



The impact of fire on mammal species: a meta-analysis and the particular case of the Iberian wolf (*Canis lupus signatus*) in Portugal

Sofia Alexandra Soares Lino
Dissertação de Mestrado apresentada à
Faculdade de Ciências da Universidade do Porto em
Ecologia, Ambiente e Território
2015





The impact of fire on mammal species: a meta-analysis and the particular case of the Iberian wolf (*Canis lupus signatus*) in Portugal

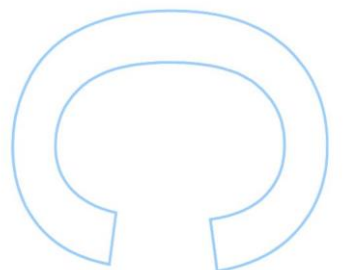
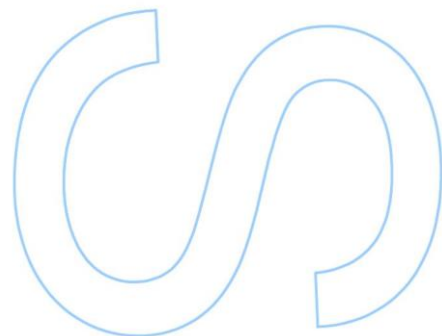
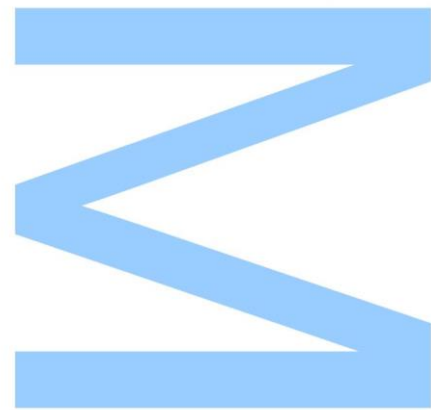
Sofia Alexandra Soares Lino
Mestrado em Ecologia, Ambiente e Território
Departamento de Biologia
2015

Orientador

Francisco Álvares, PhD, Centro de Investigação em Biodiversidade e Recursos Genéticos

Coorientador

Xavier Santos, PhD, Centro de Investigação em Biodiversidade e Recursos Genéticos

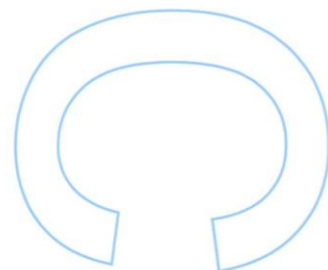
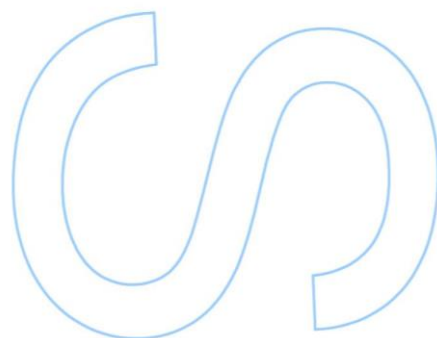
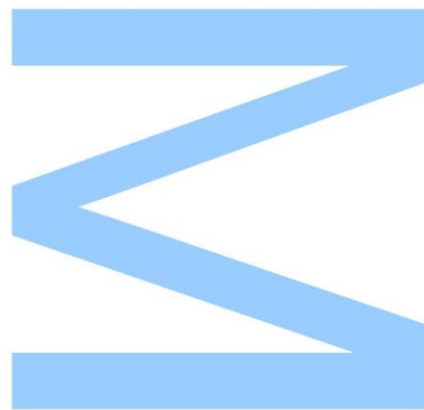




Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, ____ / ____ / ____



Acknowledgements

I would like to express my gratitude to all the people that contributed to the conclusion of this dissertation.

To my supervisors and mentors, Doctors Francisco Álvares and Xavier Santos, I would like to thank the opportunity to conduct this study. Thank you for your constant availability, for taking time between fieldwork and trips to meet up, discuss better approaches and throw some light on statistics. Thank you for your guidance and for keeping me on track.

I would also like to express my gratitude to Doctors Neftalí Sillero and João Torres, who also spent time and effort contributing to this study. Thank you for your availability, help and good humour!

To my friends Paula, Xu, Becas, Zé and João Afonso, thank you for patiently hearing me babble about things I get too much excited with every once in a while, as well as in my moments of stress. Thank you for helping me laugh it off and being there for me!

To Tiago, whom I owe infinite thanks to (and those still wouldn't be enough): We did it! For the past 6 years we've fought the same battles and, despite the struggle and the sleepless nights, I am happy I did it with you. Thank you for being the best buddy in this Master adventure and for making boring assignments and presentations a little easier (I'll never forget the face you've made upon being questioned on the functioning of our microbial fuel cell. AH!). Thank you for the moments of awe and for sharing my worries and the ill-fated anxiety. I wish you the best and wholeheartedly hope you make use of your outstanding skills, in whatever you decide to pursue.

To João, the one that has wisely learned how to deal with me. Thank you for your unconditional support throughout this stage and all the previous, for patiently listening and pretending to understand my fascination for the natural world, and for discussing fears, hopes and wishes, as well as generalized linear models, with me.

To my family, whom I owe the privilege of a high education, I am grateful for all the support and stability, not only along this year, but throughout my life. Above all, to my parents and brother: thank you for making this possible, for strolling with me "looking" for wolves, for sharing the same enthusiasm I have for nature (well, most of you!) and for understanding that there were times that I just couldn't afford to enjoy the sunlight.

Thank you for respecting my decisions and needs and, most of all, for encouraging me to pursue my dreams.

Finally, to the “wolf” that I own, my canine companion which can not read this, but can assuredly understand it: thank you for making my life happier since January, for waking me up in the morning, for (unwillingly) staying at home with me, keeping me company and dragging me to the park. Those were the work breaks that helped boost the writing of this dissertation.

*“‘Would you tell me, please, which way I ought to go from here?’
That depends a good deal on where you want to get to,’ said the Cat.
‘I don’t much care where—’ said Alice.
‘Then it doesn’t matter which way you go,’ said the Cat.
‘—so long as I get SOMEWHERE,’ Alice added as an explanation.
‘Oh, you’re sure to do that,’ said the Cat, ‘if you only walk long enough.’”*

- Lewis Carroll, Alice's Adventures in Wonderland

Abstract

Wildfires are a fundamental factor for the functioning of most ecosystems throughout the globe. However, since fire regimes are predicted to immediately respond to climate change, large-scale changes in their frequency, seasonality and severity are expected. These altered fire regimes can greatly affect biodiversity and ecosystem functioning. Thus, knowing how fire impacts plant and animal communities is a subject of great interest for biodiversity conservation and management. Several studies have addressed this subject, for most animal groups, but there is still a great lack of information. Concerning mammals in particular, few studies have addressed fires' effect on large carnivores, leaving a great gap of knowledge in relation to other trophic levels.

This study aimed to analyse the effect of fires on mammal species by focusing on several scales. First, by means of a qualitative meta-analysis based on literature review, we evaluated patterns of response to fire on mammals in relation to biological traits and eco-geographical variables. A log-linear analysis showed that the variables that fitted the model did not interact with "Response to fire", thus failing to illustrate any significant pattern. In conclusion, our results suggest that mammal's responses to fire are complex and depend on inherent species traits, rather than on global patterns or environmental characteristics. Furthermore, it was possible to confirm that there is a great lack of studies concerning fires' effect on large carnivores. We highlight the need for studies focusing on population trends and responses of large carnivores to fire disturbance.

Thus, as second analysis, this study also evaluated fires' effect on a large carnivore, the Iberian wolf (*Canis lupus signatus*), at both regional and local levels. At regional level, focused on the effects of fires on wolf range patterns, we analysed areas of wolf persistence and extinction in Portugal, considering available presence data from 1980 and 2003, in relation to variables related to fire-history, altitude and land cover. We conducted a t-test, followed by a logistic regression in which «Persistence» and «Extinction» were used as dependent binary variable. Results showed that wolf populations persisted in relatively more elevated and steeper areas, with less forest cover and more shrublands. Concerning fire patterns, wolf populations persisted in areas of high fire incidence (more than 263 000 hectares burned) mostly affected by recurrent medium (occurring every year) and large fires (occurring every four years). At local level, focused on the effects of fires on breeding patterns of wolf packs, we evaluated the effect

of fire-history, altitude and land cover variables on breeding-site selection (in relation to the remain pack territory) and breeding-site use, by considering consecutive years of reproduction. To determine variables related to breeding-site selection we used the Wilcoxon's matched-pairs test, comparing ecogeographical variables between 500 and 7000 meters radius circular buffers around each breeding site. Furthermore, we evaluated wolf behavioural response to fire in terms of breeding-site reuse, a year after fire disturbance, using a Generalized Linear Mixed Model. Results showed that reproductive cores of the breeding-sites (500m buffer) were located in extensive natural areas, at a higher altitude than the remaining pack territory (7000m buffer), but were also subjected to a higher proportion of burnt areas (a mean of 90 hectares burned). Results also showed that the packs reused their breeding-sites in consecutive years, in a similar proportion whether or not a fire event had occurred the year before. In conclusion, results suggest that wolves show a high resilience to fire, as fire events do not seem to have a major role in shaping Iberian wolf occurrence and breeding-site selection and reuse. Wolf populations in Portugal persist and reproduce in highly fire-prone areas, leading to changes in vegetation cover and refuge conditions that may promote behavioral responses and potential negative effects, especially in human-dominated landscapes, where wolves are heavily persecuted.

Keywords

Fire, mammals, meta-analysis, habitat disturbance, post-fire, Iberian wolf, *Canis lupus signatus*, habitat selection, breeding-site, conservation

Resumo

Os incêndios florestais são um fator fundamental para o funcionamento da maioria dos ecossistemas, por todo o mundo. No entanto, uma vez que se prevê uma resposta imediata dos regimes de fogo às alterações climáticas, esperam-se alterações a grande escala em termos de frequência, sazonalidade e severidade dos incêndios. Estes regimes alterados podem afetar significativamente a biodiversidade e o funcionamento dos ecossistemas. Assim, é de grande interesse para a conservação e gestão da biodiversidade conhecer o impacto do fogo nas comunidades de plantas e animais. Vários estudos têm abordado este assunto para a maioria dos grupos animais, mas há ainda uma grande falta de informação. No que diz respeito aos mamíferos, poucos estudos têm abordado o efeito dos incêndios nos grandes carnívoros, havendo uma grande lacuna de conhecimento em relação a outros níveis tróficos.

Este estudo teve como objetivo analisar o efeito dos incêndios sobre espécies de mamíferos, a diversas escalas. Primeiramente, através de uma meta-análise qualitativa com base em revisões bibliográficas, foram avaliados os padrões de resposta ao fogo em relação a características biológicas e variáveis eco-geográficas. A análise linear logarítmica demonstrou que as variáveis que melhor se ajustam ao modelo não interagem com a variável «Resposta ao fogo», falhando assim em ilustrar qualquer padrão significativo. Em conclusão, os nossos resultados sugerem que as respostas dos mamíferos ao fogo são complexas e dependem de características inerentes às espécies, em vez de padrões globais ou características ambientais. Através desta análise foi possível confirmar que existe uma grande falta de estudos sobre o efeito dos incêndios nos grandes carnívoros. Destaca-se, assim, a necessidade de estudos com foco nas tendências de distribuição e resposta dos grandes carnívoros ao fogo.

Assim, numa segunda análise, este estudo avaliou o efeito do fogo sobre o lobo ibérico (*Canis lupus signatus*), tanto a nível regional como local. Na análise a nível regional, com foco nos efeitos dos incêndios sobre os padrões de distribuição do lobo, analisaram-se a persistência e a extinção das populações em Portugal, considerando dados de presença de 1980 e 2003, em relação ao historial de incêndios, altitude e coberto do solo. Realizou-se um *t-test*, seguido de uma regressão logística que utilizou a «Persistência» e «Extinção» como variável dependente binária. Os resultados indicaram que as populações de lobo persistiram em áreas relativamente mais elevadas e íngremes, com menos extensões florestais e mais matos. No que diz respeito aos incêndios, as populações de lobo persistiram em áreas caracterizadas por uma grande

incidência de fogos (com mais de 263 000 hectares ardidos) e afetadas por incêndios recorrentes de média (ano a ano) e grande extensão (de quatro em quatro anos). Na análise a nível local, com foco no efeito dos incêndios sobre os padrões de reprodução das alcateias, avaliou-se o efeito dos incêndios, da altitude e do coberto do solo na seleção (em relação ao restante território) e utilização dos locais de reprodução, em anos consecutivos. Para determinar as variáveis relacionadas com a seleção dos locais de reprodução, utilizou-se o teste de Wilcoxon para amostras emparelhadas, comparando variáveis eco-geográficas entre dois *buffers* circulares de 500 e 7000 metros de raio à volta de cada local de reprodução. Avaliou-se, ainda, a resposta comportamental dos lobos aos incêndios, em termos da reutilização do local de reprodução pelas alcateias, um ano após o incêndio, utilizando um modelo linear generalizado misto. Os resultados mostraram que os locais de reprodução (*buffer* de 500m) estão localizados em extensas áreas naturais e em locais de maior altitude, mas que estão também sujeitos a uma maior proporção de área ardida (uma média de 90 hectares queimados), em comparação com o restante território (*buffer* de 7000m). Os resultados mostraram, ainda, que as alcateias reutilizaram os locais de reprodução numa proporção semelhante, independentemente de ter ocorrido um incêndio no ano anterior. Em conclusão, os resultados de ambas as escalas do estudo sugerem que as populações de lobo demonstram uma grande resiliência em relação aos incêndios, uma vez que estes não tiveram um papel preponderante na distribuição das populações, nem na seleção e reutilização dos locais de reprodução pelas alcateias. As populações de lobo em Portugal persistem e reproduzem-se em áreas altamente propensas a incêndios florestais que podem levar a alterações do coberto vegetal e das condições de refúgio. Estas alterações podem promover efeitos e respostas comportamentais negativos, especialmente em paisagens dominadas pelo Homem, onde as populações de lobo são fortemente perseguidas.

Palavras-chave

Incêndios florestais, mamíferos, meta-análise, perturbação do habitat, pós-fogo, lobo ibérico, *Canis lupus signatus*, seleção do habitat, local de reprodução, conservação

Index

Acknowledgements.....	i
Abstract	iv
Keywords	v
Resumo	vi
Palavras-chave	vii
Index.....	viii
List of Tables	x
List of Figures	xi
List of Acronyms	xiii
General Introduction	1
References	4
Thesis outline.....	8
Chapter I - Global patterns of fires' effects on mammals	9
1. Introduction.....	9
1.1. Objectives.....	11
2. Methodology	12
3. Results	15
4. Discussion	18
References	20
Chapter II - Patterns of fires' effects on Iberian wolf populations.....	22
1. Introduction.....	22
1.1. Fire as a major agent of habitat disturbance in Portugal	22
1.2. The Wolf as a case study.....	24
1.2.1. The Iberian wolf: challenges of living in human dominated-landscapes	26
1.3. Objectives and guiding questions	29
2. Methodology	31
2.1. Study area	31

2.2.	Wolf presence data	31
2.2.1.	Regional level.....	31
2.2.2.	Local level	32
2.3.	Eco-geographical variables.....	33
2.4.	Statistical analysis	38
3.	Results	40
3.1.	Regional level	40
3.2.	Local level.....	43
4.	Discussion	45
4.1.	Regional level	45
4.2.	Local level.....	48
4.3.	Future perspectives	50
	References	52
	General Conclusions and final remarks.....	59
	References	61
	Supplementary Material	62

List of Tables

Table 1. 1 Variables evaluated in the meta-analysis.	13
Table 1.2 - Log-linear analysis results with the best model fit.....	15
Table 1.3 – Marginal table with the cell counts of Body size concerning Response to Fire.	16
Table 1.4 – Marginal table with the cell counts of Feeding habits concerning Response to fire.....	17
Table 2.1 - Independent variables used to assess the effect of fires on wolf distribution in Portugal.	35
Table 2.2 - Independent variables used in wolf home-site eco-geographical characterization.	37
Table 2.3 - Results from the t-test analysis on the effect of eco-geographical variables in wolf persistence and extinction. Significant variables ($P < 0.05$) are indicated in bold...	41
Table 2.4 - Results from the Logit analysis on the effect of eco-geographical variables in wolf persistence. Significant variables ($p < 0.05$) are indicated in bold.	42
Table 2.5 - Wilcoxon test results with means (SD) and matched-pair differences between 500 and 7000 m radius buffers around wolf breeding-sites. Significant results ($p < 0.05$) are indicated in bold.....	43

List of Figures

Figure 0.1 – Fire activity in different ecoregions (index ranging from 0 to 1, unitless). Adapted from Pausas and Ribeiro (2013).	2
Figure 1.1 – Location of the studies (N = 19) evaluated in the meta-analysis. Red circles correspond to studies reporting wildfires, and orange circles correspond to studies reporting prescribed burns.	12
Figure 1.2 - Cell counts of Feeding habits concerning Body size.	17
Figure 2.1 - A fire-prone landscape in northern Portugal, Vieira do Minho (© F. Álvares).	23
Figure 2.2 - A fire in a pine plantation in northern Portugal, Montalegre (© F. Álvares).	23
Figure 2.3 - Wildfire's incidence in southern European countries, between 2001 and 2010. Adapted from Torres (2013).	24
Figure 2.4 - Illustration of the annual life cycle of a wolf pack. Adapted from Carbyn et al. (1993).	26
Figure 2.5 - Evolution of the Iberian wolf distribution in Portugal, during the 20th century, evaluated by records of presence in UTM 10x10 km squares. Adapted from Álvares (2011).	27
Figure 2.6 - Wolf current distribution and location of reproductive packs in the Iberian Peninsula. Adapted from Álvares (2011).	28
Figure 2.7 - A fire captured by camera-traps used for Iberian wolf monitoring in Portugal (© CIBIO/GRUPO LOBO).	29
Figure 2.8 - Areas of Iberian wolf recent Extinction (light blue) and Persistence (dark blue) in Portugal, considering distribution data from 1980 and 2003 at a scale of 10x10 km UTM squares.	32
Figure 2.9 - Location of Iberian wolf breeding-sites in Portugal assessed in this study (N=26).	33

Figure 2.10 - Map of Portugal showing (A) total burnt area extent in hectares; and (B) total number of fires per 10x10 km UTM square, for the time period of 1980-2003. 34

Figure 2.11 - Mean burnt area per year, between 1980 and 2003, in areas of wolf persistence and extinction..... 40

Figure 2.12 - Mean number of fires per year, between 1980 and 2003, in areas of wolf persistence and extinction..... 41

List of Acronyms

©	Copyright
CLC	Corine Land Cover
DGTD	Directorate-General for the Territorial Development
EEA	European Environment Agency
GLMM	Generalized Linear Mixed Model
ICNF	Institute for Nature Conservation and Forests
TSF	Time Since Fire
USGS	United States Geological Survey

General Introduction

Fire is a fundamental factor for the functioning of most ecosystems, promoting variation in habitat structure. Fire molds resource availability and population sizes (Briani *et al.*, 2004; Banks *et al.*, 2011; Plavsic, 2014; Valentine *et al.*, 2014), with several species having co-evolved with intensive fire regimes (Hantson *et al.*, 2014). The climate, weather regimes and fuel availability are constantly changing as a result of natural variability in landscapes, human activities and climate change. These factors, alongside with topography and land cover, are the most important drivers of fire activity in the world (Carmo *et al.*, 2011; Marques *et al.*, 2011; Nunes, 2012; Pereira *et al.*, 2013).

Fires affect the geophysical and biogeochemical properties of soils, influencing carbon and nitrogen cycles as well as nutrients availability and, thus, affecting the microbial composition (Bento-Gonçalves *et al.*, 2012; Mori & Johnson, 2013). They also reduce plant biomass and vegetation cover, replacing trees with shrubs and grasses (Bond *et al.*, 2005). However, fires help to maintain plant species diversity in a natural ecosystem, being the major factor driving vegetation structure, composition and distribution (Adel *et al.*, 2013). The fact that some plant species have distinct reproductive and survival strategies within different fire regimes suggests an adaptation to those particular regimes (Bowman *et al.*, 2009; Pausas & Keeley, 2009; Keeley *et al.*, 2011). The successional stages on vegetation structure following fire activity can affect animal occurrence, due to the differential availability of resources (Haslem *et al.*, 2011; Valentine *et al.*, 2014). Moreover, fire's impact in biotic interactions and abiotic conditions may also influence faunal responses (Haslem *et al.*, 2011).

Wildfires are also recognised as a main agent of habitat disturbance in many biomes throughout the globe (Figure 0.1) (Briani *et al.*, 2004; Shakesby & Doerr, 2006), especially due to the ongoing climate change and anthropogenic influence in fire regimes and activity (Pausas & Keeley, 2014). Prescribed burns are usually used as a tool for landscape management and also with the purpose of reducing the risk of uncontrollable wildfires (Haslem *et al.*, 2011; Valentine *et al.*, 2014).

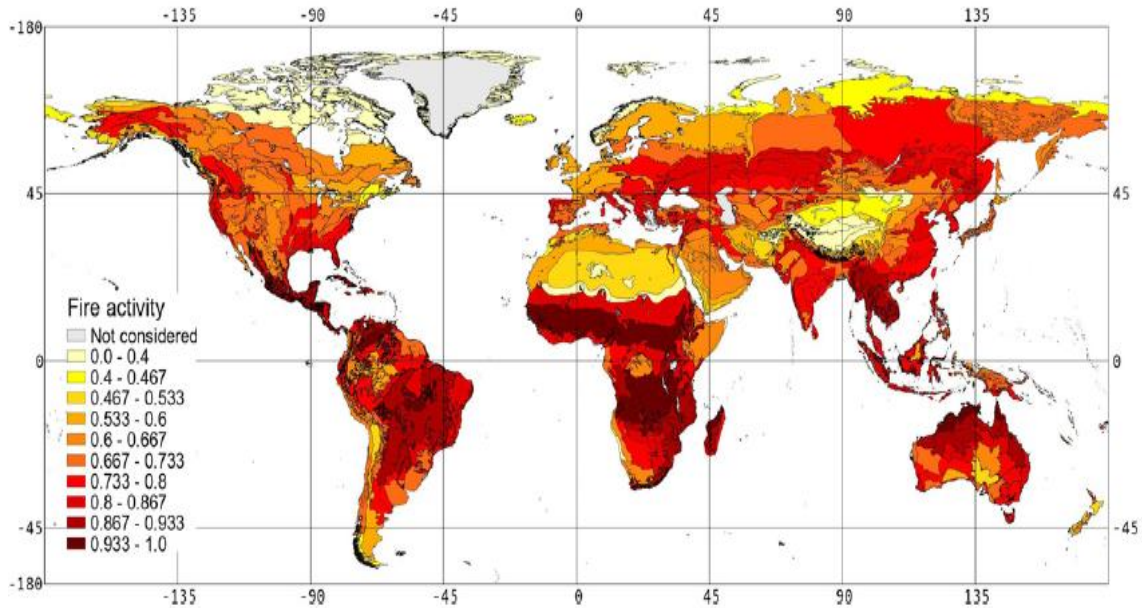


Figure 0.1 – Fire activity in different ecoregions (index ranging from 0 to 1, unitless). Adapted from Pausas and Ribeiro (2013).

Current climate and land cover changes are expected to modify natural fire regimes at a large scale (Brotons *et al.*, 2013). Models of climate change predict that wildfires will increase in frequency, seasonality and severity (Cary & Banks, 2000; Bento-Gonçalves *et al.*, 2012). These new fire regimes can greatly alter biodiversity and ecosystems functioning, having negative impacts on native plant diversity (Shive *et al.*, 2013), potentiating localized extinctions and invasions of exotic plants (Fisher *et al.*, 2009). There is also an expected impact on faunal communities, either by reducing resource availability, increasing competition and predation (Plavsic, 2014), or by direct fire hazard. Thus, it is of great interest to analyse fire's effect on biota, in order to draw management and conservation guidelines for fire-prone regions. There are several studies addressing fire's effect on most animal groups, such as gastropods (Nekola, 2002; Santos *et al.*, 2009), insects (Barrow & Kohen, 2007; Bogusch *et al.*, 2015), amphibians (Ford *et al.*, 1999; Hossack & Corn, 2007), reptiles (Ford *et al.*, 1999; Ashton & Knipps, 2011), birds (Brotons *et al.*, 2004; Valentine *et al.*, 2014) and mammals (Ford *et al.*, 1999; Ballard *et al.*, 2000; Barlow & Peres, 2006; Buchalski *et al.*, 2013; Anderson & Johnson, 2014). However, there is still a great lack of knowledge on ecological and behavioral responses to fire, as well as effects on certain taxonomic groups or trophic levels (Fisher & Wilkinson, 2005; Pastro *et al.*, 2014). For instance, among mammals there is extensive information on rodents and ungulates while, on the other hand, few studies address fire's effect on large carnivores. The gap of knowledge between these groups is critical from an ecological point of view, as predator-prey interactions are

shaped by landscape structure (Gervasi *et al.*, 2013), therefore being important dynamics to account for when analysing mammal responses to disturbance factors, such as fires (Fisher & Wilkinson, 2005).

References

- Adel, M.N., Pourbabaei, H., Omid, A., & Dey, D.C. (2013). Forest structure and woody plant species composition after a wildfire in beech forests in the north of Iran. *Journal of Forestry Research*, 24(2), 255–262.
- Anderson, T.A., & Johnson, C.J. (2014). Distribution of barren-ground caribou during winter in response to fire. *Ecosphere*, 5(10), 1-17.
- Ashton, K.G., & Knipps, A.C.S. (2011). Effects of Fire History on Amphibian and Reptile Assemblages in Rosemary Scrub. *Journal of Herpetology*, 45(4), 497–503.
- Ballard, W.B., Krausman, P.R., Boe, S., Cunningham, S., & Whitlaw, H.A. (2000). Short-term Response of Gray Wolves, *Canis lupus*, to Wildfire in Northwestern Alaska. *Canadian Field-Naturalist*, 114(2), 241-247.
- Banks, S.C., Dujardin, M., McBurney, L., Blair, D., Barker, M., & Lindenmayer, D.B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos*, 120, 26–37.
- Barlow, J., & Peres, C.A. (2006). Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest. *Biodiversity and Conservation*, 15, 985–1012.
- Barrow, L.P., C.L., & Kohen, J.L. (2007). Habitat type influences fire resilience of ant assemblages in the semi-arid tropics of Northern Australia. *Journal of Arid Environments*, 69, 80-95.
- Bento-Gonçalves, A., Vieira, A., Úbeda, X., & Martin, D. (2012). Fire and soils: Key concepts and recent advances. *Geoderma*, 191, 3–13.
- Bogusch, P., Blazej, L., Tryzna, M., & Heneberg, P. (2015). Forgotten role of fires in Central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). *Eur J Forest Res*, 134(1), 153-166.
- Bond, W.J., Woodward, F.I., & Midgley, G.F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525–538.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., et al. (2009). Fire in the Earth System. *Science*, 324, 481-484.
- Briani, D.C., Palma, A.R.T., Vieira, E.M., & Henriques, R.P.B. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation*, 13, 1023–1037.

- Brotons, L., Aquilué, N., de Cáceres, M., Fortin, M.-J., & Fall, A. (2013). How Fire History, Fire Suppression Practices and Climate Change Affect Wildfire Regimes in Mediterranean Landscapes. *PLoS ONE*, *8*(5).
- Brotons, L., Herrando, S., & Martin, J.-L. (2004). Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires. *Landscape Ecology*, *19*, 663–675.
- Buchalski, M.R., Fontaine, J.B., Heady, P.A.I., Hayes, J.P., & Frick, W.F. (2013). Bat Response to Differing Fire Severity in Mixed-Conifer Forest California, USA. *PLoS ONE*, *8*(3), 7.
- Carmo, M., Moreira, F., Casimiro, P., & Vaz, P. (2011). Land use and topography influences on wildfire occurrence in northern Portugal. *Landscape and Urban Planning*, *100*(169-176).
- Cary, G.J., & Banks, J.C.G. (2000). Fire Regime Sensitivity to Global Climate Change: An Australian Perspective. In J. L. Innes, M. Beniston, & M. M. Verstraete (Eds.), *Biomass Burning and Its Inter-Relationships with the Climate System Advances in Global Change Research* (Vol. 3, pp. 233 – 246): Springer Netherlands.
- Fisher, J.L., Loneragan, W.A., Dixon, K., Delaney, J., & Veneklaas, E.J. (2009). Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. *Biological Conservation*, *142*, 2270–2281.
- Fisher, J.T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev*, *35*, 51-81.
- Ford, W.M., Menzel, M.A., McGill, D.W., Laerm, J., & McCay, T.S. (1999). Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management*, *114*, 233-243.
- Gervasi, V., Sand, H.Z., B, Mattisson, J., Wabakken, P., & Linnell, J.D.C. (2013). Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, *23*(7), 1722-1734.
- Hantson, S., Salvador Pueyo, S., & Chuvieco, E. (2014). Global fire size distribution is driven by human impact and climate. *Global Ecol. Biogeogr*, 1-10.
- Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A., Taylor, R.S., et al. (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, *48*, 247–256.

- Hossack, B.R., & Corn, P.S. (2007). Responses of Pond-Breeding Amphibians to Wildfire: Short-Term Patterns in Occupancy and Colonization. *Ecological Applications*, 17(5), 1403–1410.
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., & Bradstock, R.A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16(8), 406-411.
- Marques, S., Borges, J.G., Garcia-Gonzalo, J., Moreira, F., Carreiras, J.M.B., Oliveira, M.M., et al. (2011). Characterization of wildfires in Portugal. *Eur J Forest Res*, 130, 775-784.
- Mori, A.S., & Johnson, E.A. (2013). Assessing possible shifts in wildfire regimes under a changing climate in mountainous landscapes. *Forest Ecology and Management*, 310, 875–886.
- Nekola, J.C. (2002). Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Animal Biodiversity and Conservation*, 25(2), 53–66.
- Nunes, A.N. (2012). Regional variability and driving forces behind forest fires in Portugal an overview of the last three decades (1980-2009). *Applied Geography*, 34, 576-586.
- Pastro, L.A., Dickman, C.R., & Letnic, M. (2014). Fire type and hemisphere determine the effects of fire on the alpha and beta diversity of vertebrates: a global meta-analysis. *Global Ecol. Biogeogr.*, 23, 1146–1156.
- Pausas, J.G., & Keeley, J.E. (2009). A Burning Story: The Role of Fire in the History of Life. *BioScience*, 59, 593–601.
- Pausas, J.G., & Keeley, J.E. (2014). Abrupt Climate-Independent Fire Regime Changes. *Ecosystems*, 17(6), 1109-1120.
- Pausas, J.G., & Ribeiro, E. (2013). The global fire–productivity relationship. *Global Ecol. Biogeogr.*, 22(6), 728–736.
- Pereira, M.G., Calado, T.J., Da Camara, C.C., & Calheiros, T. (2013). Effects of regional climate change on rural fires in Portugal. *Climate Research*, 57, 187–200.
- Plavsic, M.J. (2014). Proximate and ultimate drivers of small-mammal recolonization after fire: microhabitat conditions, rainfall and species traits. *Animal Conservation*, 1-10.
- Santos, X., Bros, V., & Miño, À. (2009). Recolonization of a burned Mediterranean area by terrestrial gastropods. *Biodivers Conserv*, 18(12), 3153-3165.
- Shakesby, R.A., & Doerr, S.H. (2006). Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews*, 74(3-4), 269- 307.

- Shive, K.L., Kuenzi, A.M., Sieg, C.H., & Fulé, P.Z. (2013). Pre-fire fuel reduction treatments influence plant communities and exotic species 9 years after a large wildfire. *Applied Vegetation Science*, 16(3), 457–469.
- Valentine, L.E., Rebecca Fisher, R., Wilson, B.A., Sonneman, T., Stock, W.D., P.A, F., et al. (2014). Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape. *Biological Conservation*, 175, 1-9.

Thesis outline

Considering that wildfires influence faunal communities and there is lack of knowledge concerning some mammal groups, such as large carnivores, this study has two major objectives presented in separate chapters:

Chapter I: Global patterns of fires' effects on mammals

This chapter presents a meta-analysis on fire's effect on mammal species, based on data from an extensive literature review. In order to identify patterns of response to fire, we searched published studies concerning mammal species in post-fire environments and modeled a response according to their persistence or abundance after the fire disturbance, using a log-linear analysis.

Chapter II: Patterns of fires' effects on Iberian wolf populations

This chapter presents an analysis on fire's effect on a large carnivore, using as a model the Iberian wolf population in Portugal, at two geographical scales. At a regional scale, we analysed the effect of fires on wolf distribution trends by considering wolf persistence and extinction areas in Portugal, based in available presence records from 1980 and 2003, in relation to variables related to fire-history, altitude and land cover. At a local scale, we analysed home-site selection by wolf packs, concerning fire-history, altitude and land cover variables. We have also evaluated wolf behavioural responses to fire in terms of breeding-site reuse, a year after fire disturbance.

Chapter I - Global patterns of fires' effects on mammals

1. Introduction

Fires affect the landscape by changing vegetation structure and composition (Torres, 2013), which creates changes in availability of food and shelter for some animal species, affecting local wildlife communities (Allard-Duchêne *et al.*, 2014; Green *et al.*, 2014). Thus, the short and long-term responses of mammal species to fire would be driven by particular life-history traits of species, such as diet, habitat use, territory size and predator-prey interactions. At a short term, fire's effects can be minimised by refuges, which typically occur within the fire boundaries as isolated patches surrounded by burnt areas (Robinson *et al.*, 2013). These refuges may facilitate the persistence of individuals or populations within the burnt area, as they enable the survival of species (Banks *et al.*, 2011; Robinson *et al.*, 2013). There is also a dynamic fire-grazing interaction affecting herbivore mammal species. From the North American grasslands and boreal forests to the African savannahs, ungulates are often documented to preferentially select recently burned areas (Fisher & Wilkinson, 2005; Allred *et al.*, 2011; Green *et al.*, 2014). This fact may be due to forage quality, which is inversely related to time since fire (Allred *et al.*, 2011). Thus, although fire removes the vegetation cover where these animals feed and find refuge on, it may also benefit them at a short-term, by enabling the growth of a more nutritious vegetation, such as grasses (Allred *et al.*, 2011; Silva *et al.*, 2014). This early-successional habitats produce not only shrubs, but a large quantity of seeds as well, which attract ground-foraging herbivorous and granivorous species, such as snowshoe hares (*Lepus americanus*), meadow voles (*Microtus pennsylvanicus*) and jumping mice (*Zapus hudsonius* and *Napaeozapus insignis*) (Fisher & Wilkinson, 2005; Allard-Duchêne *et al.*, 2014). Some authors refer to the increased risk of predation in early-successional post-fire habitats as result of the increased prey visibility, due to the lack of vegetation (de Ronde *et al.*, 2004; Allred *et al.*, 2011). However, this is an arguable topic, as predation risk should be reduced due to the fact that predators are more easily spotted in sparse vegetation (Eby *et al.*, 2014) and, furthermore, due to the slow recovery of predator populations after fire (Torre & Díaz, 2004).

Not all herbivores seek recent burns for feeding. Caribous (*Rangifer tarandus spp*), for example, feed primarily on lichens and were reported to select mature (long

unburned) stands significantly more than younger (recently burned) stands, due to the slow recovery of their main diet (Fisher & Wilkinson, 2005; Joly *et al.*, 2007; Anderson & Johnson, 2014). Also, some small mammal species, such as southern red-backed voles (*Myodes gapperi*), northern flying squirrels (*Glaucomys sabrinus*), red squirrels (*Tamiasciurus hudsonicus*), delicate vesper mice (*Calomys tener*) and Brant's climbing mouse (*Dendromus mesomelas*), are documented to avoid recent burns and select mature habitats instead (Briani *et al.*, 2004; Fisher & Wilkinson, 2005; Zwolak & Foresman, 2007; Plavsic, 2014), due to the canopy heterogeneity that ensures better protection and locomotion (Fisher & Wilkinson, 2005; Zwolak & Foresman, 2007; Allard-Duchêne *et al.*, 2014).

Concerning bat's activity, a study conducted in the Australian tropical savannah, have reported the combined influence of post-fire habitat structure and bats' morphological features in the selection and use of burned areas. The less manoeuvrable and faster-flying species, such as the hoary wattled bat (*Chalinolobus nigrogriseus*), the northern free-tail bat (*Chaerephon jobensis*) and species belonging to the *Saccolaimus* genus, had preferentially selected forest canopies opened by fire (Inkster-Draper *et al.*, 2013).

Despite the abundant literature on the response of mammal species to fire, there are taxonomic biases towards groups, such as Ungulates and Rodents, which are more studied than, for instance, large carnivores. In fact, few studies have addressed the responses of canids, felids or ursids to fire (Fisher & Wilkinson, 2005). One of the few studies on canids, focused on wolf (*Canis lupus*) packs in Alaska. The authors concluded that the analysed packs tended to avoid the burned areas for two years, but returned to use them the third year after fire (Ballard *et al.*, 2000). A study located on the African savannah reported that large carnivores responded to prescribed fires in parallel to syntopic ungulates (Green *et al.*, 2014). This study concluded that African lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and cheetahs (*Acinonyx jubatus*) numbers coincided with the abundance of Thomson's gazelles (*Eudorcas thomsoni*), during the first 120 days after fire. However, since these carnivores were not detected before burning had occurred, the authors could not account for detection probability. Since top-predator species are more vulnerable to habitat disturbance, large carnivores are expected to be negatively affected by fires (Plavsic, 2014), but it is difficult to draw any conclusions for this group of animals based on such few studies. Furthermore, within mammals, this subject lacks an overview of the general patterns that influence responses to fire according to biological traits or biogeographic regions.

1.1. Objectives

The main objective of this chapter was to uncover general patterns of fire's effect on mammal species. This objective has been achieved by a qualitative meta-analysis on data from published papers. By compiling studies on this subject, we aimed at investigating whether mammal species' persistence or abundance in burned areas was governed by ecological species traits, namely taxonomic group, feeding habits and body size. Concerning taxonomic group and feeding habits, herbivores are expected to select recently-burned areas significantly more than long-unburned areas, for feeding on the growing vegetation. Concerning body size, we expected larger bodied animals to select burned areas significantly less than unburned ones, due to their higher locomotion ability which enables them to move away from fire disturbed areas.

2. Methodology

We have initially searched and compiled a total of 27 published studies addressing fire's effect on mammal species. However, only 19 of these studies were retained (Figure 1.1), for holding the data that best suited this analysis. We found several differences between studies, especially concerning methodological approaches to examine mammal responses to fire, according to the taxonomic group that was addressed. These methodological differences preclude to obtain a quantitative measure of relative abundances of species between unburned and burned areas. For this reason, we conducted a qualitative meta-analysis in which all numeric and nominal information was categorized in classes. All data was extracted from the text, figures or tables of the studies, and the following variables were analysed: Taxonomic group (7 classes), Body size (3 classes), Feeding habits (4 classes), Biome (5 classes; the evaluated studies took place in different ecoregions which we reclassified into five biomes based on the classification elaborated by Olson *et al.* (2001)), Fire type (2 classes), and Time since fire (3 classes) (Table 1.1). For each species and published paper, we classified the variable "Response to fire" as Negative, Positive or Equal, according to differences in species persistence or abundance in burned areas compared to unburned ones. A log-linear analysis was performed in order to examine the relationship between the categorical variables. This analysis was performed with a backward elimination procedure, in order to identify which variables fit the model and better interact with the variable "Response to fire".

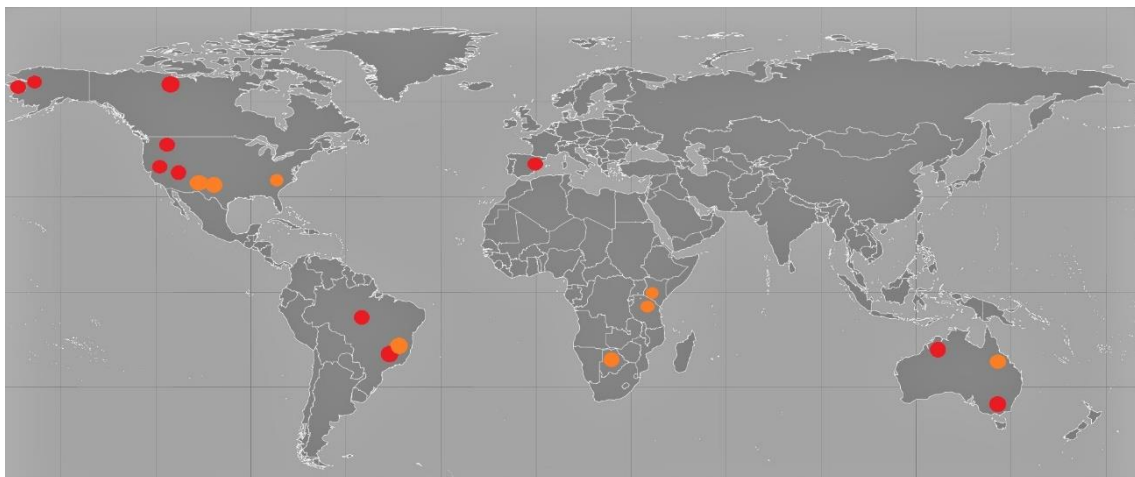


Figure 1.1 – Location of the studies (N = 19) evaluated in the meta-analysis. Red circles correspond to studies reporting wildfires, and orange circles correspond to studies reporting prescribed burns.

Table 1.1 Variables evaluated in the meta-analysis.

	Definition	Classes Definition	N studies	N species
Taxonomic Group	Mammal species classified into seven taxonomic groups	Bats	2	17
		Carnivora	2	4
		Marsupials	3	6
		Primates	1	7
		Rodents	12	53
		Ungulates	5	16
		Xenartha	1	3
Bodysize	Head-Body lenght	Small	14	82
		Medium	4	14
		Large	4	9
Biome	Ecoregions reclassified in five biomes	Arid/semi-arid grasslands and Desert/Xeric shrublands	3	18
		Boreal forests/taiga, Montane grassland and shrublands	4	11
		Mediterranean coniferous and oak forests	2	9
		Temperate broadleaf and mixed forests, grasslands, savannas and shrublands	2	13
		Tropical and subtropical moist broadleaf forests, grasslands, savannas and shrublands	8	60
Feeding habits		Carnivore	6	13
		Herbivore	13	44
		Insectivore	7	29
		Omnivore	12	23
Fire Type		Wildfire	10	50
		Prescribed fire	9	65
TSF	Time since fire	<1 year post-burn	8	45
		1 to 2years post-burn	11	62
		>2 years post-burn	9	48
Response to fire	Mammal species persistence or abundance after fire	Negative presence or abundance in burned areas concerning unburned ones	17	60
		Positive presence or abundance in burned areas concerning unburned ones	16	55
		Equal presence or abundance in burned areas concerning unburned ones	14	39

Despite the compilation of several biological variables, we have neglected several unbalanced ones, due to the small sample size for some classes, as these variables produced marginal tables with several null values. Thus, only suitable variables were analysed. We have retained Body Size, since locomotion ability is a key factor when responding to a disturbance event, and Feeding habits, as main diet may influence species' response and recolonization of post-fire environments. Furthermore, wildfires (Fire Type) and higher times since fire (TSF>1 year) were also analysed as variables in the model.

The statistical analysis was performed using SPSS Statistics 21 software for Windows (IBM Corp., 2012).

3. Results

We evaluated nineteen studies comprising a total of 105 mammalian species. Nine studies were located in North America, three in South America, one in Europe, three in Africa and three in Australia (Figure 1.1). Rodents were the main subject studied in the majority of papers (N = 12), with 53 species analysed. The second most studied group was Ungulates, with 16 species analysed over five studies. On the other hand, very few studies (N = 2) were found concerning Carnivora group which focused only 4 different species. Most studies (N = 14) analysed small sized mammal species (N = 82). Concerning feeding habits, the majority of species were herbivores (N = 44) or omnivores (N = 23), analysed in 13 and 12 studies respectively. Furthermore, the majority of studies (N = 8) was conducted in tropical and subtropical eco-regions, focusing a total of 60 species. Both fire type and time since fire had comparable sample sizes, with similar number of studies and species (Table 1.1).

The backward log-linear analysis indicated that the best fitting model (Table 1.2) consisted of the interactions between Body Size and Feeding habits ($X^2 = 15.581$; $df = 22$; $p = 0.836$). The variable Response to fire did not significantly interact with the variables Body Size or Feeding habits. After removing the studies based on prescribed fires, we observed that these patterns did not vary when only studies based on Wildfires were examined. Likewise, the pattern did not vary when we examined separately studies based on plots with different times since fire, as a proxy for long-term responses ($X^2 = 15.309$, $df = 22$, $p = 0.848$; $X^2 = 11.242$, $df = 22$, $p = 0.971$, for each factor respectively).

Table 1.2 - Log-linear analysis results with the best model fit.

Step ^a		Effects	Chi-Square	df	Sig.
0	Generating Class ^b	Bodysize*Feeding*Response	0.000	0	
	Deleted Effect	1 Bodysize*Feeding*Response	.342	12	1.000
1	Generating Class ^b	Bodysize*Feeding, Bodysize*Response, Feeding*Response	.342	12	1.000
	Deleted Effect	1 Bodysize*Feeding	67.760	6	0.000
	Deleted Effect	2 Bodysize*Response	5.289	4	0.259
2	Deleted Effect	3 Feeding*Response	9.339	6	0.155
	Generating Class ^b	Bodysize*Feeding, Feeding*Response	5.631	16	0.992

Step ^a	Effects	Chi-Square	df	Sig.
Deleted Effect	1 Bodysize*Feeding	68.371	6	0.000
	2 Feeding*Response	9.950	6	0.127
Generating Class ^b	Bodysize*Feeding, Response	15.581	22	0.836
3 Deleted Effect	1 Bodysize*Feeding	68.371	6	0.000
	2 Response	12.112	2	0.002
4 Generating Class ^b	Bodysize*Feeding, Response	15.581	22	0.836

a. At each step, the effect with the largest significance level for the Likelihood Ratio Change is deleted, provided the significance level is larger than 0.050.

b. Statistics are displayed for the best model at each step after step 0.

No significant relationship was found between the biological variables (Body size and Feeding habits) and Response to fire, as cell counts were similar between the three Response classes (Table 1.3 and Table 1.4). We examined separately the response of herbivores to fire and observed that herbivores did not preferably select burned areas ($X^2 = 3.842$, $df = 2$, $p = 0.146$). This result contradicts one of the presented hypotheses.

Table 1.3 – Marginal table with the cell counts of Body size concerning Response to Fire.

		Body size			Total	
		Small	Medium	Large		
Response	Negative	Count	90	6	7	103
		% within Body size	41.5%	28.6%	24.1%	38.6%
	Equal	Count	47	5	11	63
		% within Body size	21.7%	23.8%	37.9%	23.6%
	Positive	Count	80	10	11	101
		% within Body size	36.9%	47.6%	37.9%	37.8%
Total	Count	217	21	29	267	
	% within Body size	100.0%	100.0%	100.0%	100.0%	

Table 1.4 – Marginal table with the cell counts of Feeding habits concerning Response to fire.

		Feeding				Total	
		Carnivore	Herbivore	Insectivore	Omnivore		
Response	Negative	Count	15	37	21	30	103
		% within Feeding	41.7%	32.5%	35.0%	52.6%	38.6%
	Equal	Count	5	30	18	10	63
		% within Feeding	13.9%	26.3%	30.0%	17.5%	23.6%
	Positive	Count	16	47	21	17	101
		% within Feeding	44.4%	41.2%	35.0%	29.8%	37.8%
Total	Count	36	114	60	57	267	
	% within Feeding	100.0%	100.0%	100.0%	100.0%	100.0%	

Both biological variables, Body size and Feeding habits, showed a significant interaction (Figure 1.2). Most species included in the meta-analysis of three major feeding groups, i. e. carnivores, herbivores and omnivores; were of small body size (88.9%, 67.5% and 84.2% respectively). Also, all insectivorous species were small sized. On the other hand, the largest bodied species were herbivorous.

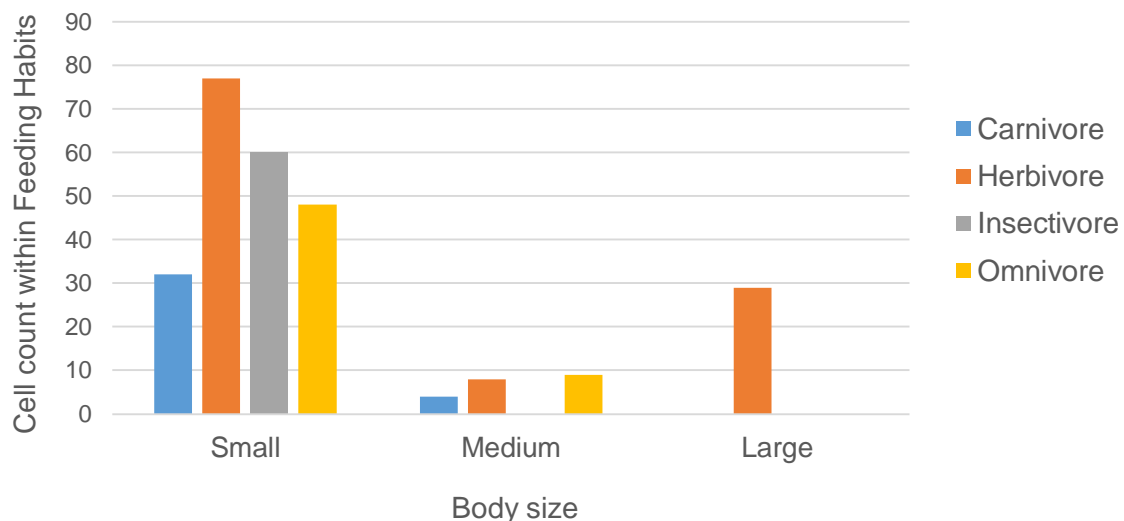


Figure 1.2 - Cell counts of Feeding habits concerning Body size.

4. Discussion

This study performed a meta-analysis on mammal species' response to fire. As a result from the literature review, the lack of studies concerning large carnivores was evident, in opposition to a great amount of studies concerning the response to fire on large ungulates and small mammal species, such as rodents. This bias on the scientific knowledge of fires' effects on wildlife has been already addressed by previous studies (Fisher & Wilkinson, 2005). Thus, it is worth mention that our results reflect the average effects of all studies analysed, and therefore, might present biased conclusions. Nevertheless, our results were in accordance with the review on vertebrates' diversity after fire conducted by Pastro and collaborators (2014). In their meta-analysis, Pastro *et al.* (2014) analysed fire's effects on alpha and beta diversity of some vertebrate groups, by compiling studies on amphibian, reptile, bird and mammal diversity after fire, and analysing patterns for each taxonomic group concerning fire type, time since fire, geographical location and ecoregion. Pastro *et al.* (2014) concluded that taxa and ecoregions were poor predictors of fire's effects on alpha diversity, as denoted by an absence of broad-scale response. Likewise, wildfires did not significantly affect mammal alpha diversity, probably due to their occurrence in a range of geographical locations and ecoregions. Our results, focused only in mammal species, showed that taxonomic group, biome, fire type and time since fire did not explain any pattern of response to fire within mammals. This is contrary to Pastro *et al.* (2014) findings, as they have found patterns of response for birds: wildfires increased the alpha diversity of temperate coniferous birds, while prescribed burns increased their diversity in temperate grasslands and shrublands.

In our analysis, the best fitting model consisted of the interaction between body size and feeding habits, failing to draw a pattern for mammal response to fire. We expected herbivores to select recently burned areas as suggested by some local studies (Allred *et al.*, 2011; Green *et al.*, 2014), but results were not significant to conclude any preference at a large scale. Moreover, our expectation that large bodied mammals would select burned areas significantly less than unburned ones was not verified (Table 1.3). In fact, the analysed large bodied mammals were all herbivorous, thus would be expected to select burned areas more, as well as areas with smaller time since fire, however, as stated before, results were not statistically significant.

Our lack of a general pattern of response may be due to the wide variability of biological traits within mammals, and fire regimes considering a small amount of

available studies. In fact, the small number of studies analysed cover a large number of taxonomic groups (N = 7) and biomes (N = 5), the latter comprising different fire types and times since fire. Also, vegetation type determines fire intensity (Pausas & Keeley, 2009) which, in turn, may have a preponderant effect on its recovery, affecting refuge and feeding conditions (Allard-Duchêne *et al.*, 2014; Green *et al.*, 2014). This variable is difficult to quantify and its absence in the analysis may be precluding a general pattern of response to fire. Among mammals, there is also a high variability in body size, feeding habits and other general life-history traits, which further preclude the identification of a general and large-scale pattern of response to fires. Thus, the effect of fires should be mostly dependent on the scale of the analysis, such as the biological traits of certain species, living in particular environmental conditions. This assumption renders the need for research focused on specific species and locations, and on different levels of behavioural responses to fire besides presence or abundance. In this context, our meta-analysis stresses the need for local studies focusing on population trends and responses of large size carnivores under particular fire regimes.

References

- Allard-Duchêne, A., Pothier, D., Dupuch, A., & Fortin, D. (2014). Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. *Forest Ecology and Management*, 313, 17-25.
- Allred, B.W., Fuhlendorf, S.M.E., D.M., & Elmore, R.D. (2011). Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecology and Evolution*, 1(2), 132-144.
- Anderson, T.A., & Johnson, C.J. (2014). Distribution of barren-ground caribou during winter in response to fire. *Ecosphere*, 5(10), 1-17.
- Ballard, W.B., Krausman, P.R., Boe, S., Cunningham, S., & Whitlaw, H.A. (2000). Short-term Response of Gray Wolves, *Canis lupus*, to Wildfire in Northwestern Alaska. *Canadian Field-Naturalist*, 114(2), 241-247.
- Banks, S.C., Dujardin, M., McBurney, L., Blair, D., Barker, M., & Lindenmayer, D.B. (2011). Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? *Oikos*, 120, 26–37.
- Briani, D.C., Palma, A.R.T., Vieira, E.M., & Henriques, R.P.B. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation*, 13, 1023–1037.
- de Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B., & Geldenhuys, C.J. (2004). Fire Effects on Flora and Fauna. In J. G. Goldammer & C. de Ronde (Eds.), *Wildland Fire Management Handbook for Sub-Sahara Africa* (pp. 77-87): Global Fire Monitoring Center.
- Eby, S.L.A., T.M., Mayemba, E.P., & Ritchie, M.E. (2014). The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology*, 83, 10.
- Fisher, J.T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev*, 35, 51-81.
- Green, D.S., Roloff, G.J., Heath, B.R., & Holekamp, K.E. (2014). Temporal dynamics of the responses by African mammals to prescribed fire. *The Journal of Wildlife Management*, 79(2).
- IBM Corp. (2012). *IBM SPSS Statistics for Windows (Version 21.0)*. Armonk, NY.
- Inkster-Draper, T.E., Sheaves, M., Johnson, C.N., & Robson, S.K.A. (2013). Prescribed fire in eucalypt woodlands: immediate effects on a microbat community of northern Australia. *Wildlife Research*, 40, 70–76.

- Joly, K., Bente, P., & Dau, J. (2007). Response of Overwintering Caribou to Burned Habitat in Northwest Alaska. *Arctic*, 60(4), 401–410.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience*, 5(11), 933-938.
- Pastro, L.A., Dickman, C.R., & Letnic, M. (2014). Fire type and hemisphere determine the effects of fire on the alpha and beta diversity of vertebrates: a global meta-analysis. *Global Ecol. Biogeogr.*, 23, 1146–1156.
- Pausas, J.G., & Keeley, J.E. (2009). A Burning Story: The Role of Fire in the History of Life. *BioScience*, 59, 593–601.
- Plavsic, M.J. (2014). Proximate and ultimate drivers of small-mammal recolonization after fire: microhabitat conditions, rainfall and species traits. *Animal Conservation*, 1-10.
- Robinson, N.M., Leonard, S.W.J., Ritchie, E.G., Bassett, M., Chia, E.K., Buckingham, S., et al. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology*.
- Silva, J.S., Catry, F., Moreira, F., Lopes, T., Forte, T., & Bugalho, M.N. (2014). Effects of deer on the post-fire recovery of a Mediterranean plant community in Central Portugal. *J For Res*, 19, 276–284.
- Torre, I., & Díaz, M. (2004). Small mammal abundance in Mediterranean post-fire habitats: a role for predators? *Acta Oecologica*, 25, 137–143.
- Torres, J. (2013). *Patterns and drivers of wildfire occurrence and post-fire vegetation resilience across scales in Portugal*. (Doutoramento em Biologia), Faculdade de Ciências da Universidade do Porto, Porto.
- Zwolak, R., & Foresman, K.R. (2007). Effects of a stand-replacing fire on small-mammal communities in montane forest. *Can. J. Zool.*, 85, 815-822.

Chapter II - Patterns of fires' effects on Iberian wolf populations

1. Introduction

Wildfires are recognised as a main agent of habitat disturbance, as well as a fundamental factor in landscape evolution, particularly in the Mediterranean basin (Carmo *et al.*, 2011; Silva *et al.*, 2011; De la Rosa *et al.*, 2012; Nunes, 2012). This region is highly prone to the occurrence of numerous fire events due to its climate (rainy and mild winters followed by hot and dry summers), which produce a high amount of fuel-potential biomass (Nunes *et al.*, 2005; Nunes, 2012; Amraoui *et al.*, 2013; Pereira *et al.*, 2013). Concerning the Iberian Peninsula, in particular, burning together with grazing, farming and mining are human-related activities that have performed deep landscape transformation since Mid-Holocene (Carrión *et al.*, 2007). In this context, fire disturbance is expected to have profound effects on the occurrence and responses of wildlife, particularly in species where refuge is a major habitat requirement in fire-prone landscapes already deeply transformed by humans (Carrión *et al.*, 2007; Moreira *et al.*, 2009; Nunes, 2012). This is the case of large carnivores living in Iberian Peninsula, such as the Iberian wolves, making this setting a perfect model to study responses of a large mammal to intensive fire regimes.

1.1. Fire as a major agent of habitat disturbance in Portugal

In Continental Portugal, wildfires have devastated over 100 000 hectares per year, during the past thirty years (De la Rosa *et al.*, 2012; Ferreira-Leite *et al.*, 2013). Due to socio-economic and political changes that occurred in Portugal during the 1960's and 1970's, many rural areas have experienced human population decreases (Nunes *et al.*, 2005; Silva *et al.*, 2011; Ferreira-Leite *et al.*, 2013), leading to the abandonment of agricultural fields and livestock production. These lands were converted into forest plantations, dominated by maritime pine (*Pinus pinaster* Ait.) and eucalyptus (*Eucalyptus globulus* Labill.), or left abandoned to secondary succession processes, turning into shrublands (Lourenço *et al.*, 2012; Nunes, 2012; Machado *et al.*, 2015). Due to the plantation of these highly inflammable tree species, and in absence of livestock to graze the vegetation and labour to clean the fields, the progressive accumulation of fuel

generated a fire-prone landscape throughout the country (Figure 2.1) (Nunes et al., 2005), especially in the districts located in northern Portugal (Figure 2.2) (Nunes, 2012), increasing the risk of wildfires in the last decades (Carmo et al., 2011).



Figure 2.1 - A fire-prone landscape in northern Portugal, Vieira do Minho (© F. Álvares).



Figure 2.2 - A fire in a pine plantation in northern Portugal, Montalegre (© F. Álvares).

According to the Portuguese Institute for Nature and Forest Conservation (ICNF), over the past thirty years, the years of 2003 and 2005 stand out with significantly higher

numbers of burnt forested areas (425 839 and 339 088 ha, respectively). Furthermore, the majority of fires in Portugal are caused by arson or negligence (Nunes, 2012; Amraoui *et al.*, 2013). The significant increase of burnt area in recent decades, complemented with the highest number of ignitions, distinguish Portugal from other southern European countries (Figure 2.3) (Lourenço *et al.*, 2012; Nunes, 2012; Torres, 2013). These factors make wildfires the cause of several economic and ecological losses in Portugal, with human casualties associated (Nunes *et al.*, 2005; Amraoui *et al.*, 2013). According to Pereira *et al.* (2013), a large increase of burnt area in Portugal is expected at the end of the present century.

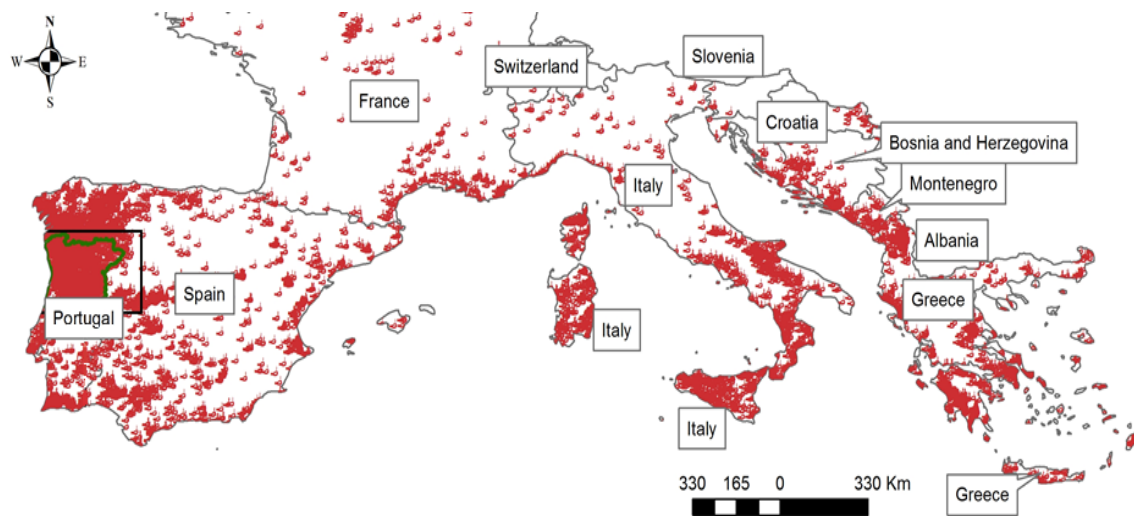


Figure 2.3 - Wildfire's incidence in southern European countries, between 2001 and 2010. Adapted from Torres (2013).

Induced by fires, landscape changes can influence the persistence and distribution trends of animal species. However, impacts on species are not symmetric and some groups, such as large mammals, are expected to experience higher effects due to their low reproductive rate, large spatial requirements, as well as susceptibility to human persecution and disturbance (Cardillo *et al.*, 2005; Chapron *et al.*, 2014). A particular species of mammal highly related to these biological traits is the grey wolf (*Canis lupus* Linnaeus, 1758) (Mech & Boitani, 2003).

1.2. The Wolf as a case study

Wolves are habitat generalists and the most distributed canid species (Mech & Boitani, 2003). They occupy large territories, inhabiting all vegetation types existing in the northern hemisphere, and are able to persist in human dominated landscapes, with

a high heterogeneity of land uses, as far as minimum requirements of refuge and food availability are fulfilled (Mech & Boitani, 2003; Rodríguez-Freire & Crecente-Maseda, 2008). However, wolves are highly vulnerable to human persecution and habitat disturbance, and even for a generalist species there are disturbance thresholds where changes on landscape may limit their survival (Sunquist & Sunquist, 2001).

Wolves tend to particularly avoid human presence and disturbance during the breeding season (Person & Russell, 2009; Eggermann *et al.*, 2010; Llaneza *et al.*, 2011). In Europe, wolves mate during February and March, and use holes, caves and pits as dens (Mech & Boitani, 2003). Pups are born during late April and early May, and until they are around 4 months old, the pack centers its activities in certain areas near the den called the rendezvous sites. These sites are where wolves raise and leave their pups until late summer or early autumn, before they are able to travel with adults and move throughout the pack territory (Figure 2.4) (Álvares, 2011; Iliopoulos *et al.*, 2013; Bassi *et al.*, 2015). Home-sites comprise dens and rendezvous sites. Wolves can use the same home-site for several consecutive years even when suffering direct human disturbance (Argue *et al.*, 2008). However, excessive disturbances around home-sites may lead to their abandonment and to pup translocation (Argue *et al.*, 2008; Iliopoulos *et al.*, 2013). Pup mortality is usually higher during the first six months of age (Kartinen *et al.*, 2010; Iliopoulos *et al.*, 2013; Bassi *et al.*, 2015), therefore home-site selection may have a large impact in wolf pack reproductive success. Breeding-site selection depends on a number of environmental and anthropogenic factors (Person & Russell, 2009) such as elevated and protected areas (Capitani *et al.*, 2006; Bassi *et al.*, 2015) probably due to the decreased risk of human disturbance. Higher altitudes and slopes could however affect adult wolf movements between home-sites and the remain territory (Norris *et al.*, 2002). Regarding land cover, wolves are reported to preferentially locate home-sites in coniferous forest, probably due to its sandy soil (Norris *et al.*, 2002; Theuerkauf *et al.*, 2003), and to avoid urban areas, paved roads (Theuerkauf *et al.*, 2003; Capitani *et al.*, 2006; Kartinen *et al.*, 2010; Bassi *et al.*, 2015) and major water bodies (Norris *et al.*, 2002; Kartinen *et al.*, 2010) in the immediate vicinity of their dens.

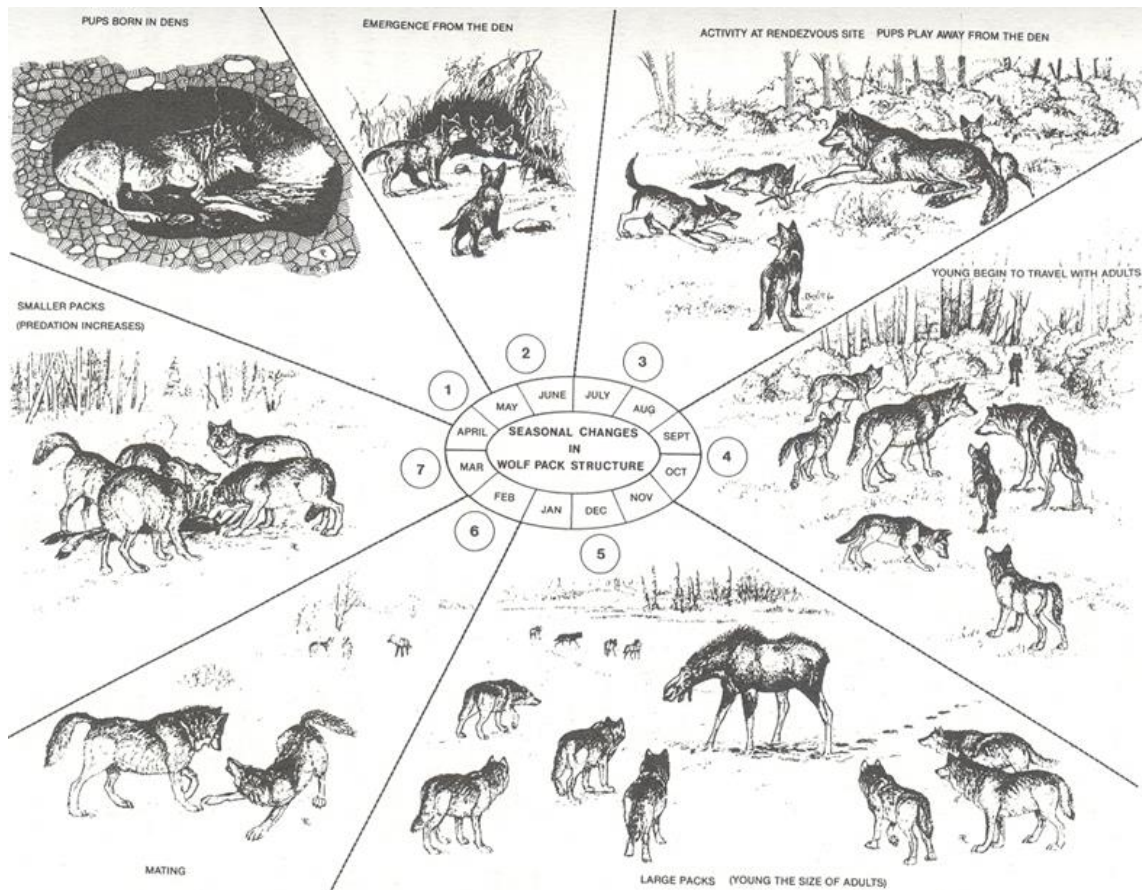


Figure 2.4 - Illustration of the annual life cycle of a wolf pack. Adapted from Carbyn et al. (1993).

1.2.1. The Iberian wolf: challenges of living in human dominated-landscapes

The complex interactions between human, biological and environmental factors affecting wolf distribution patterns and home-site selection, in human dominated landscapes, raise important conservation implications, especially in small, endangered and marginal wolf populations (Rodríguez-Freire & Crecente-Maseda, 2008). This is the case of Portugal, where wolves are protected by law since 1988 and listed as “Endangered” in the Red Book of Vertebrates of Portugal (Pimenta *et al.*, 2005). Iberian wolves (*Canis lupus signatus* Cabrera, 1907) were still present across Portugal around 1930, occurring at coastal lowlands and areas near Lisbon (Figure 2.5). However, around mid 20th century and due to ferocious human persecution, habitat fragmentation, decrease in vegetation cover and food scarcity, wolf distribution drastically declined in south and central Portugal (Petrucci-Fonseca, 1990; Álvares, 2004; Pimenta *et al.*, 2005). In Portugal, wolf breeding packs distribution overlaps with highly humanised landscapes, suggesting that refuge for breeding may represent a limiting factor in wolf range (Pimenta *et al.*, 2005; Eggermann *et al.*, 2010; Álvares, 2011).

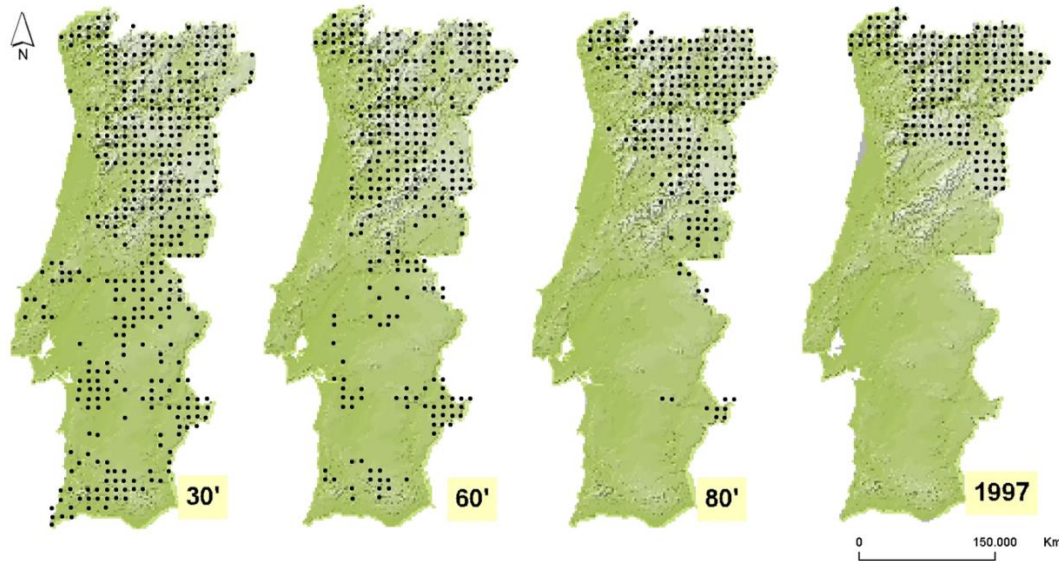


Figure 2.5 - Evolution of the Iberian wolf distribution in Portugal, during the 20th century, evaluated by records of presence in UTM 10x10 km squares. Adapted from Álvares (2011).

Currently, the Portuguese wolf population is estimated in 300 individuals and some of its main threats are habitat disturbance and loss, and population fragmentation, by constraining breeding rates and connectivity (Grilo *et al.*, 2002; Álvares, 2004). These factors are directly or indirectly related to human activities, and have led to population declines and even local extinctions. Wolf range in Portugal overlaps with several municipalities of Minho, Trás-os-Montes and Beira-Alta regions, and is fragmented into two population nuclei, located at north and south of the Douro river, respectively (Grilo *et al.*, 2002; Pimenta *et al.*, 2005). The north Douro population is contiguous with the Spanish population (Figure 2.6), extending to Galicia and Castilla y León, whilst the south Douro population is isolated and shows a high degree of fragmentation (Álvares, 2004; Pimenta *et al.*, 2005).

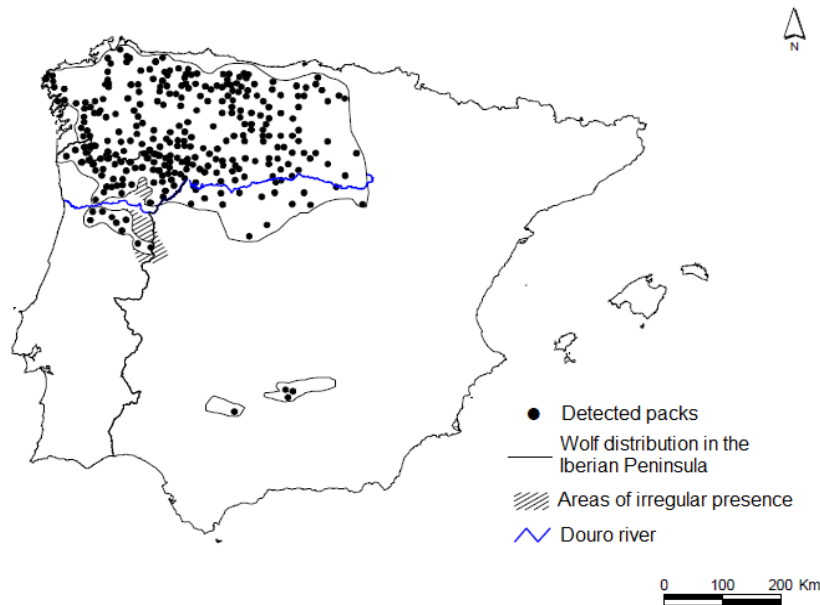


Figure 2.6 - Wolf current distribution and location of reproductive packs in the Iberian Peninsula. Adapted from Álvares (2011).

In this context, the Iberian Peninsula is a good example of wolf resilience in highly humanised and disturbed landscapes. Iberian wolves show positive selection towards areas with low human pressure, such as elevated and less accessible sites that provide refuges, while food availability does not seem to be a limiting factor (Eggermann *et al.*, 2010; Llanaezza *et al.*, 2011). Altitude and land cover have been identified as the main environmental factors influencing current Iberian wolf distribution and represent the main drivers for wolf persistence, despite the species being persecuted for decades (Grilo *et al.*, 2002; Eggermann *et al.*, 2010; Llanaezza *et al.*, 2011). In Iberia, altitude is inversely related to human density, and thus, higher altitudes are selected by wolves to provide refuge and minimise the risk of encounters with people (Llanaezza *et al.*, 2011). Concerning land cover, Iberian wolves tend to be more present in open areas rather than forested ones. In fact, although woodlands could potentially provide refuge and wild prey, Iberian wolves select open areas and shrublands despite being areas where animals tend to be conspicuous (Llanaezza *et al.*, 2011). These areas are often related to higher altitudes and are used as grazing pastures for livestock, which constitutes the main food source for wolves in the Iberian Peninsula (Blanco *et al.*, 1992; Vos, 2000; Álvares & Blanco, 2014).

Simulations based on trends of socio-economic indicators related to human activities and landscape changes (e.g. anthropogenic infrastructures, land use and livestock availability) predict a high risk of extinction for the Portuguese wolf population (Santos *et al.*, 2007). In this context, determining the immediate importance of landscape

changes in wolf distribution patterns and, in particular, the effect of disturbances in their habitat, such as fire activity (Figure 2.7), is crucial to support efficient measures for wolf conservation and management. In fact, great proportions of burnt areas occur in northern and central Portugal (Nunes, 2012), suggesting a wide overlap with wolf range. However, there is poor knowledge concerning fire's effect on wolf populations worldwide (Ballard *et al.*, 2000; Fisher & Wilkinson, 2005) and particularly in Portugal, as no study addressing this topic has ever been made for the Iberian wolf population.



Figure 2.7 - A fire captured by camera-traps used for Iberian wolf monitoring in Portugal (© CIBIO/GRUPO LOBO).

1.3. Objectives and guiding questions

The main goal of this study is to analyse patterns of fire's effect on Iberian wolf populations, at two geographical scales:

- a) At a regional level, considering current wolf range and areas of recent extinction (since 1980), we aimed to assess whether fire was an explanatory variable of wolf persistence and extinction, according to the decreasing trend of wolf distribution in continental Portugal. We examined patterns of fire activity, by comparison to other eco-geographical variables known to affect wolf distribution (Grilo *et al.*, 2002;

Eggermann *et al.*, 2010; Llana *et al.*, 2011). At this scale, we intended to answer the following questions:

- i. What is the fire regime in terms of geographical incidence, burnt extent and number of fires in current wolf range?
 - ii. Does the fire regime explain wolf extinction?
- b) At a local level, we used available data on breeding-site location of eleven wolf packs during consecutive years of confirmed reproduction, in Portugal, at both north and south Douro river. We aimed at evaluating home-site selection considering fire descriptors together with other eco-geographical variables known to affect wolf home-site selection (Capitani *et al.*, 2006; Kaartinen *et al.*, 2010; Iliopoulos *et al.*, 2013; Bassi *et al.*, 2015). Furthermore, we aimed at evaluating wolf behavioural response to fire disturbance, in terms of breeding-site reuse a year after fire occurrence. At this scale, we intended to answer the following questions:
- i. Which are the eco-geographical conditions, including fire descriptors, related to wolf home-site selection?
 - ii. Do wolves select different breeding-sites the year following a fire event?

2. Methodology

2.1. Study area

Continental Portugal is located mainly in the Mediterranean biogeographic region, with the exception of northwest, which is included in the Atlantic region (Costa *et al.*, 1998; Pimenta *et al.*, 2005; ICNB, 2010). Wolf range in Portugal corresponds to areas of moderate human density with less than 50 inhabitants per km², with the majority of the areas (60%) accounting less than 25 inhabitants per km² (Pimenta *et al.*, 2005). In these areas, wolves are found mostly above 400 meters of altitude, with the majority of the packs being located above 700 meters (Pimenta *et al.*, 2005). The climate is temperate, with a mean annual temperature ranging from 7°C to 16°C (ICNB, 2010), and with an average annual precipitation ranging from 400 mm at the eastern lowlands to 2800 mm in the western mountains (Carmo *et al.*, 2011). Land cover is dominated by agricultural and agro-forestry areas alternating with mixed forests and shrub patches (Nunes *et al.*, 2005; Pimenta *et al.*, 2005). Within wolf range, wild prey populations are scarce but there is a great availability of livestock, especially in the mountainous areas, which comprises the main food resource for wolves (Álvares, 2004; Pimenta *et al.*, 2005).

2.2. Wolf presence data

2.2.1. Regional level

Wolf presence data was available at 10x10 km UTM grid based on wolf distribution assessments at a national level, conducted in 1980 (Petrucci-Fonseca, 1990) and 2002/2003 (Pimenta *et al.*, 2005). Due to the lack of data from fire-related and eco-geographical variables respecting the decades before 1980, it was not possible to consider the wolf distribution data from previous years. The areas of wolf persistence, extinction and absence were assessed for each square by taking into account the differences between both time periods, 1980 and 2002/2003:

- (1) Persistence: wolf presence detected in both periods;
- (2) Extinction: wolf presence detected in 1980, but not in 2002/2003;
- (3) Absence: no presence detected in any period.

Wolf occurrence was detected in 267 squares (persistence N = 207; extinction N = 60), consisting in 30% of the entire Portuguese territory (Figure 2.8). Single squares with no record of wolves in 1980 which were, nevertheless, located within the area of

persistence and adjacent to presence squares, were considered as presences (N=39), as they represent less than the average size of pack home ranges and therefore were assumed to result from lack of sampling. Likewise, areas of occasional wolf presence (considered as “probable” presence in Pimenta *et al.* (2005)) were considered as areas of wolf persistence in the analysis (N=104). Wolves have faced a drastic reduction of their population numbers during the 20th century, with high extinction rates in each decade (Petrucci-Fonseca, 1990; Álvares, 2004; Pimenta *et al.*, 2005). In fact, few years before 1980 wolves were still present in large areas classified as Absence in this study. For this reason, absence squares were not considered for statistical analysis.

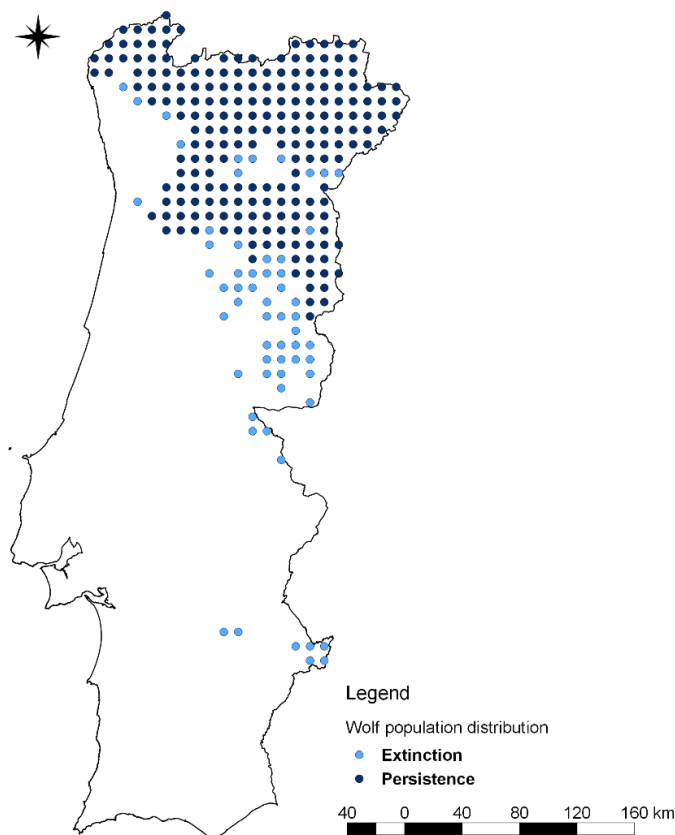


Figure 2.8 - Areas of Iberian wolf recent Extinction (light blue) and Persistence (dark blue) in Portugal, considering distribution data from 1980 and 2003 at a scale of 10x10 km UTM squares.

2.2.2. Local level

Data on wolf breeding was available from continuous wolf population monitoring conducted by CIBIO since 1996 (Álvares, 2011; Nakamura *et al.*, 2013; Roque *et al.*, 2013), involving visual and acoustic detection of wolf pups in their rendezvous-sites (pup-rearing areas) during breeding season, from July to September (Álvares, 2011). We have assessed a total of 26 breeding-sites from eleven packs in which reproduction had

occurred in consecutive years, nine of them located in north Douro wolf population (Peneda-Gerês National Park, covering the districts of Braga, Viana do Castelo and Vila Real) and two in south Douro wolf population (mountain ranges in the district of Viseu) (Figure 2.9). However, different numbers of sites were selected for home-site selection (N = 12) and breeding-site reuse (N = 22) analysis.

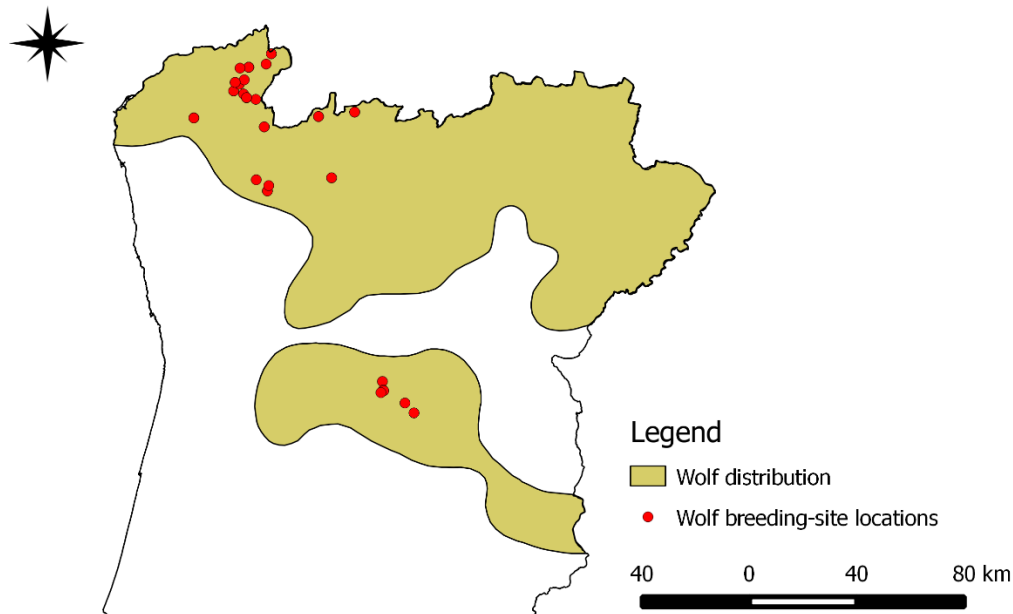


Figure 2.9 - Location of Iberian wolf breeding-sites in Portugal assessed in this study (N=26).

2.3. Eco-geographical variables

Three types of variables were considered for the analysis: fire-history, altitude and land cover (Table 2.1). These two latter types are reported in previous studies as the main drivers for wolf occurrence (Grilo *et al.*, 2002; Eggermann *et al.*, 2010; Llaneza *et al.*, 2011) and for home-site selection (Capitani *et al.*, 2006; Bassi *et al.*, 2015). Thus, these variables were included to assess whether other eco-geographical traits besides fire-history could explain wolf distribution trends and home-site selection. There are some differences in the assessed eco-geographical variables regarding both study levels.

2.3.1. Regional level

i. Fire-history

The fire dataset for continental Portugal covering the time period between 1975-2009 was obtained from an Atlas of fires in Portugal (Pereira & Santos, 2003; Oliveira *et*

al., 2012) and was kindly provided by the leading researcher of that project, José M.C Pereira from Instituto Superior de Agronomia (pers. comm., September 2014). However, only fires concerning the period from 1980 to 2003 were considered in the analysis, corresponding with the data period related to wolf distribution. According to Marques *et al.* (2011), small fires (<50 ha burnt) were the most abundant ones in Portugal, for the time period between 1987-1994 and 2000-2004, nevertheless, they only represented 0.5% of the total surface of a 10x10 km UTM square. Thus, we considered that such small burnt areas would not have important impacts on wolf presence within a 100 km² square. Consequently, each UTM square was characterised according to total burnt area and number of fires (Figure 2.10) and time since fire, taking into account all fires and those larger than 50 and 500 ha, respectively (i.e. one fold higher than the 50 ha threshold) (Table 2.1). Concerning time since fire, we neglected those corresponding to a burnt area smaller than 50 hectares, for the stated above reason.

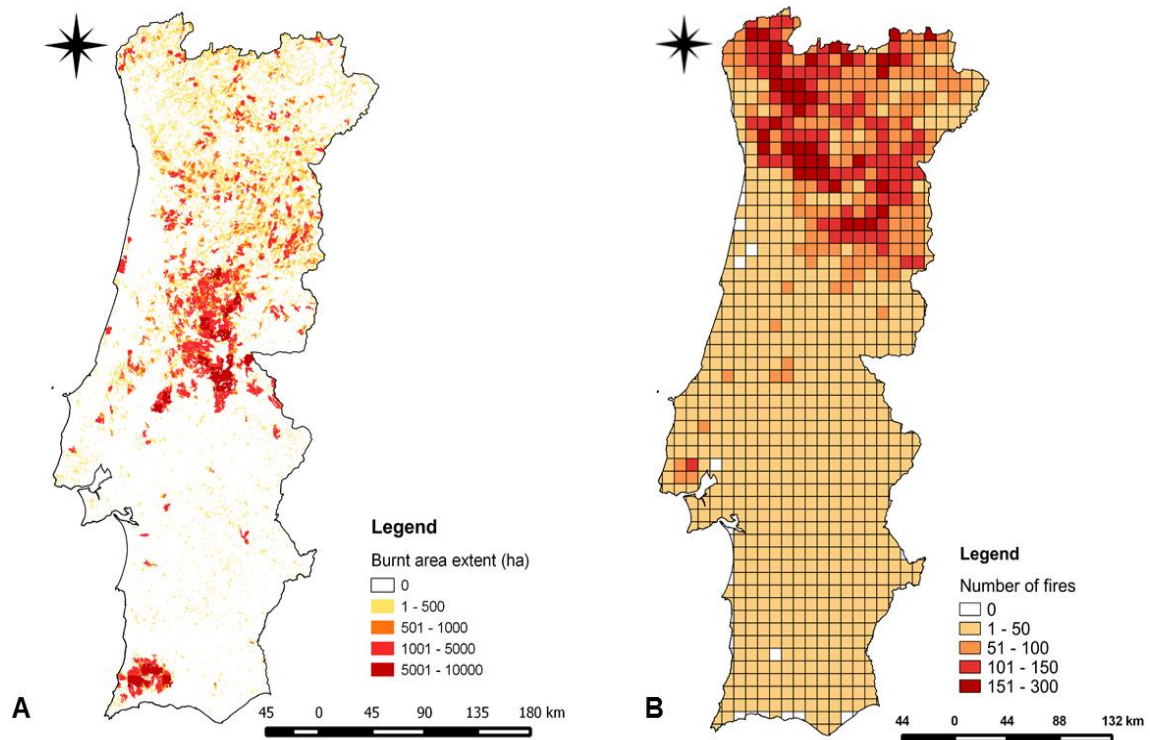


Figure 2.10 - Map of Portugal showing (A) total burnt area extent in hectares; and (B) total number of fires per 10x10 km UTM square, for the time period of 1980-2003.

ii. Altitude

Altitude values (maximum, minimum, mean and range) were calculated for each 10x10km grid-cell (Table 2.1), from a raster file obtained from the Shuttle Radar Topography Mission (SRTM), provided by the U.S. Geological Survey (USGS, 2006).

Range altitude was calculated from the difference between the maximum and minimum values of altitude, as a potentially more informative and complementary variable than the mean value.

iii. Land cover

Land cover data was accessed from the Directorate-General for the Territorial Development (DGTD) website and obtained from Corine Land Cover (CLC) 2006 map of continental Portugal. Thirty two land classes were primarily considered, and were then reclassified into five land use classes (see Table 1, Supplementary Material), on regard of the vegetation structure, namely: Urban Areas, Agricultural Land, Forests, Shrubland and Open Areas (see Figure 3 and Figure 4, Supplementary Material). This criteria is considered relevant for the Iberian wolf occurrence since it reflects favourable conditions for wolf refuge according to previous studies (Grilo *et al.*, 2002; Cayuela, 2004; Eggermann *et al.*, 2010). Area extent (in hectares) of each land cover type was calculated for each 10x10 km grid-cell (Table 2.1). Pielou's evenness index (Heip *et al.*, 1998) was calculated as a measure of habitat heterogeneity, to ascertain if the different land cover types occur in the same proportion, being numerically even, in each square. Evenness values vary from 0 (variation in proportion) to 1 (no variation, even).

Table 2.1 - Independent variables used to assess the effect of fires on wolf distribution in Portugal.

Variable group/class	Variable name	Description	Data source
	Burn_Total	Total burnt area (in hectares)	
	Burn+50HA	Burnt area with more than 50 ha burned (in hectares)	
	Burn+500HA	Burnt area with more than 500 ha burned (in hectares)	
	Nfire_Total	Total number of fires	
Fire-history	Nfire_+50HA	Number of fires with more than 50 ha burnt	JMC Pereira (pers. comm.)
	Nfire_+500HA	Number of fires with more than 500 ha burnt	
	TSF_+50HA	Time (in years) since the last fire with more than 50 ha burnt	
	TSF_+500HA	Time (in years) since the last fire with more than 500 ha burnt	

Variable group/class	Variable name	Description	Data source
Altitude	Alti_Max	Maximum altitude (in meters)	(USGS)
	Alti_Min	Minimum altitude (in meters)	
	Alti_Mean	Mean altitude (in meters)	
	Alti_Range	Altitudinal range (Alti_Max – Alti_Min) (in meters)	
Land cover	UrbanArea	Urban area extent (in hectares)	(DGTD); (EEA)
	AgricLand	Agricultural land extent (in hectares)	
	Forest	Forested area extent (in hectares)	
	Shrubland	Shrub/Heath vegetated areas extent (in hectares)	
	OpenAreas	Extent of areas with little or no vegetation (in hectares)	

2.3.2. Local level

i. Eco-geographical variables related to home-site selection

From the twenty six breeding-sites, we selected twelve assigned to different packs and drew two circular buffers of 500 and 7000 meters radius, around each site. These buffers represent, respectively, the reproductive core and the pack territory extent, which comprises areas between 150-300 km² (Álvares, 2011). The smaller buffer was deducted to the larger one in order to avoid repeated measurements of the same variables. For each buffer, we quantified each eco-geographical variable considered most relevant to use in this fine-scale analysis (Table 2.2). We added “Natural areas” as a variable comprising the sum of Forest, Shrubland and Open Areas extent, in order to evaluate the importance of natural areas as a whole in wolf home-site selection.

Table 2.2 - Independent variables used in wolf home-site eco-geographical characterization.

Variable group/class	Variable name	Description	Data source
Fire-history	%BurntArea_15y	Proportion of total burnt area, burned in the last 15 years until the year of reproduction	JMC Pereira (pers. comm.)
	Nfire_15y	Number of fires per a hundred hectares, with more than 50 ha burned, in the last 15 years until the year of reproduction	
Altitude	Alti_Mean	Mean altitude (in meters)	(USGS)
Land cover	%UrbanArea	Proportion of urban area extent	(DGTD); (EEA)
	%AgricLand	Proportion of agricultural land extent	
	%Forest	Proportion of forested area extent	
	%Shrubland	Proportion of shrub/heath vegetated areas extent	
	%OpenAreas	Proportion of areas with little or no vegetation extent	
	%Natural_areas	Proportion of natural and semi-natural areas (sum of Forest, Shrubland and Open Areas)	

The proportions of the burnt area, number of fires per a hundred hectares, altitude and the different land cover types were determined around each breeding-site within the 500 and 7000 meters radius. Concerning land cover characterization, the use of data from time periods representative of all reproduction years was mandatory. Therefore, Corine Land Cover changes for the years 1990-2000 and 2000-2006, in continental Portugal, respectively obtained from European Environment Agency (EEA) and Directorate-General for the Territorial Development (DGTD), were used accordingly to each breeding period.

ii. Fire-history variables related to breeding-site use

To assess whether fires had an impact on the selection and reuse of breeding-sites between consecutive years, two fire-related variables were selected: burnt area

proportion (%BurntArea) and time since fire (TSF); both regarding the previous year of breeding occurrence. We have analysed previous years' breeding locations in order to evaluate reuse or selection of a different site a year after fire disturbance. Focusing on the second year of reproduction led some previous breeding locations to be neglected on the analysis. Thus, only 22 breeding-sites were selected with a 500 m radius circular buffer drawn around each. The above-mentioned variables were assessed for each buffer. Details concerning these variables are described in section 2.2.3., related to the Regional level analysis.

All data on wolf occurrence and eco-geographical variables, at both study levels, were compiled and analysed in QGIS Geographic Information System, version 2.0.1 Dufour (QGIS, 2013).

2.4. Statistical analysis

2.4.1. Regional level

To assess how each variable affects wolf distribution patterns, a t-test was firstly conducted by comparing the set of eighteen eco-geographical variables (8 fire-history, 4 altitude, 6 land cover) between squares of wolf persistence (N = 207) and extinction (N = 60). Then, both non-significant and high correlated ($r > 0.75$) variables were excluded. Secondly, six eco-geographical variables (Nfire_+50HA, TSF_+500HA, Alti_Mean, Alti_Range, Forest and Shrubland) were retained and selected as predictors on a logistic regression analysis, using wolf presence data in Portugal as a binary dependent variable with two categories: extinction and persistence. The logistic regression analysis was conducted with a backward stepwise procedure, which intends to remove non-significant variables, testing their significance using Wald statistic test.

2.4.2. Local level

To assess the variables related to home-site selection, the Wilcoxon's matched-pairs test was employed to compare scores for nine eco-geographic variables, between the 500 and 7000 m buffers at each breeding-site (Table 2.2).

To assess the effect of fire on breeding-site use in consecutive years, we conducted qualitative and quantitative approaches. Qualitatively, we examined whether

packs re-used or displaced breeding-sites, regarding fire occurrence in the previous year. Thus, a 2x2 contingency table, with “displacement” and “non-displacement” as rows and “burn” and “not-burn” as columns, was prepared and a chi-square test was then performed. Quantitatively, we examined which fire-history variables could explain pack displacement in meters, between consecutive years, by Generalized Linear Mixed Model (GLMM). This method allows to analyse non-normal data and to model a response (dependent) variable through fixed (independent variables) and random effects (Bolker *et al.*, 2008; Che & Xu, 2012). In this study, breeding-site use from one year to the next, was analysed as a dependent variable, while different wolf packs were considered a random effect, since different quantities of data were collected for each pack, during several years. The independent variables analysed for each breeding location were %BurntArea and TSF.

All statistical analysis, for both study levels, were completed using SPSS Statistics 21 software for Windows (IBMCorp., 2012).

3. Results

3.1. Regional level

In 1980 the Iberian wolf was present in approximately 30% of the Portuguese territory (comprising 2 747 ha). By 2003 its total distribution area consisted in 23% of the country (comprising 2 130 ha). From 1980 to 2003 fires had burned 977 970 hectares in areas of wolf occurrence in Continental Portugal. The mean burnt area per square was 970 hectares, with a minimum of 7 961 hectares burnt in the year 1997 and a maximum of 210 238 hectares burnt in 2003. In areas of wolf persistence a total of 263 054 hectares were burned by medium and large fires (>50 hectares burnt), between 1980 and 2003. For the same time period, a total of 85 222 hectares was burned in areas of wolf extinction. The burnt extent was overall higher in areas of persistence compared to areas of extinction (Figure 2.11). An exception is made for the years of 1983, 1986, 1987, 1990, 1992, 1995, 1999 and 2001-2003, in which areas of wolf extinction had a higher mean burnt extent when compared to the ones of wolf persistence.

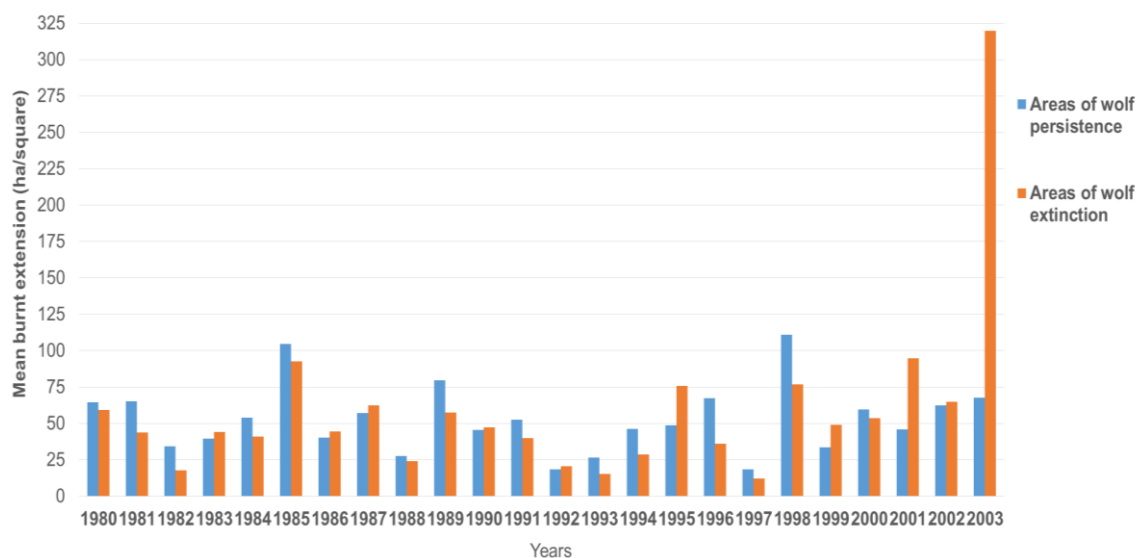


Figure 2.11 - Mean burnt area per year, between 1980 and 2003, in areas of wolf persistence and extinction.

Likewise, the mean number of fires per year was higher in areas of wolf persistence (Figure 2.12), being consistent with the overall results from mean burnt extent. This part did not change in the years 1986, 1987, 1990, 1995, 1999, and 2001-2003 as the number of fires showed relatively higher values in areas of wolf persistence.

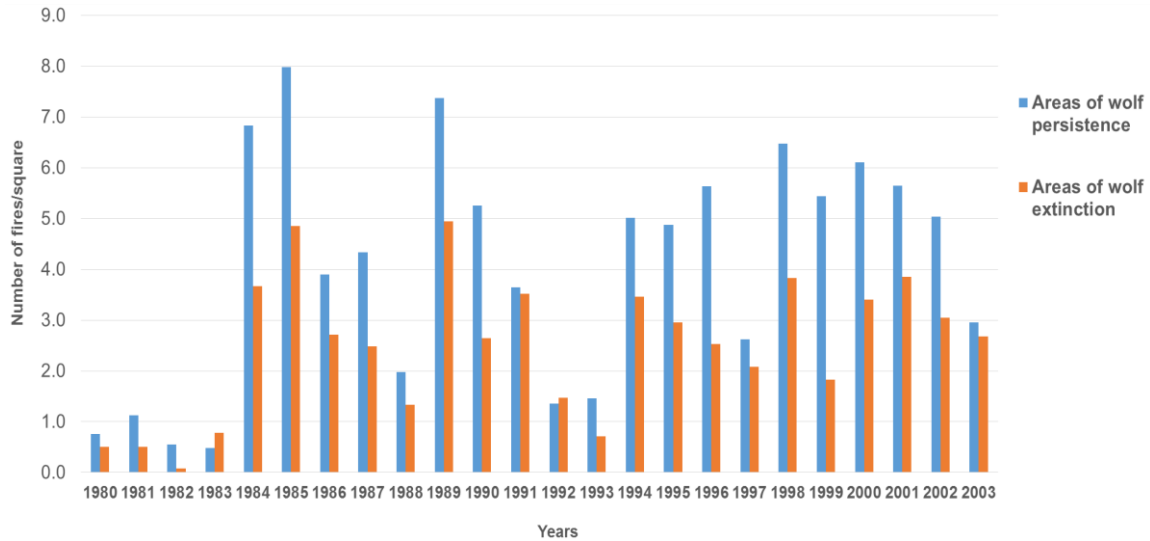


Figure 2.12 - Mean number of fires per year, between 1980 and 2003, in areas of wolf persistence and extinction.

From the eighteen eco-geographical variables primarily used to assess wolf distribution patterns, only nine variables resulted significant on the t-test analysis (Table 2.3): *Alti_Max*, *Alti_Min*, *Alti_Mean*, *Alti_Range*, *Nfire_Total*, *Nfire_+50HA*, *TSF_+500HA*, *Forest*, and *Shrubland*. All these variables showed higher mean values in areas of wolf persistence, with exception of *Forest*. No significant differences were found between land cover heterogeneity concerning areas of wolf persistence and extinction, as *Evenness Index* was not significant. Nonetheless, results showed different mean values for each variable, particularly *Forest* and *Shrubland* which presented significant opposite outcomes, the first being higher in areas of wolf extinction and the second in areas of wolf persistence.

Table 2.3 - Results from the t-test analysis on the effect of eco-geographical variables in wolf persistence and extinction. Significant variables ($P < 0.05$) are indicated in bold.

Variables	Mean Persist (N = 207)	Mean Extinct (N = 60)	t-value	p
Burn_Total	1270.81	1420.38	1.085	0.279
Burn+50HA	1270.81	1419.97	1.082	0.280
Burn+500HA	1227.81	1366.43	1.891	0.341
Nfire_Total	96.83	59.90	-4.752	0.000
Nfire_+50HA	32.57	23.24	-3.298	0.001
Nfire_+500HA	4.43	4.21	-0.344	0.7
TSF_+50HA	1.17	1.86	1.581	0.115
TSF_+500HA	4.52	2.50	-2.470	0.014

Alti_Max	692.52	524.33	-4.516	0.000
Alti_Min	572.55	435.23	-3.771	0.000
Alti_Mean	632.78	480.05	-4.189	0.000
Alti_Range	119.97	89.10	-2.976	0.003
UrbanArea	112.08	186.23	1.937	0.054
AgricLand	4076.63	4303.07	0.563	0.574
Forest	1250.43	1712.67	2.422	0.016
Shrubland	998.07	645.94	-2.053	0.041
OpenAreas	2967.67	3568.60	0.784	0.434
Evenness	0.40	0.42	1.463	0.145

Finally, only 6 eco-geographical variables were retained for conducting the logistic regression, after exclusion of the non-significant and high correlated ($r>0.75$) ones (see Table 2, Supplementary Material). Five variables resulted significant to explain differences in areas of wolf extinction and persistence (Table 2.4). Concerning the fire-history variables, Nfire_+50HA and TSF_+500HA were significant, with wolves persisted in squares with higher numbers of medium and large fires (Nfire_+50HA) and larger periods free of large fires (higher TSF_+500HA values). As for the altitudinal variables, Alti_Mean and Alti_Range were significant, meaning that there is higher altitudinal range (steeper slopes) in squares of wolf persistence, in opposition to a lower range (smoother slopes) in areas of wolf extinction. Concerning the land cover, areas of wolf persistence were less forested than areas of wolf extinction.

Table 2.4 - Results from the Logit analysis on the effect of eco-geographical variables in wolf persistence. Significant variables ($p<0.05$) are indicated in bold.

	Variable	B	Std error	Wald	p
	NFire_+50HA	0.018	0.010	3.433	0.064
	TSF_+500Ha	0.102	0.044	5.342	0.021
	Alti_Mean	0.002	0.001	6.622	0.010
Step 1	Alti_Range	0.005	0.003	3.473	0.062
	Forest	0.000	0.000	5.309	0.021
	Shrubland	0.000	0.000	0.905	0.342
	Constant	-0.830	0.505	2.708	0.100

Step 2	NFire_+50HA	0.019	0.010	3.946	0.047
	TSF_+500Ha	0.099	0.044	5.152	0.023
	Alti_Mean	0.002	0.001	7.738	0.005
	Alti_Range	0.005	0.003	4.086	0.043
	Forest	0.000	0.000	5.344	0.021
	Constant	-0.820	0.504	2.653	0.103

3.2. Local level

3.2.1. Effects of fires and other variables on home-site selection by wolves

The 500 meters radius buffer comprising the reproductive core area, was significantly more burnt during the 15 years before reproduction, than the surrounding territory within the 7000 meters radius buffer. Furthermore, the number of fires per 100 hectares was significantly lower in the reproductive core areas. According to our results (Table 2.5), the reproductive cores are established in significantly higher mean altitude when compared to the surrounding territory. Urban areas did not occur within the reproductive cores and were found in low proportion within the larger area, representing the remain pack territory. As for agricultural lands, its proportion was significantly lower in reproductive core areas. There were no significant differences in forest, shrubland and open areas proportion between both buffers, but natural areas proportion was significantly higher in the smaller buffer, representing the reproductive core.

Table 2.5 - Wilcoxon test results with means (SD) and matched-pair differences between 500 and 7000 m radius buffers around wolf breeding-sites. Significant results ($p < 0.05$) are indicated in bold

Factor	Buffer 500m (N=12)	Buffer 7000m (N=12)	p
%BurntArea_15y	89.98 (±58.84)	52.41 (±16.29)	0.034
Nfire_15y	0.005 (±0.007)	0.55 (±0.15)	0.002
Alti_Mean	954.72 (±199.97)	783.65 (±232.64)	0.003
%UrbanArea	0.00 (±0.00)	0.43 (±0.43)	0.008

Factor	Buffer 500m (N=12)	Buffer 7000m (N=12)	p
%AgricLand	0.30 (±1.02)	20.43 (±13.33)	0.002
%Forest	12.25 (±18.14)	14.74 (±8.84)	0.272
%Shrubland	33.83 (±34.90)	12.03 (±5.49)	0.110
%OpenAreas	53.62 (±35.61)	43.70 (±14.91)	0.239
%Natural_areas	99.70 (±1.02)	70.46 (±14.77)	0.002

3.2.2. Effect of fires on breeding-site use by wolves

We did not find a significant association between breeding-site displacement in consecutive years and fire occurrence in the previous year (Chi square test $X^2 = 0.65$, $df = 1$, $p = 0.42$). Regarding pack displacement ($N = 7$), only two packs (~28%) have moved their breeding site when a fire event occurred the previous year. However, along with the other five packs, these two packs had also moved when no fire event had previously occurred. Regarding wolf pack reuse of breeding-sites ($N = 9$), eight (~88%) maintained their breeding-sites in fire undisturbed areas, and five (~55%) maintained them despite fires had occurred the year before breeding. Furthermore, the GLMM analysis demonstrated that %BurntArea and TSF variables were not significant ($p = 0.26$) to explain pack displacement between years with wolf packs as a random effect, thus failing to explain consecutive uses between breeding-sites from the same pack.

4. Discussion

This study contributed to evaluate the occurrence of a large carnivore, the Iberian wolf, in a fire-prone landscape. We have performed the first analysis on Iberian wolf distribution patterns, by assessing the extinction and persistence range since 1980, and home-site selection and breeding-site use, under a major habitat disturbance factor such as fire.

4.1. Regional level

4.1.1. The effect of eco-geographical variables in wolf distribution patterns

In anthropogenic landscapes large carnivores' persistence seems to be modulated by interactions between factors as human presence and landscape attributes (Llaneza *et al.*, 2011). Regarding altitude variables, the Portuguese wolf population persisted in relatively more elevated and steeper areas and became extinct in lower ones, probably due to the presence of suitable land cover and grazing livestock in higher altitudes. Altitude does not directly reflect wolf presence, but rather the conditions associated with higher altitudes which allow the species to persist over time (Pimenta *et al.*, 2005). A study on the variables affecting habitat selection by wolves in northern Italy concluded that wolves avoid widespread urbanised and arable areas, as well as lower altitudinal areas, due to the anthropic pressure associated (Massolo & Meriggi, 1998). Moreover, wolves positively select higher altitudes and inaccessible sites in search for refuge and to avoid contact with humans (Grilo *et al.*, 2002; Llaneza *et al.*, 2011). Our results are in agreement with the previous literature addressing this topic, where wolves got extinct in relatively more urbanised, agricultural and open areas, as well as in areas of lower altitudes and flatter topography.

Massolo and Meriggi (1998) defined wolf suitable habitats as rich in wild preys, with low human impact and extensive forest cover. Our results seem inconsistent with this last variable, since forest extent was higher in areas of wolf extinction. The extent of native forest in Portugal has drastically decreased over the past decades, due to the widespread plantation of eucalypt (*Eucalyptus globulus*) and maritime pine (*Pinus pinaster*), two species of great commercial interest (Maia *et al.*, 2014) which together constitute 50% of the forest cover in the country (ICNF, 2013). Despite being considered as forests in the Corine Land Cover, these plantations are not natural forest extents. Rodríguez-Freire and Crecente-Maseda (2008) stated that wolves in Galicia (northern

Spain) prefer semi-natural deciduous woodland in opposition to eucalypt and pine plantations. Accordingly to our findings, Eggermann *et al.* (2010) showed that wolves in northern Portugal occur in less forested areas, probably due to the selection of areas where livestock grazes, mainly open areas and shrublands. In fact, in the mountainous areas of northern and central Portugal, shepherds usually burn the land to facilitate the growth of shrubs and grasses for livestock foraging (Nunes, 2012), explaining our results on the intensive fire regime in wolf persistence area. Besides, these evidences may explain wolf extinction in larger extents of forest where, arguably, there are less forage conditions for grazing livestock. On the other hand, open woodland areas, which are usually used for livestock grazing in the Iberian Peninsula, seem to promote wild boar (*Sus scrofa*) abundance by providing attractive foraging areas (Mangas & Rodríguez-Estival, 2010). As the wild boar constitutes one of main wild prey for Iberian wolves (Álvares, 2004), wolves probably also take advantage of these areas to hunt one of their most important natural prey.

Carmo *et al.* (2011) reported that shrublands were the most fire-prone land cover, in fires assessed between 1990-1991 in northern Portugal, as well as the most common cover type in steeper slopes, where the fire spread rate is higher (Carmo *et al.*, 2011; Nunes, 2012). However, susceptibility to fire increases with slope regardless the land cover type (Carmo *et al.*, 2011). Extrapolating these conclusions to our study, it can be stated that the Iberian wolf populations seem highly resilient, persisting in less forested but more fire-prone areas, such as shrublands. In this context, the increasing human disturbance and infrastructure development, such as wind farms and roads, across wolf range (Álvares, 2011), particularly in highlands, is becoming an issue for wolf conservation (Eggermann *et al.*, 2010; Houle *et al.*, 2010). These infrastructures may enhance wildfire's effect on wolf populations by constraining habitat connectivity or selection of alternative refuge areas (Linnell, 2013).

4.1.2. The relevance of fire-related variables in wolf distribution patterns

During the analysed time period, comprising more than two decades, fire was a constant event in the wolf distribution area and seemed not to play an important role in wolf extinction. Higher values of mean burnt extent and mean number of fires were associated with areas of wolf persistence (Figure 2.11 and Figure 2.12). Furthermore, a large number of fires (see Figure 2, Supplementary Material), as well as larger periods of time free of large fires, occurred in the current wolf range, which includes the districts of Viana do Castelo, Vila Real, Viseu and Guarda (Pimenta *et al.*, 2005). These results

suggest that wolves are able to persist in frequently burned areas, but occur in areas where large fires are more spaced in time. Both north and south Douro river wolf populations have persisted in these areas affected by medium and large fires (see Figure 2, Supplementary Material), showing high resilience to this source of habitat disturbance. In particular, areas of higher fire incidence (measured as total number of fires) mostly overlap with two of the most important wolf population nuclei in Portugal: Peneda-Gerês population, which comprises one of the most stable and high-density wolf areas in Portugal; and south Douro population which, in contrast, comprises a small, isolated and highly endangered wolf population (Pimenta *et al.*, 2005).

In most southern regions of Portugal, where the wolf has been absent in the last decades, the overall smaller burnt area, pictured in Figure 2.10A, is derived from fewer fires (Figure 2.10B), and may reflect the characteristic low human population density, drier climate, lower altitudinal range and, especially, the land cover (Nunes, 2012; Torres, 2013). A particular result stands out concerning areas of wolf extinction. As it has been explored by some authors before (Marques *et al.*, 2011; Ferreira-Leite *et al.*, 2013; Tedim *et al.*, 2013), the low number of fires that occurred in 2003 correspond to a high value of burnt area. This fact is due to the occurrence of a small number of large fires during the late-spring and summer of 2003, resulting from consecutive heatwaves and drought (Trigo *et al.*, 2006). This atypical year was characterised by anomalies of meteorological variables like maximum and minimum surface temperature, humidity level and wind speed, which together favored ignition and fire spread (Trigo *et al.*, 2006).

Despite Portugal's fire regime, according to our results fires do not seem to have a role shaping Iberian wolf persistence or extinction, as wolves both persisted and became extinct in areas affected by recurrent medium and large fires. Fire assuredly induces changes in landscape structure, creating a mosaic of areas with greater risk of encounters with humans and fewer refuges for both wolves and wild prey (Lyon *et al.*, 2000b; Gervasi *et al.*, 2013; Robinson *et al.*, 2013), thus affecting their reproduction and population numbers (Sand *et al.*, 2006). However, wolves can travel great distances and have large home ranges (Hentrup, 2011), which allows them to avoid burned areas and select different parts of their territories when necessary. Fire can influence prey availability and space use, making prey species more vulnerable to wolf predations. In fact, several studies have found that herbivores are attracted to recently burned areas, due to plant regrowth and increased safety from predators, which are easily spotted due to the lack of vegetation (de Ronde *et al.*, 2004; Allred *et al.*, 2011; Eby *et al.*, 2014). Changes in herbivore distribution are influenced by season, location and time since fire (Green *et al.*, 2014). However, some species may become more vulnerable to predation

as prey visibility is also increased (de Ronde *et al.*, 2004; Allred *et al.*, 2011). Large carnivores thrive in areas where their prey, both wild and domestic, is plentiful (Lyon *et al.*, 2000a), as may occur in recent burns. Thus, negative effects of burnt areas on the Iberian wolves' hunting success are not expected. Furthermore, the fact that both wild and domestic prey may occupy these burned areas can promote Iberian wolf persistence in the territory under a strong fire regime. However, fires are expected to induce a negative effect on the vegetation cover of sites used for refuge and breeding by wolves, although no previous study have yet addressed this potential effect. Forestry activities, involving logging and drastic changes in vegetation cover, may disturb wolves in a similar way that fires do. Contrary to effects of fire, forestry activities' effect have been widely studied on mammals (Fisher & Wilkinson, 2005; Allard-Duchêne *et al.*, 2014), and even on wolves (Hebblewhite *et al.*, 2009; Houle *et al.*, 2010). Cumulative effects of logging activities, i.e removal of forest stands, alter habitat selection by wolves in boreal ecosystems, influencing their predator-prey dynamics (Houle *et al.*, 2010), and can also negatively influence wolves breeding and denning behaviour, by removing vegetation cover and, hence, conditions that may foster refuge (Robinson *et al.*, 2013). Thus, fire activity is expected to induce similar effects and responses on wolves.

4.2. Local level

4.2.1. Eco-geographical variables related to home-site selection

The comparison between 500m and 7000m buffers around breeding-sites indicated that the smaller buffers, which constitute wolf reproductive cores, were located in higher altitudes and extensive natural areas, in opposition to urban and agricultural ones. The reproductive cores were also characterized by greater proportions of burnt areas, burned for the last fifteen years before reproduction, when compared to the larger buffer, comprising the surrounding areas attributed to the remain pack territory. However, reproductive core sites occurred in areas with a lower number of fires per a hundred hectares, meaning a few number of fires are responsible for the large burnt area observed. Concerning fire-history, the large proportion of burnt areas in the reproductive cores may be explained by land cover extent in this area. In Portugal, shrublands and mixed conifer forests tend to burn more than agricultural and urban areas, mainly because they are frequently burned for renovation of pastures for livestock (Moreira *et al.*, 2009; Carmo *et al.*, 2011; Nunes, 2012) and also due to their eco-geographical attributes, which make them especially fire-prone (Nunes *et al.*, 2005; Moreira *et al.*, 2009; Carmo *et al.*, 2011). In opposition to what happens with shrublands, agricultural

areas are usually close to urban settlements, making fire detection and subsequent firefighting quicker and easier (Moreira *et al.*, 2009). Comparing mean values between both buffers it is evident that the smaller buffer, comprising the reproductive cores, hold conditions for wolf refuge (Grilo *et al.*, 2002; Cayuela, 2004; Eggermann *et al.*, 2010; Llaneza *et al.*, 2011), having a higher proportion of natural areas and a higher mean altitude. However, within natural lands it is worth mention that reproductive core sites were not found in any specific natural cover type, thus Iberian wolves do not seem to prefer a specific vegetation type when selecting their breeding locations, as far as they provide vegetation cover for refuge. This fact is in accordance with previous studies on this subject (Theuerkauf *et al.*, 2003; Kaartinen *et al.*, 2010; Iliopoulos *et al.*, 2013). Several studies in North America reported breeding-site selection at low altitudes and gentle slopes (Ballard & Dau, 1983; Person & Russell, 2009), far from clearcuts and logged stands, but close to water courses (Norris *et al.*, 2002; Trapp *et al.*, 2008; Person & Russell, 2009). However, studies from Europe shed a different light on the subject, as European wolves occupy areas with greater proximity to human settlements (Kaartinen *et al.*, 2010). Two studies, conducted on different regions of Italy, reported altitude and distance to protected areas as the best predictors of wolf breeding-site selection (Capitani *et al.*, 2006; Bassi *et al.*, 2015). Both studies concluded that wolf rendezvous sites were significantly more frequent inside protected areas, and far from roads. Moreover, Bassi *et al.* (2015) indicate that rendezvous sites are associated to altitudes between 800 and 1200 meters, in the mountainous areas of central Italy. In Poland, Theuerkauf *et al.* (2003) reported wolves selection of home and resting sites to be far from forest roads and near a strict reserve with low human activity. Likewise, a study in Greece by Iliopoulos *et al.* (2013) concluded that wolves generally avoid semi-forested and open habitats, as well as roads, when establishing rendezvous sites. Another European study, conducted in the Finnish boreal forests (Kaartinen *et al.*, 2010), used generalized linear mixed models to explain den-site location distances to human-modified areas (villages, cities, built-up areas, roads and agriculture fields), as well as forest type, vegetation and water bodies around home-sites. The authors concluded that wolves avoided these urbanised areas and selected younger successional stages of conifer forests, presumably due to high abundance of moose (*Alces alces*), which is one of the main wolf prey in those areas. Similarly, our results suggest human disturbance to be the main factor affecting wolf home-site selection in Portugal. For breeding, wolves' selection of fire-prone areas seem to be preferable than proximity to humans. These fire-prone areas, however, involve fire-related disturbances, such as direct fire hazard and regular modifications in vegetation structure and composition (Torres, 2013). These

disturbances may alter refuge conditions and prey distribution (Allard-Duchêne *et al.*, 2014; Green *et al.*, 2014); and possibly compromise breeding-site suitability.

4.2.2. Fire's effect on breeding-site selection and use

Our results showed no significant effects of fire-related variables in breeding-site use during consecutive years of reproduction, despite the majority of fires in Portugal occurring during summer months (Trigo *et al.*, 2006; Lourenço *et al.*, 2012; Nunes, 2012; Pereira *et al.*, 2013), when wolves are breeding and raising their pups (Iliopoulos *et al.*, 2013; Bassi *et al.*, 2015). In our study, a total of seven packs selected different breeding-sites in consecutive years. Wolf packs' displacement from one site to another did not show any association to fire disturbance (2 in 7 packs changed breeding-sites the year after fire disturbance, while 5 in 7 changed breeding-sites the year after no fire disturbance had occurred). Despite no significant results, we hypothesize that this frequent breeding-site displacement may be caused by several other factors not considered in this study, such as prey distribution or anthropogenic disturbances, like infrastructure development and tourism-related activities (Argue *et al.*, 2008; Eggermann *et al.*, 2010; Houle *et al.*, 2010; Linnell, 2013). Moreover, fire intensity, with strong implications on vegetation cover, was yet another factor not addressed in this study, as no quantified information was found. The same applies for post-fire management of burnt areas, either by removal of burnt logs or replantation. Fire management influences resource availability (Valentine *et al.*, 2014), which may affect the permanence of wolf breeding-sites. Furthermore, wolf mortality due to human persecution, as frequently occurs in Portugal (Pimenta *et al.*, 2005; Álvares, 2011), can also explain breeding-site displacement, as it leads to pack disruption and to changes of the breeding pair (Rutledge *et al.*, 2010), which may alter the selection of a specific breeding location.

4.3. Future perspectives

Regional and local approaches are coincident to report that distribution and breeding activity of the Iberian wolf in Portugal do not seem correlated to fire disturbance as, despite the great proportion of fires in wolf range, the species is able to persist. In contrast, we acknowledge that other factors, not addressed in our study, could also predict and explain wolf distribution at the regional scale, and breeding-site selection and use at the local scale. In fact, some events of wolf persistence and extinction correspond to areas geographically close to the Spanish border, and so, wolf occurrence in these

areas may be reflecting ecological processes occurring in the neighbour country. Also, as we have previously mentioned, factors such as infrastructure development and prey availability are potential threats to wolf persistence in the territory and may potentiate fire's effect as a factor of habitat disturbance and unsuitability. A new study model comprising these, and possibly more, disturbance factors would be of major importance for better understanding wolf distribution patterns and selection of breeding sites. Another factor that assuredly has a great impact on wolf persistence and reproduction success is direct human disturbance. There are several studies reporting direct human disturbance effects in wolf home-sites (Argue *et al.*, 2008; Person & Russell, 2009), but none concerning the Iberian wolf. Also, since wolves seem not to avoid burned areas, we suggest a more in-depth study on the behavioural responses of wolves. In fact, changes in circadian activity and movement patterns are expected, since wolves become more exposed and vulnerable to human persecution in recently burned areas. Moreover, as another complement of this study, a similar analysis could be drawn concerning wild prey species of Iberian wolves, such as wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) (Álvares, 2011). Since there is lack of information on their response to fire, such approach would complement this study's results and help explain wolf distribution trends and selection of burned areas.

References

- Allard-Duchêne, A., Pothier, D., Dupuch, A., & Fortin, D. (2014). Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. *Forest Ecology and Management*, 313, 17-25.
- Allred, B.W., Fuhlendorf, S.M.E., D.M., & Elmore, R.D. (2011). Ungulate preference for burned patches reveals strength of fire–grazing interaction. *Ecology and Evolution*, 1(2), 132-144.
- Álvares, F. (2004). Status and Conservation of the Iberian Wolf in Portugal. *Wolf Print*, 4-6.
- Álvares, F. (2011). *Ecologia e conservação do lobo (Canis lupus, L.) no Noroeste de Portugal. Tese de Doutoramento.*, Universidade de Lisboa, Portugal.
- Álvares, F., & Blanco, J.C. (2014). Recovering traditional husbandry practices to reduce wolf predation on free-ranging cattle in Iberia. *Carnivore Damage Prevention News*, 10, 4-9.
- Amraoui, M., Liberato, M.L.R., Calado, T.J., Da Camara, C.C., L.P, C., Trigo, R.M., et al. (2013). Fire activity over Mediterranean Europe based on information from Meteosat-8. *Forest Ecology and Management*, 294, 62–75.
- Argue, A.M., Mills, K.J., & Patterson, B.R. (2008). Behavioural response of eastern wolves (*Canis lycaon*) to disturbance at homesites and its effects on pup survival. *Can. J. Zool.*, 86, 400-406.
- Ballard, W.B., & Dau, J.R. (1983). Characteristic of Gray Wolf, *Canis lupus*, Den and Rendezvous sites in Southcentral Alaska. *Canadian Field-Naturalist*, 97(3), 299-302.
- Ballard, W.B., Krausman, P.R., Boe, S., Cunningham, S., & Whitlaw, H.A. (2000). Short-term Response of Gray Wolves, *Canis lupus*, to Wildfire in Northwestern Alaska. *Canadian Field-Naturalist*, 114(2), 241-247.
- Bassi, E., Willis, S.G., Passilongo, D., Mattioli, L., & Apollonio, M. (2015). Predicting the Spatial Distribution of Wolf (*Canis lupus*) Breeding Areas in a Mountainous Region of Central Italy. *PLoS ONE*, 10(6), 1-14.
- Blanco, J.C., Reig, S., & Cuesta, L. (1992). Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation*, 60, 73-80.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., et al. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24(3), 127-135.

- Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., et al. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica*, 51, 395–404.
- Carbyn, L.N., Oosenbrug, S.M., & Anions, D.W. (1993). *Wolves and bisons...and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park* (Vol. 4). University of Alberta: Canadian Circumpolar Institute.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., et al. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, 309, 1239-1241.
- Carmo, M., Moreira, F., Casimiro, P., & Vaz, P. (2011). Land use and topography influences on wildfire occurrence in northern Portugal. *Landscape and Urban Planning*, 100(169-176).
- Carrión, J.S., Fuentes, N., González-Sampériz, P., Sánchez-Quirante, L., Finlayson, J.C., Fernández, S., et al. (2007). Holocene environmental change in a montane region of southern Europe with a long history of human settlement. *Quaternary Science Reviews*, 26, 1455-1475.
- Cayuela, L. (2004). Habitat evaluation for the Iberian wolf *Canis lupus* in Picos de Europa National Park, Spain. *Applied Geography*, 24, 199-215.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., et al. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346, 1517-1519.
- Che, X., & Xu, S. (2012). Generalized linear mixed models for mapping multiple quantitative trait loci. *Heredity*, 109, 41–49.
- Costa, J.C., Aguiar, C., Capelo, J.H., Lousã, M., & Neto, C. (1998). Biogeografia de Portugal Continental. *Quercetea*, 0.
- De la Rosa, J.M., Faria, S.R., Varela, M.E., Knicker, H., González-Vila, F.J., González-Pérez, J.A., et al. (2012). Characterization of wildfire effects on soil organic matter using analytical pyrolysis. *Geoderma*, 191, 24-30.
- de Ronde, C., Trollope, W.S.W., Parr, C.L., Brockett, B., & Geldenhuys, C.J. (2004). Fire Effects on Flora and Fauna. In J. G. Goldammer & C. de Ronde (Eds.), *Wildland Fire Management Handbook for Sub-Sahara Africa* (pp. 77-87): Global Fire Monitoring Center.
- DGTD. Corine Land Cover (CLC) for Continental Portugal. Retrieved http://www.dgterritorio.pt/cartografia_e_geodesia/cartografia/cartografia_tematica/cartas_de_ocupacao_do_solo/corine_land_cover/ Accessed November 2014

- Eby, S.L.A., T.M., Mayemba, E.P., & Ritchie, M.E. (2014). The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology*, 83, 10.
- EEA. Corine Land Cover 1990 - 2000 changes Retrieved <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2> Accessed June 2015
- Eggermann, J., Ferrão-da-Costa, G., Guerra, A.M., Kirchner, W.H., & Petrucci-Fonseca, F. (2010). Presence of Iberian wolf (*Canis lupus signatus*) in relation to land cover, livestock and human influence in Portugal. *Mammalian Biology*, 76(2), 217-221.
- Ferreira-Leite, F., Bento-Gonçalves, A., Lourenço, L., Úbeda, X., & Vieira, A. (2013). Grandes Incendios Florestais em Portugal Continental como Resultado das Perturbações nos Regimes de Fogo no Mundo Mediterrâneo. *Silva Lusitana, nº Especial*, 127-142.
- Fisher, J.T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev*, 35, 51-81.
- Gervasi, V., Sand, H.Z., B, Mattisson, J., Wabakken, P., & Linnell, J.D.C. (2013). Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, 23(7), 1722-1734.
- Green, D.S., Roloff, G.J., Heath, B.R., & Holekamp, K.E. (2014). Temporal dynamics of the responses by African mammals to prescribed fire. *The Journal of Wildlife Management*, 79(2).
- Grilo, C., Moço, C., Cândido, A.T., Alexandre, A.S., & Petrucci-Fonseca, F. (2002). Challenges for the recovery of the Iberian wolf in the Douro river south region. *Revista Biol. (Lisboa)*, 20, 121-131.
- Hebblewhite, M., Munro, R.H., & Merrill, E.H. (2009). Trophic consequences of postfire logging in a wolf–ungulate system. *Forest Ecology and Management*, 257, 1053–1062.
- Heip, C.H.R., Herman, P.M.J., & Soetaert, K. (1998). Indices of diversity and evenness. *Oceanis*, 24(4), 80-83.
- Hentrup, M. (2011). *The effect of social relations on joint object interactions in wolves (Canis lupus)*. (Masterthesis), University of Münster.
- Houle, M.F., D, Dussault, C., Courtois, R., & Ouellet, J.-P. (2010). Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecol*, 25, 419-433.

- IBM Corp. (2012). IBM SPSS Statistics for Windows (Version 21.0). Armonk, NY.
- ICNB. (2010). *Fourth National Report to the Convention on Biological Diversity -Portugal*. Instituto da Conservação da Natureza e da Biodiversidade.
- ICNF. (2013). *IFN6 – Áreas dos usos do solo e das espécies florestais de Portugal continental em 1995, 2005 e 2010. Resultados preliminares*. Instituto da Conservação da Natureza e das Florestas. Lisboa.
- Iliopoulos, Y., Youlatos, D., & Sgardelis, S. (2013). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *European Journal of Wildlife Research*, 12.
- Kaartinen, S., Luoto, M., & Kojola, I. (2010). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology*, 281, 99–104.
- Linnell, J.D.C. (2013). *From conflict to coexistence? Insights from multi-disciplinary research into the relationships between people, large carnivores and institutions*. IUCN/SSC Large Carnivore Initiative for Europe.
- Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2011). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions*, 18(5), 459-469.
- Lourenço, L., Nunes, A.N., Bento-Gonçalves, A., & Vieira, A. (2012). Soil Erosion After Wildfires in Portugal: What Happens When Heavy Rainfall Events Occur? In D. Godone & S. Stanchi (Eds.), *Research on Soil Erosion* (pp. 65-88). Croatia.
- Lyon, L.J., Huff, M.H., S. Telfer, E.S., Schreiner, D.S., & Smith, J.K. (2000a). Fire Effects on Animal Populations. In J. K. Smith (Ed.), *Wildland fire in ecosystems: effects of fire on fauna* (pp. 25-34): United States Department of Agriculture.
- Lyon, L.J., Huff, M.H., & Smith, J.K. (2000b). Fire Effects on Fauna at Landscape Scales. In J. K. Smith (Ed.), *Wildland fire in ecosystems: effects of fire on fauna* (pp. 43-49): United States Department of Agriculture.
- Machado, A.I., Serpa, D., Ferreira, R.V., Rodríguez-Blanco, M.L., Pinto, R., Nunes, M.I., et al. (2015). Cation export by overland flow in a recently burnt forest area in north-central Portugal. *Science of the Total Environment*, 524-525, 201-212.
- Maia, P., Keizer, J., Vasques, A., Abrantes, N., Roxo, L., Fernandes, P., et al. (2014). Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal: Effects of biogeography, topography, forest type and post-fire management. *Forest Ecology and Management*, 334, 154-162.
- Mangas, J.G., & Rodríguez-Estival, J. (2010). Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. *Forest Ecology and Management*, 260, 1274-1281.

- Marques, S., Borges, J.G., Garcia-Gonzalo, J., Moreira, F., Carreiras, J.M.B., Oliveira, M.M., et al. (2011). Characterization of wildfires in Portugal. *Eur J Forest Res*, 130, 775-784.
- Massolo, A., & Meriggi, A. (1998). Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. *Ecography*, 21, 97-107.
- Mech, L.D., & Boitani, L. (2003). *Wolves; Behavior, Ecology and Conservation*: The University of Chicago Press.
- Moreira, F., Vaz, P., Catry, F., & Silva, J.S. (2009). Regional variations in wildfire susceptibility of land-cover types in Portugal: implications for landscape management to minimize fire hazard. *International Journal of Wildland Fire*, 18, 563–574.
- Nakamura, M., Rio-Maior, H., Godinho, R., & Álvares, F. (2013). *Investigação Aplicada à Conservação do Lobo no Noroeste de Portugal. Relatório Técnico – Ano II*. Retrieved from
- Norris, D.R., Theberge, M.T., & Theberge, J.B. (2002). Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. *Can. J. Zool.*, 80, 866–872.
- Nunes, A.N. (2012). Regional variability and driving forces behind forest fires in Portugal an overview of the last three decades (1980-2009). *Applied Geography*, 34, 576-586.
- Nunes, M.C.S., Vasconcelos, M.J., Pereira, J.M.C., Dasgupta, N., Alldredge, R.J., & Rego, F.C. (2005). Land cover type and fire in Portugal: do fires burn land cover selectively? *Landscape Ecology*, 20, 661–673.
- Oliveira, S.L.J., Pereira, J.M.C., & Carreiras, J.M.B. (2012). Fire frequency analysis in Portugal (1975–2005), using Landsat-based burnt area maps. *International Journal of Wildland Fire*, 21, 48-60.
- Pereira, J.M.C., & Santos, T.N. (2003). *Fire Risk and Burned Area Mapping in Portugal*. Retrieved from
- Pereira, M.G., Calado, T.J., Da Camara, C.C., & Calheiros, T. (2013). Effects of regional climate change on rural fires in Portugal. *Climate Research*, 57, 187–200.
- Person, D.K., & Russell, A.L. (2009). Reproduction and Den Site Selection by Wolves in a Disturbed Landscape. *Northwest Science*, 83(3), 211-224.
- Petrucci-Fonseca, F. (1990). *O lobo (Canis lupus signatus Cabrera, 1907) em Portugal: Problemática da sua conservação.*, Faculdade de Ciências da Universidade de

- Lisboa. (Dissertação apresentada à Faculdade de Ciências da Universidade de Lisboa para a obtenção do grau de doutor)
- Pimenta, V., Barroso, I., Álvares, F., Correia, J., Ferrão da Costa, G., Moreira, L., et al. (2005). *Situação populacional do Lobo em Portugal, resultados do Censo Nacional 2002/2003. Relatório Técnico*. Retrieved from
- QGIS. (2013). QGIS Geographic Information System: Open Source Geospatial Foundation Project. Retrieved from <http://qgis.osgeo.org>
- Robinson, N.M., Leonard, S.W.J., Ritchie, E.G., Bassett, M., Chia, E.K., Buckingham, S., et al. (2013). Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology*.
- Rodríguez-Freire, M., & Crecente-Maseda, R. (2008). Directional Connectivity of Wolf (*Canis lupus*) Populations in Northwest Spain and Anthropogenic Effects on Dispersal Patterns. *Environ Model Assess*, 13, 35-51.
- Roque, S., Bernardo, J., Godinho, R., Petrucci-Fonseca, F., & Álvares, F. (2013). *Plano de Monitorização do Lobo a Sul do Rio Douro – Zona Este. Relatório Técnico, Ano I*. Retrieved from
- Rutledge, L.Y., Patterson, B.R., Mills, K.J., Loveless, K.M., Murray, D.L., & White, B.N. (2010). Protection from harvesting restores the natural social structure of eastern wolf packs. *Biological Conservation*, 143, 332–339.
- Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, 72, 781-789.
- Santos, M., Vaz, C., Travassos, P., & Cabral, J.A. (2007). Simulating the impact of socio-economic trends on threatened Iberian wolf populations *Canis lupus signatus* in north-eastern Portugal. *Ecological Indicators*, 7, 649-664.
- Silva, J.S., Vaz, P., Moreira, M., Catry, F., & Rego, F.C. (2011). Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal. *Landscape and Urban Planning*, 101, 349-358.
- Sunquist, M.E., & Sunquist, F. (2001). Changing landscapes: consequences for carnivores. In J. L. Gittleman, S. M. Funk, D. Macdonald, & R. K. Wayne (Eds.), *Carnivore Conservation* (Vol. 5, pp. 399-418). Cambridge: Cambridge University Press.
- Tedim, F., Remelgado, R., Borges, C., Carvalho, S., & Martins, J. (2013). Exploring the occurrence of mega-fires in Portugal. *Forest Ecology and Management*, 294, 86-96.

- Theuerkauf, J., Rouys, S., & Jedrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can. J. Zool.*, 81, 163–167.
- Torres, J. (2013). *Patterns and drivers of wildfire occurrence and post-fire vegetation resilience across scales in Portugal*. (Doutoramento em Biologia), Faculdade de Ciências da Universidade do Porto, Porto.
- Trapp, J.R., Beier, P., Mack, C., Parsons, D.R., & Paquet, P.C. (2008). Wolf, *Canis lupus*, Den Site Selection in the Rocky Mountains. *Canadian Field-Naturalist*, 122(1), 49-56.
- Trigo, R.M., Pereira, J.M.C., Pereira, M.G., Mota, B., Calado, T.J., Da Camara, C.C., et al. (2006). Atmospheric conditions associated with the exceptional fire season of 2003 in Portugal. *Int. J. Climatol*, 26, 1741–1757.
- USGS. (2006). Shuttle Radar Topography Mission (SRTM). from Global Land Cover Facility, University of Maryland
- Valentine, L.E., Rebecca Fisher, R., Wilson, B.A., Sonneman, T., Stock, W.D., P.A, F., et al. (2014). Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape. *Biological Conservation*, 175, 1-9.
- Vos, J. (2000). Food habits and livestock depredation of two iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *J.Zool*, 251, 457-462.

General Conclusions and final remarks

This study evaluated fire's effect on mammal species by means of a meta-analysis, and performed the first analysis on fire's effect on the Iberian wolf distribution patterns and reproductive behaviour.

Concerning the first chapter focused in the meta-analysis, results failed to identify a global pattern of mammals' response to fire, possibly due to the small number of studies and the large variability among the classes of the evaluated variables. The only statistically significant interaction occurred between the variables Body Size and Feeding habits, unrelated to Response to fire disturbance. However, during the bibliographic compilation process, we were able to verify that there is, indeed, a great lack of studies concerning fires' effect on large size carnivores. Fires' effect on mammals should mostly depend on the scale of the analysis.

Concerning the second chapter of the study, focused on the effects of fires on wolves, results suggest that fires do not have a role on the persistence and extinction of wolf populations in Portugal, nor in their breeding-site selection and use. In fact, wolves clearly persist and reproduce in fire-prone areas, despite the expected effects on changing vegetation structure and influencing prey distribution. Concerning wolf breeding-site selection and use in consecutive years, we tested fire as the only source of disturbance. Nonetheless, we acknowledge that factors such as human-mediated disturbances and prey availability may also be influencing breeding-site selection and use. Models of climate change predict an increase in frequency of large wildfires (Cary & Banks, 2000), as fire regimes are expected to respond to climate change (Bento-Gonçalves 2012), as well as an increase in burnt extent for Portugal, by the end of the century (Pereira *et al.*, 2013). These predictions together with the increasing socio-economic development within wolf range (Santos *et al.*, 2007) may lead to a decrease in availability of suitable habitats for wolves to find food, refuge and breeding conditions. In fact, since wolves feed mostly on livestock (Blanco *et al.*, 1992; Vos, 2000; Álvares & Blanco, 2014), and since wild prey is scarce, an increased human-wolf conflict is also expected. In conclusion, fire alone does not seem to be an issue for Iberian wolf conservation in Portugal, however, its effects added to other sources of disturbance, in a human-dominated and heterogeneous landscape, may have a devastating effect on the long-term survival of wolf populations.

Hopefully, this study's results will incite new researches concerning fires' effects on large mammals in Portugal, where fire has been a constant factor of habitat disturbance but where, controversially, its effects on faunal communities have not yet received the deserved attention. Furthermore, we hope that our results will lead to a better understanding of the conditions that favour wolf persistence in the territory, allowing managers to improve measures for Iberian wolf management and conservation in Portugal.

References

- Álvares, F., & Blanco, J.C. (2014). Recovering traditional husbandry practices to reduce wolf predation on free-ranging cattle in Iberia. *Carnivore Damage Prevention News*, 10, 4-9.
- Blanco, J.C., Reig, S., & Cuesta, L. (1992). Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation*, 60, 73-80.
- Cary, G.J., & Banks, J.C.G. (2000). Fire Regime Sensitivity to Global Climate Change: An Australian Perspective. In J. L. Innes, M. Beniston, & M. M. Verstraete (Eds.), *Biomass Burning and Its Inter-Relationships with the Climate System Advances in Global Change Research* (Vol. 3, pp. 233 – 246): Springer Netherlands.
- Pereira, M.G., Calado, T.J., Da Camara, C.C., & Calheiros, T. (2013). Effects of regional climate change on rural fires in Portugal. *Climate Research*, 57, 187–200.
- Santos, M., Vaz, C., Travassos, P., & Cabral, J.A. (2007). Simulating the impact of socio-economic trends on threatened Iberian wolf populations *Canis lupus signatus* in north-eastern Portugal. *Ecological Indicators*, 7, 649-664.
- Vos, J. (2000). Food habits and livestock depredation of two iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *J.Zool*, 251, 457-462.

Supplementary Material

Figures

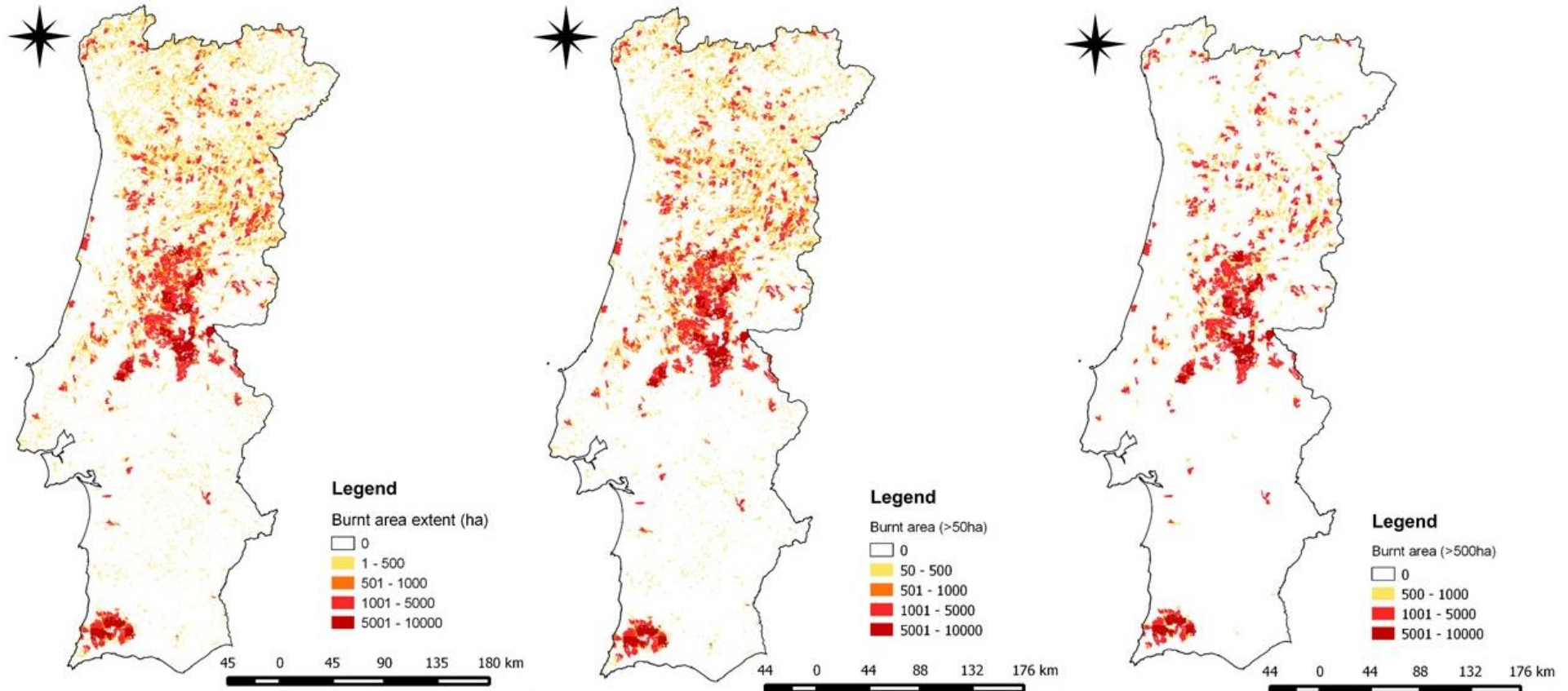


Figure 1 - Map of Portugal showing total burnt area extent (left), burnt area extent with more than 50 ha burned (centre) and burnt area extent with more than 500 ha burned (right), for the time period of 1980-2003. Units are in hectares.

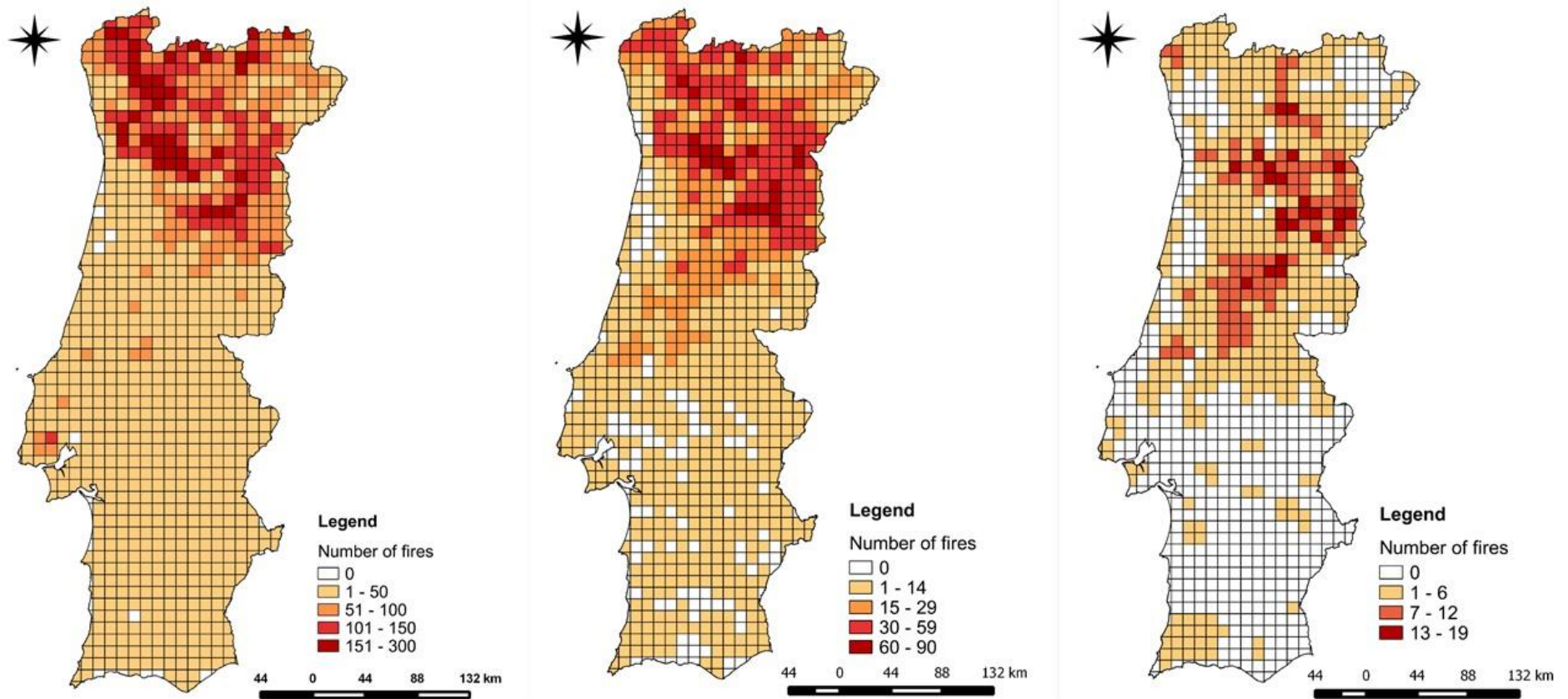


Figure 2 - Map of Portugal showing total number of fire ignitions (left), and fire ignitions resulting in burned areas larger than 50 ha (centre) and 500 ha (right), for the time period of 1980-2003.

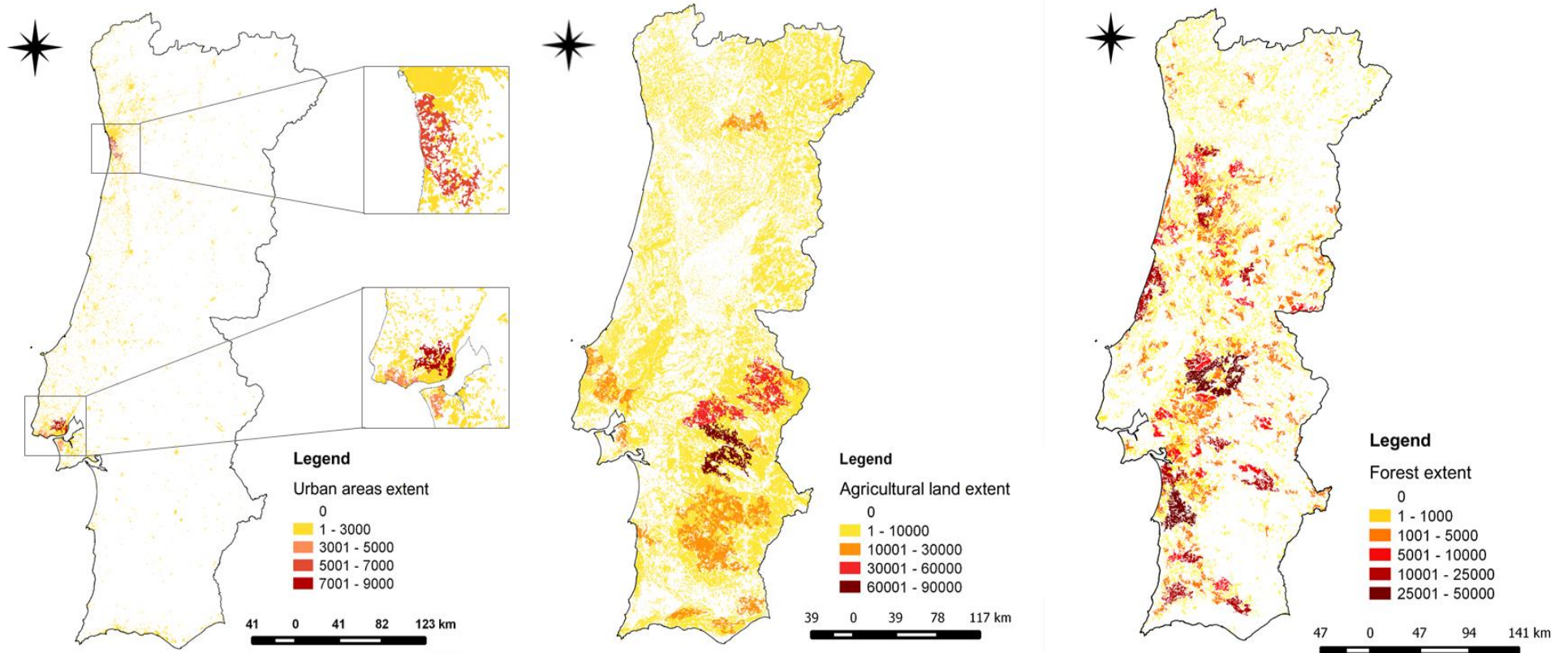


Figure 3 - Map of Portugal showing urban areas (left), agricultural land (centre) and forest extent (right). Units are in hectares.

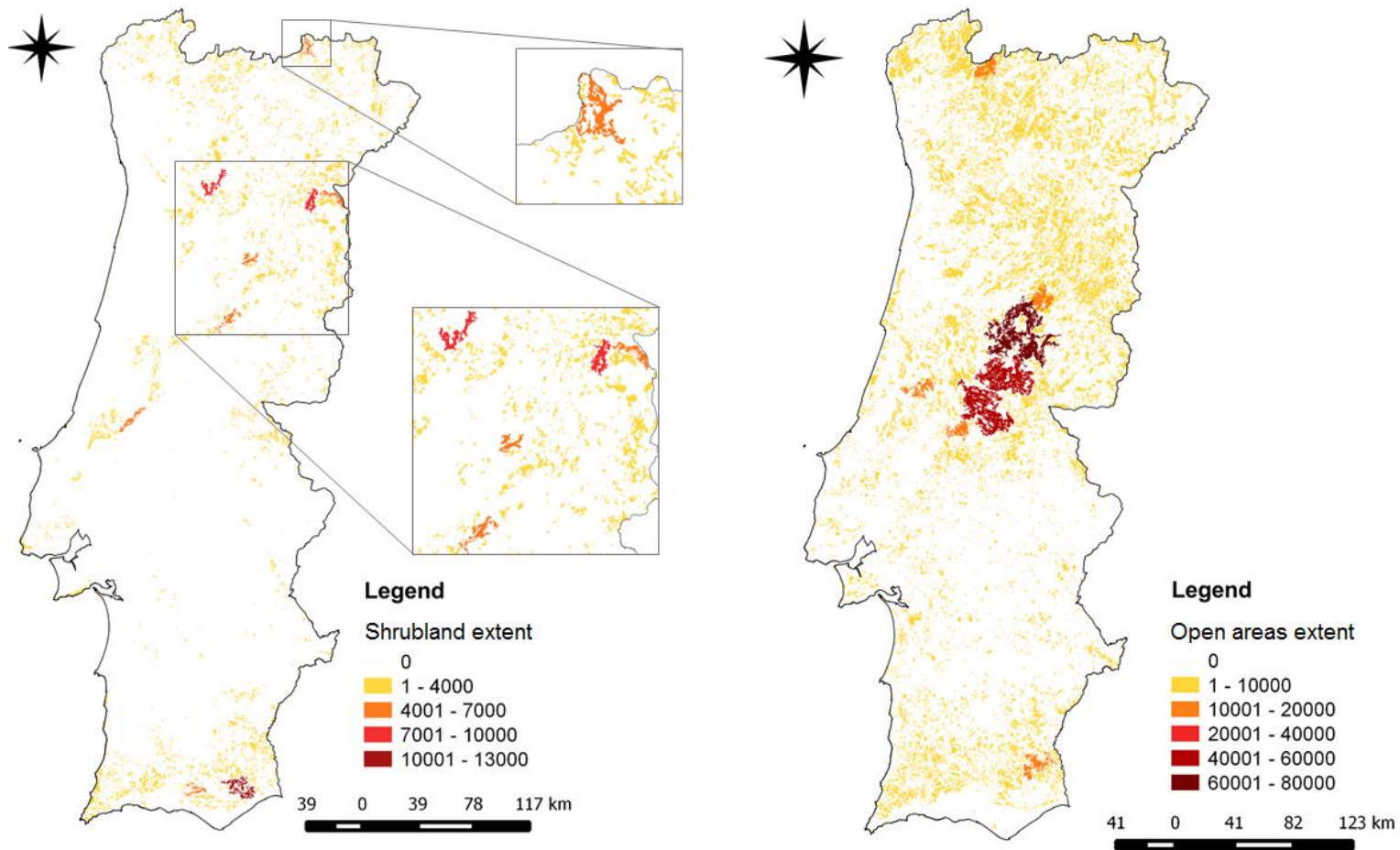


Figure 4 - Map of Portugal showing shrubland (left) and open areas extent (right). Units are in hectares.

Tables

Table 1 - Land use reclassification. CLC code and CLC level 3 obtained from Directorate-General for the Territorial Development's website.

CLC code	CLC level 3 category	Reclassified
111	Continuous urban fabric	Urban Areas
112	Discontinuous urban fabric	
121	Industrial or commercial units	
122	Road and rail networks and associated land	
123	Port areas	
124	Airports	
131	Mineral extraction sites	
132	Dump sites	
133	Construction sites	
141	Green urban areas	
142	Sport and leisure facilities	
211	Non-irrigated arable land	
212	Permanently irrigated land	
213	Rice fields	
221	Vineyards	
222	Fruit trees and berry plantations	

CLC code	CLC level 3 category	Reclassified
223	Olive groves	
231	Pastures	
241	Annual crops associated with permanent crops	
242	Complex cultivation patterns	
243	Land principally occupied by agriculture, with significant areas of natural vegetation	
244	Agro-forestry areas	
311	Broad-leaved forest (includes eucalyptus)	
312	Coniferous forest	Forest
313	Mixed forest	
322	Moors and heathland	Shrubland
323	Sclerophyllous vegetation	
321	Natural grasslands	
324	Transitional woodland-shrub	Open Areas
332	Bare rocks	
333	Sparsely vegetated areas	
334	Burnt areas	Urban Areas, Agricultural Land, Forest, Shrubland and Open Areas

Table 2 – Correlation matrix. The high correlated ($r>0.75$) are indicated in bold.

		Burn_Total	Burn+50HA	Burn+500HA	Nfire_Total	Nfire_+50HA	Nfire_+500HA	TSF_+50HA	TSF_+500HA	Alti_Max	Alti_Min	Alti_Mean	Alti_Range
Burn_Total	Pearson Correlation	1	1.000**	.993**	-.012	.270**	.458**	-.248**	-.293**	.214**	.197**	.208**	.085
	Sig. (2-tailed)		0.000	.000	.847	.000	.000	.000	.000	.000	.001	.001	.165
	N	267	267	267	267	267	267	265	220	267	267	267	267
Burn+50HA	Pearson Correlation	1.000**	1	.993**	-.012	.271**	.458**	-.248**	-.293**	.214**	.197**	.208**	.085
	Sig. (2-tailed)	0.000		.000	.849	.000	.000	.000	.000	.000	.001	.001	.165
	N	267	267	267	267	265	220	265	220	267	267	267	267
Burn+500HA	Pearson Correlation	.993**	.993**	1	.017	.300**	.460**	-.247**	-.294**	.190**	.170**	.182**	.093
	Sig. (2-tailed)	.000	.000		.787	.000	.000	.000	.000	.002	.005	.003	.128
	N	267	267	267	267	265	220	265	220	267	267	267	267
Nfire_Total	Pearson Correlation	-.012	-.012	.017	1	.843**	.282**	-.345**	-.115	.194**	.102	.150*	.351**
	Sig. (2-tailed)	.847	.849	.787		.000	.000	.000	.088	.001	.097	.014	.000
	N	267	267	267	267	265	220	265	220	267	267	267	267
Nfire_+50HA	Pearson Correlation	.270**	.271**	.300**	.843**	1	.631**	-.400**	-.306**	.233**	.180**	.209**	.214**
	Sig. (2-tailed)	.000	.000	.000	.000		.000	.000	.000	.000	.003	.001	.000
	N	267	265	265	265	267	220	265	220	267	267	267	267
Nfire_+500HA	Pearson Correlation	.458**	.458**	.460**	.282**	.631**	1	-.295**	-.440**	.219**	.219**	.221**	.028
	Sig. (2-tailed)	.000	.000	.000	.000	.000		.000	.000	.000	.000	.000	.653
	N	267	220	220	220	220	267	265	220	267	267	267	267

TSF_+50HA	Pearson Correlation	-.293**	-.248**	-.247**	-.345**	-.400**	-.295**	1	.456**	-.109	-.079	-.095	-.120
	Sig. (2-tailed)	.000	.000	.000	.000	.000	.000		.000	.075	.199	.121	.051
	N	220	265	265	265	265	265	265	220	265	265	265	265
TSF_+500HA	Pearson Correlation	-.456**	-.293**	-.294**	-.115	-.306**	-.440**	.456**	1	.080	.066	.074	.058
	Sig. (2-tailed)	.000	.000	.000	.088	.000	.000	.000		.235	.326	.272	.394
	N	220	220	220	220	220	220	220	220	220	220	220	220
Alti_Max	Pearson Correlation	.214**	.214**	.190**	.194**	.233**	.219**	-.109	.080	1	.962**	.991**	.255**
	Sig. (2-tailed)	.000	.000	.002	.001	.000	.000	.075	.235		.000	.000	.000
	N	267	267	267	267	267	267	265	220	267	267	267	267
Alti_Min	Pearson Correlation	.197**	.197**	.170**	.102	.180**	.219**	-.079	.066	.962**	1	.990**	-.018
	Sig. (2-tailed)	.001	.001	.005	.097	.003	.000	.199	.326	.000		.000	.770
	N	267	267	267	267	267	267	265	220	267	267	267	267
Alti_Mean	Pearson Correlation	.208**	.208**	.182**	.150*	.209**	.221**	-.095	.074	.991**	.990**	1	.122*
	Sig. (2-tailed)	.001	.001	.003	.014	.001	.000	.121	.272	.000	.000		.046
	N	267	267	267	267	267	267	265	220	267	267	267	267
Alti_Range	Pearson Correlation	.085	.085	.093	.351**	.214**	.028	-.120	.058	.255**	-.018	.122*	1
	Sig. (2-tailed)	.165	.165	.128	.000	.000	.653	.051	.394	.000	.770	.046	
	N	267	267	267	267	267	267	265	220	267	267	267	267
UrbanArea	Pearson Correlation	-.014	-.015	-.021	.009	-.008	.005	-.013	.118	-.277**	-.272**	-.277**	-.052
	Sig. (2-tailed)	.824	.812	.735	.882	.894	.930	.838	.081	.000	.000	.000	.397
	N	267	267	267	267	267	267	265	220	267	267	267	267

AgricLand	Pearson Correlation	-.148 [*]	-.148 [*]	-.182 ^{**}	-.177 ^{**}	-.158 ^{**}	-.140 [*]	.049	-.115	-.260 ^{**}	-.204 ^{**}	-.235 ^{**}	-.230 ^{**}
	Sig. (2-tailed)	.016	.016	.003	.004	.010	.023	.426	.089	.000	.001	.000	.000
	N	267	267	267	267	267	267	265	220	267	267	267	267
Forest	Pearson Correlation	-.122 [*]	-.122 [*]	.029	-.051	-.117	-.157 [*]	.072	.080	-.056	-.096	-.077	.136 [*]
	Sig. (2-tailed)	.047	.046	.642	.409	.056	.010	.246	.235	.362	.116	.212	.026
	N	267	267	267	267	267	267	265	220	267	267	267	267
Shrubland	Pearson Correlation	.126 [*]	.126 [*]	.077	.175 ^{**}	.174 ^{**}	.129 [*]	-.043	-.036	.168 ^{**}	.131 [*]	.151 [*]	.154 [*]
	Sig. (2-tailed)	.039	.039	.208	.004	.004	.035	.487	.593	.006	.033	.013	.012
	N	267	267	267	267	267	267	265	220	267	267	267	267
OpenAreas	Pearson Correlation	.127 [*]	.127 [*]	.005	.037	.085	.150 [*]	-.085	-.087	.062	.063	.063	.004
	Sig. (2-tailed)	.038	.038	.941	.551	.165	.014	.165	.199	.310	.304	.302	.942
	N	267	267	267	267	267	267	265	220	267	267	267	267
Evenness	Pearson Correlation	-.187 ^{**}	-.187 ^{**}	-.249 ^{**}	-.286 ^{**}	-.284 ^{**}	-.157 [*]	.118	.015	-.089	-.022	-.057	-.245 ^{**}
	Sig. (2-tailed)	.002	.002	.000	.000	.000	.010	.054	.830	.149	.715	.357	.000
	N	267	267	267	267	267	267	265	220	267	267	267	267

Table 3 –Correlation matrix (continued). The high correlated ($r > 0.75$) are indicated in red.

		UrbanArea	AgricLand	Forest	Shrubland	OpenAreas	Evenness
Burn_Total	Pearson Correlation	-.014	-.148*	-.122*	.126*	.127*	-.187**
	Sig. (2-tailed)	.824	.016	.047	.039	.038	.002
	N	267	267	267	267	267	267
Burn+50HA	Pearson Correlation	-.015	-.148*	-.122*	.126*	.127*	-.187**
	Sig. (2-tailed)	.812	.016	.046	.039	.038	.002
	N	267	267	267	267	267	267
Burn+50HA	Pearson Correlation	-.021	-.182**	.029	.077	.005	-.249**
	Sig. (2-tailed)	.735	.003	.642	.208	.941	.000
	N	267	267	267	267	267	267
Nfire_Total	Pearson Correlation	.009	-.177**	-.051	.175**	.037	-.286**
	Sig. (2-tailed)	.882	.004	.409	.004	.551	.000
	N	267	267	267	267	267	267
Nfire_+50HA	Pearson Correlation	-.008	-.158**	-.117	.174**	.085	-.284**
	Sig. (2-tailed)	.894	.010	.056	.004	.165	.000
	N	267	267	267	267	267	267
Nfire_+500HA	Pearson Correlation	.005	-.140*	-.157*	.129*	.150*	-.157*
	Sig. (2-tailed)	.930	.023	.010	.035	.014	.010
	N	267	267	267	267	267	267
TSF_+50HA	Pearson Correlation	-.013	.049	.072	-.043	-.085	.118
	Sig. (2-tailed)	.838	.426	.246	.487	.165	.054
	N	265	265	265	265	265	265

		UrbanArea	AgricLand	Forest	Shrubland	OpenAreas	Evenness
TSF_+500HA	Pearson Correlation	.118	-.115	.080	-.036	-.087	.015
	Sig. (2-tailed)	.081	.089	.235	.593	.199	.830
	N	220	220	220	220	220	220
Alti_Max	Pearson Correlation	-.277**	-.260**	-.056	.168**	.062	-.089
	Sig. (2-tailed)	.000	.000	.362	.006	.310	.149
	N	267	267	267	267	267	267
Alti_Min	Pearson Correlation	-.272**	-.204**	-.096	.131*	.063	-.022
	Sig. (2-tailed)	.000	.001	.116	.033	.304	.715
	N	267	267	267	267	267	267
Alti_Mean	Pearson Correlation	-.277**	-.235**	-.077	.151*	.063	-.057
	Sig. (2-tailed)	.000	.000	.212	.013	.302	.357
	N	267	267	267	267	267	267
Alti_Range	Pearson Correlation	-.052	-.230**	.136*	.154*	.004	-.245**
	Sig. (2-tailed)	.397	.000	.026	.012	.942	.000
	N	267	267	267	267	267	267
UrbanArea	Pearson Correlation	1	.019	.209**	-.121*	.019	-.165**
	Sig. (2-tailed)		.761	.001	.048	.757	.007
	N	267	267	267	267	267	267
AgricLand	Pearson Correlation	.019	1	-.033	.075	.042	.497**
	Sig. (2-tailed)	.761		.591	.223	.499	.000
	N	267	267	267	267	267	267
Forest	Pearson Correlation	.209**	-.033	1	-.003	.037	-.244**
	Sig. (2-tailed)	.001	.591		.967	.545	.000
	N	267	267	267	267	267	267

		UrbanArea	AgricLand	Forest	Shrubland	OpenAreas	Evenness
Shrubland	Pearson Correlation	-.121*	.075	-.003	1	.036	-.255**
	Sig. (2-tailed)	.048	.223	.967		.555	.000
	N	267	267	267	267	267	267
OpenAreas	Pearson Correlation	.019	.042	.037	.036	1	.211**
	Sig. (2-tailed)	.757	.499	.545	.555		.001
	N	267	267	267	267	267	267
Evenness	Pearson Correlation	-.165**	.497**	-.244**	-.255**	.211**	1
	Sig. (2-tailed)	.007	.000	.000	.000	.001	
	N	267	267	267	267	267	267