traps it was possible to detect significant differences on the diet of the lizards and on arthropod communities inhabiting the two areas (burned and unburned). The availability of prey items varied according to the different areas, as well as the amount of Coleoptera consumed by *P. algirus*. Both factors seem connected and can explain network metrics measured.

According to the insects collected in pitfall traps I argue that the diet from the unburned area is less diverse when compared with the diet of the animals in the burned area due to dominance of Coleoptera (Table VI). Lizards inhabiting the undisturbed area have access to less variety of prey (Figure 17). On the individual diet analysis, these results point to a lower clustering for the lizards composing the burned area, meaning that, despite the diet variation, there is no individual specialization and there is higher competition. The presence of individual specialization has been reported in other taxa (Araújo *et al.*, 2008; Araújo *et al.*, 2010) but in this area perhaps this specialization is not so notable because *P. algirus* has a generalist diet. However, competition may explain why animals in the undisturbed area consumed one specific insect order (Coleoptera) above all others (higher consumption accordingly to higher availability) (Figure 22).

In the burned area, prey availability is greater, and with less dominance of Coleoptera (Table X) in pitfall traps. According to its availability, it is also less consumed by individuals (Table VIII), and this also reflects more diversity of consumed prey (Table IX) traduced by higher diet variation and clustering.

I found some controversial information with some studies reporting an increase in Coleoptera abundance after fire, as a result of an increase in species that feed on injured or dead trees (Saint-Germain *et al.*, 2005; Rodrigo *et al.*, 2008), and others reporting low Coleoptera abundances right after fire probably due to lethal surface temperature, loss of litter and predation (Harris & Whitcomb, 1974; Elia *et al.*, 2012). However, Zou *et al.*, (2013) found a negative correlation for shrub diversity and a positive correlation for herbaceous and woody diversity when compared with Coleoptera abundance. Both of my areas were poor in herbaceous vegetation, but the unburned area was mainly composed by pine plantations, whereas the burned area was only constituted by shrubs. These results are consistent with those found by Zou *et al.*, (2013) since the Coleoptera abundance was higher in the unburned area than in the burned area, which could also explain the differences in consumption between areas. Anyway, differences in the availability of Coleoptera is critical to understand the trophic ecology of *P. algirus* since this is one of the most predated prey in diet studies conducted in other Iberian areas (e.g. Valverde, 1967; Pérez-Mellado, 1982; Román, 1984; Pérez-Quintero, 1997). The results found when I compared the availability with the consumed prey in both areas show a positive relation between availability and the consumed arthropods for the unburned area (Figure 22; particularly evident for Coleoptera). No correlation was found for the burned area (Table XI). Díaz & Carrascal (1991) reported that the abundance of *P. algirus* is correlated with the abundance of prey, and consequentially, the abundance of prey items is correlated with vegetation cover and litter. My results are consistent with those found by these authors, since the lizards on the burned area feed less on Coleoptera, probably because the conditions of the habitat are not yet favorable for higher abundances of these arthropods.

Chapter Three – Discussion

Different levels of intraspecific competition and prey availability may also explain why animals consumed different prey types in the two areas. This suggests that in the burned area, Coleoptera would be consumed in greater quantities, if the abundances were as high as in the unburned area. Nevertheless, lizards seem to have feeding habits adapted to both disturbed and undisturbed areas since their abundances are extremely high when compared with other reptile species of the Serra da Estrela Natural Park.

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Conclusions and Future Perspectives

Reptiles are indeed a taxon with outstanding features, highly adapted, but also highly specific and dependent on a number of environmental factors. Reptile communities may show a negative response immediately after fire (probably due to direct mortality), but recover quickly and neither their richness, nor their abundances seem to be strongly affected by this disturbance. On the one hand, the thermal properties of microhabitats could facilitate reptiles' fast recover in the early stages of post-fire succession whereas, on the other hand, they may also intervene on the latter post-fire stages, where the complexity of the habitat increases, and both the abundance and species richness decreases. For some species (*P. algirus*), the increase in canopy cover and density seem not to affect the overall performance and distribution range, probably because of their generalist habits. Nevertheless, reptile presence is positively related with the diversity of vegetation at a local scale, enhancing the importance of habitat structure to these animals.

Also, in a general way, dietary habits of *P. algirus* appear to be adapted to the different availability of prey. Moreover, these animals do not present individual specialization but, in undisturbed areas, they seem to be more selective over their prey, preying over the most abundant prey type. In disturbed areas the lack of dominance of preferred prey types reflect more diversity of consumed prey and accordingly, more dietary variation and clustering. Still, they present an effective used of food resources in the burned area, suggesting reptiles are well adapted to post-fire conditions.

To conclude, three major assumptions can be taken from this study:

- In fire prone habitats, where most species are well adapted, other factors than fire history may play a more important role on reptile communities;

Conclusions and Future Perspectives

- Reptiles are highly dependent on habitat structure variables;
- Their dietary requirements are adapted to disturbed areas.

Predictions in a future scenario indicate an increase in fire frequency and extension over this next century. Although the effect of repeated fire regimes is scarcely examined, I speculate that changes in fire regimes might put in particular danger the communities that occur in Mediterranean areas (since these areas are prone to burn). A large number of endemic species and especially late colonizers of long-term unburned areas can be severely affected. This study provides new findings that may help to better understand the response of reptile communities to fires, thus improving our knowledge to fill research gaps and to draw conservation strategies to protect this and another taxa. Although there is no “one size fits all” approach, by understanding which species may be more affected by fire, we may be helping also, another species that share the same habitats.

More studies need to be done to better understand the general responses of reptiles to fire. It could be of great importance to examine how biotic interactions may be affected by fire, and how these interactions vary along the post-fire succession. Following this study, the inclusion of a larger number of studies (considering different methodological aspects), or even the inclusion of other variables that can modulate the different responses of reptiles to fire (e.g. number of fires; life-history traits) in the analysis can help to better understand the responses of reptiles to this disturbance. My next step is to include in my analysis some life-history traits for each species, and understand if there are any common characteristics that can allow reptile species to persist or avoid an area affected by fire.

Conclusions and Future Perspectives

Future studies could also include a long-term study (for several years), which would imply several more visits to my replicates in PNSE (in order to track more species and individuals) and would be of great value to examine how the communities behave along the post-fire succession. This together with higher individual captures (to collect sufficient data to perform diet analysis between burned and unburned plots to the other species present in PNSE) would increase our knowledge in this particular matter, and could be a starting point to draw and apply conservation measures to this and other taxonomical groups.

Supplementary Materials

Supplementary Materials I - Fire studies and data used in the analysis (Chapter One). Explanation of codes: Fire

Type: WF (Wildfire), PF (Prescribed Fire), BF (Both fire types (prescribed and wildfire)), NA (Not applicable).

Biomes: ecoregions according to Olson *et al.*, (2001); Location: study's location. Experience method: CT (control-treatment); BAF (before after fire). Group: groups of animals caught in each study (Liz= Lizard; Sn= Snake; TT= turtle). Method sampling: method used in each study sampling. Mean time since fire (months).

References of studies used in the analysis of this chapter.

Supplementary Materials

Ref	Author	Fire Type	Biomes	Location	Rep.	Exp. Method	Group	Method sampling	Mean time since fire (months)
1.	(Ashton & Knipps, 2011)	NA	TCF	North America	R	CT	Liz+Sh	pitfall	134
2.	(Brown & Nelson, 1993)	WF	TMBF	Australia	U	CT	Liz	transects	457
3.	(Brown <i>et al.</i> , 2014)	BF	TGS	North America	U	BAF	Liz+Sh	pitfall	3
4.	(Cano & Leynaud, 2010)	PF	TSGS	South America	U	CT	Liz	pitfall	22
5.	(Costa <i>et al.</i> , 2013)	PF	TSBF	South America	U	BAF	Liz	pitfall	6
6.	(Cunningham <i>et al.</i> , 2002)	WF	DXS	North America	R	CT	Liz	pitfall	22
7.	(Driscoll & Henderson, 2008)	WF	MFS	Australia	R	CT	Liz	pitfall	53
8.	(Driscoll <i>et al.</i> , 2012)	PF	MFS	Australia	R	CT	Liz+Sh	pitfall	51
9.	(Fredericksen & Fredericksen, 2002)	WF	TMBF	South America	U	CT	Liz+Sh	pitfall	48
10.	(Greenberg & Waldrop, 2008)	PF	TBF	North America	U	CT	Liz+Sn+TT	pitfall	10
11.	(Jones <i>et al.</i> , 2000)	PF	TSBF	North America	U	CT	Liz+Sn+TT	pitfall/ transect	48
12.	(Keyser <i>et al.</i> , 2004)	PF	TSBF	North America	U	CT	Liz	pitfall	14
13.	(Langford <i>et al.</i> , 2007)	PF	TSBF	North America	R	CT	Liz+Sn+TT	pitfall/ transect	12
14.	(Legge <i>et al.</i> , 2008)	WF	TSGS	Australia	R	CT	Liz+Sn	pitfall	1
15.	(Letnic <i>et al.</i> , 2004)	WF	DXS	Australia	R	CT	Liz	pitfall	12

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16.	(Mateus <i>et al.</i> , In Press)	WF	MFS	Europe	R	CT	Liz+Sn	transect	74
17.	(Matthews <i>et al.</i> , 2010)	PF	TBF	North America	U	CT	Liz+Sn	pitfall	24
18.	(McCoy <i>et al.</i> , 2013)	PF	TCF	North America	R	CT	Liz+Sn	pitfall	108
19.	(McLeod & Gates, 1998)	PF	TBF	North America	U	CT	Liz+Sn+TT	pitfall	12
20.	(Moseley <i>et al.</i> , 2003)	PF	TCF	North America	R	CT	Liz+Sn	pitfall	6
21.	(Mott <i>et al.</i> , 2010)	PF	TBF	Australia	U	CT	Liz+Sn	pitfall/ transect	27
22.	(Pastro <i>et al.</i> , 2011)	PF	DXS	Australia	R	CT	Liz	pitfall	6
23.	(Pastro <i>et al.</i> , 2013)	WF	DXS	Australia	U	CT	Liz	pitfall	60
24.	(Rochester <i>et al.</i> , 2010)	WF	MFS	North America	U	BAF	Liz+Sn	pitfall	24
25.	(Santos & Cheylan, 2013)	WF	MFS	Europe	R	CT	Liz+Sn+TT	transect	84
26.	(Santos & Poquet, 2010)	WF	MFS	Europe	R	CT	Liz+Sn	pitfall/ transect	150
27.	(Santos <i>et al.</i> , In Press)	WF	MFS	Europe	R	CT	Liz+Sn+TT	transect	172
28.	(Slavchev <i>et al.</i> , 2014)	WF	MFS	Europe	U	CT	TT	transect	12
29.	(Thompson <i>et al.</i> , 2013)	PF	MFS	North America	U	CT	Sn	pitfall	15
30.	(Virkki <i>et al.</i> , 2013)	PF	TSGS	Australia	R	CT	Liz+Sn	pitfall/ transect	11
31.	(Wilgers & Horne, 2006)	PF	TGS	North America	R	CT	Liz+Sn+TT	pitfall	30

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Supplementary Materials II – Generalized Linear Mixed Model’s output for the models in Chapter Two. Significant results are presented in bold.
Visit schedule

Table I. Number of reptiles according to time since last fire

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	0.9753658	0.1094081	8.915	<0.00001
<u>TSF</u>	-0.0002529	0.0046203	-0.055	0.956

Table II. Reptile Abundance according to the different fire classes

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	1.10966	0.14349	7.733	<0.00001
<u>Class A</u>	-0.36623	0.17999	-2.035	0.04188
<u>Class B</u>	0.07697	0.15983	0.482	0.63010
<u>Class C</u>	0.01588	0.14525	0.109	0.91294
<u>Class D</u>	-0.39550	0.15203	-2.601	0.00929

Table III. Species Richness according to fire class

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	0.15415	0.18898	0.816	0.415
<u>Class A</u>	-0.24116	0.28490	-0.846	0.397
<u>Class B</u>	0.03509	0.26495	0.132	0.895
<u>Class C</u>	0.20002	0.23078	0.867	0.386
<u>Class D</u>	0.06899	0.22887	0.302	0.763

Table IV. Number of reptiles according to the number of fires

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	1.08016	0.11125	9.709	<0.00001
<u>Number of Fires</u>	-0.06411	0.03278	-1.956	0.0505

Table V. Species richness according to the number of fires

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	0.18056	0.10829	1.667	0.0954
<u>Number of Fires</u>	0.01268	0.04571	0.277	0.7815

Table VII. Reptile presence in relation to plant diversity

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	-0.46833	0.20357	-2.301	0.02142
<u>Plant Species</u>	0.12245	0.04174	2.934	0.0034

Table VIII –Response of *Psammodromus algirus* over the different vegetation cover types (tree, shrub and herbaceous cover)

	<u>Estimate</u>	<u>Std. Error</u>	<u>z value</u>	<u>p value</u>
<u>(Intercept)</u>	0.619380	0.121937	5.079	<0.00001
<u>% Tree Cover</u>	0.004700	0.001636	2.873	0.0407
<u>(Intercept)</u>	0.599133	0.158902	3.770	0.0001
<u>% Shrub Cover</u>	0.003538	0.002280	1.552	0.1208
<u>(Intercept)</u>	1.139132	0.142537	7.992	<0.00001
<u>% Herbaceous Cover</u>	-0.006426	0.001775	-3.620	0.0003

Supplementary Materials III – Distance where reptiles were observed across the different fire classes. This distance was calculated from the observation point until the middle of the transect (in a perpendicular way).

