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From global to local: impacts of human disturbance on niche partitioning among carnivores

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Copyright Statement

Dissemination of research

Chapter 2 is published in the peer-reviewed journal *Biological Reviews* (Appendix I):

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Chapter 3 has been accepted for publication in the peer-reviewed journal *Mammal Review* (Appendix II):

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Chapter 4 has been prepared for submission in a peer-reviewed journal.

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“Better to yield when it is folly to resist, than to resist stubbornly and be destroyed.“

— Aesop, The Oak and the Reed

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All 147 species included in the literature reviews are depicted individually at the bottom of this thesis. Credit goes to Anaïs Tallon: I cannot thank you enough for your time, and for these beautiful drawings.

Abstract

Interspecific competition and resource partitioning are strong evolutionary forces, shaping communities. The mechanisms of coexistence and competition among species have been a central topic within community ecology, with a particular focus on mammalian carnivore community research. However, the influence of humans and their activities on those processes is still poorly understood. This thesis first reviews the existing literature on spatial, temporal, and trophic niche partitioning in carnivore communities. After extracting any reported effects of human disturbance, a theoretical framework is proposed, covering the three main outcomes of the impact of humans on resource partitioning, intraguild competition and community structure. Then, generalized linear mixed models are employed to evaluate the relative influence of a range of human, meteorological and ecological variables on the coefficients of temporal overlap within carnivore communities on a global scale, using data extracted from the existing literature. Findings show that the regulation of activity pattern is subject to strong site-specificity, and that temporal avoidance of both humans and competitors may be regulated by short, reactive responses, rather than long-term changes in behaviour. In addition, the methodology and reasoning employed by the currently available literature to calculate the coefficient of temporal overlap between pairs of species are evaluated. Key guidelines and recommendations are provided to future studies to develop an improved and standardised research practice on the study of animal activity pattern and temporal partitioning. Finally, multispecies occupancy models are used on secondary raw camera trap data to explore the fine-scale patterns of co-occurrence between red foxes and domestic cats within a rural–urban gradient in England, in relation to anthropogenic features in the landscape. This thesis fills an important knowledge gap on the effects of human pressures on carnivore communities, by focusing on the impacts on niche partitioning and coexistence. The research questions are addressed through an innovative gradient of spatial scales, human disturbance types, ecosystems and carnivore communities, thus yielding findings of global value. This study presents evidence that the disturbance humans impose on carnivores is reflected on their behaviour, which can modify interspecific interactions within the carnivore communities, and have cascading effects on community structure and ecosystem functioning.

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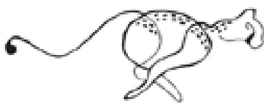
Chapter 1

General introduction

1.1. Welcome to the Anthropocene

Human encroachment into natural ecosystems is increasing at an alarming rate (Geldmann et al. 2014, Venter et al. 2016, Watson et al. 2016), and an estimated 60 to 80% of terrestrial land now faces some level of anthropogenic disturbance (Ellis & Ramankutty 2008, Watson et al. 2016, Ward et al. 2020). The Anthropocene refers to the current epoch, in which global human activities have become the dominant influence on climate and the environment (Crutzen & Stoermer 2000). The unrelenting increase in global human footprint severely impacts wildlife, and is responsible for what has been widely accepted as the start of the sixth mass extinction (Ceballos et al. 2015, 2017, Di Marco et al. 2018). Two dualistic conservation models have been proposed to reduce the deleterious effects of humans on wildlife, akin to the land-sparing versus land-sharing models used within a broader biodiversity conservation context (Green et al. 2005, Phalan et al. 2011, Kremen & Merenlender 2018). The separation model seeks to isolate people and nature by confining endangered wildlife to highly managed protected areas or to remote, uninhabited areas (e.g. Wilson 2016). However, this paradigm requires large wilderness regions, which may be difficult to attain in regions heavily colonized by humans (Woodroffe & Ginsberg 1998, Chapron et al. 2014). Contrastingly, the coexistence model strives to enable people and wildlife to share the landscape at finer spatial scales, whilst minimising human–wildlife conflicts. For this strategy to work, anthropogenic habitats and public attitudes need to be reshaped to accommodate wildlife and ensure human–wildlife coexistence (Rosenzweig 2003, Dickman 2010, Carter & Linnell 2016).



In shared landscapes, the alteration of landscapes for human residence or resource exploitation, in combination with the direct presence of humans and human activities, can give rise to behavioural responses and adaptations of wildlife to human disturbance (Sih et al. 2011, Tuomainen & Candolin 2011, Candolin & Wong 2012, Gaynor et al. 2018, Tucker et al. 2018). In addition, changes in the behaviour of one species can influence other species by reshaping population and community dynamics (Bolnick et al. 2011). Indeed, human-induced behavioural changes can have cascading effects on species interactions, with ecological implications for community structure and ecosystem function (Wilson et al. 2020). Thus, to fully understand the impact of humans on animal behaviour and communities, we need to improve our understanding of how species interact with each other, and how humans might influence such interactions.

1.2. Competition and coexistence in carnivore communities in a natural setting

According to Hutchinson's (1957) definition, the range of resources and environmental conditions allowing a species to persist in an ecosystem forms its ecological niche. The competitive exclusion principle (Gause 1934, Hardin 1960) states that two interacting species occupying similar ecological niches, and therefore competing for the same resources, cannot co-exist in the long term. Interspecific competition may result in the exclusion of the least competitive species from the habitat by its superior competitor, or in the local extinction of one or more species. Interspecific competition can also lead to niche differentiation, which facilitates coexistence among sympatric species. Indeed, the limiting similarity theory of

MacArthur & Levins (1967) highlights the existence of a threshold in niche similarity under which stable coexistence is possible. Thus, to achieve coexistence, competing species can segregate one or more dimensions of their ecological niche, a process commonly referred to as resource partitioning (or niche partitioning; Schoener 1974a). For instance, populations of coyotes —*Canis latrans*— and bobcats —*Lynx rufus*— in Florida can facilitate sympatry by segregating their diets (coyotes prey primarily upon large ungulates and complement their diets with large quantities of fruits, whereas bobcats primarily consume rodents and lagomorphs), and by having non-overlapping core areas in their home ranges (Thornton et al. 2004). Interspecific competition and resource partitioning regulate the strength of interactions among species, and are significant evolutionary forces shaping community structures (Schoener 1983, Wisheu 1998). In fact, the differentiations in ecological niches observed in contemporary competing species may well be the result of a stronger interspecific competition in the past (i.e. the ghost of competition past; Connell 1980).

Interspecific competition has been identified as a key mechanism structuring mammalian carnivore guilds (e.g. Linnell & Strand 2000, Caro & Stoner 2003, Hunter & Caro 2008). As is the case for all animals, two major forms of competitive interactions exist among carnivores: the first, exploitation competition, occurs when two species compete for the same resource indirectly (e.g. consumption of similar prey species; Hayward & Kerley 2008); the second, interference competition, happens when one species prevents another species from obtaining a resource directly (e.g. aggressive interactions near kill sites; Creel & Creel 1996).

In the carnivore guild, interference interactions can directly result in the injury or death of one of the competitors (i.e. intraguild predation; Palomares & Caro 1999), and has important implications for carnivore demography (Linnell & Strand 2000).

In both forms of competition, dominant predators can reduce the fitness of subordinate species (Jiménez et al. 2019). Subordinate carnivores can diminish this deleterious impact by partitioning resources from their dominant counterparts, and typically do so through a combination of three niche dimensions (Schoener 1974a): spatially, where subordinate species adjust their habitat use to limit sympatry with dominant predators (e.g. Durant 1998, Viota et al. 2012); temporally, where competitors alter their activity pattern to reduce the amount of time species are active simultaneously (e.g. Hayward & Slotow 2009); and trophically, where competitors segregate their diets by using different food resources (e.g. Karanth & Sunquist 1995).

Accumulating evidence, however, has reported high values of niche overlap within different competing carnivore guilds worldwide (e.g. Mitchell & Banks 2005, Glen & Dickman 2008, Cozzi et al. 2012, Davis et al. 2018), suggesting that niche segregation alone is not the fundamental mechanism driving coexistence, and may be the outcome of more complex processes (Vanak et al. 2013). For example, risk avoidance may often be a reactive, rather than predictive, process (Broekhuis et al. 2013, López-Bao et al. 2016). In this case, carnivore species can maintain awareness of their nearest competitors at all times and adapt their use of space and time to prevent risky encounters. As such, competing species live in a landscape in which contrasting habitats result in different levels of risk of interference competition (i.e. the landscape of fear; Laundré et al. 2001, Ritchie & Johnson 2009). Therefore, accurately characterising competitive interactions among carnivores may require investigating these processes at various spatiotemporal scales, to capture local variability. In addition, incorporating anthropogenic factors may be required to fully comprehend how these processes operate in landscapes shared with humans.

Typically, members of the carnivore guild are connected to a wide array of species in the ecosystem via interspecific interactions (Beschta & Ripple 2009, Prugh et al. 2009). Indeed, carnivores have been suggested to regulate ecosystem structures and functioning via density-mediated and behaviourally-mediated trophic cascades (Estes et al. 2011, Ripple et al. 2014). Similarly, intraguild interactions between a dominant large carnivore and a subordinate mesocarnivore may have indirect effects on the behaviour and demographic of a third smaller carnivore species (i.e. the carnivore cascade hypothesis; Levi & Wilmers 2012). However, as a result of a deeply rooted history of conflicts with humans (Treves & Karanth 2003), carnivores often change their behaviour in the face of anthropogenic disturbance, which can, in turn, interfere with their ecological role in the ecosystem (Ordiz et al. 2013a, Kuijper et al. 2016). Yet, the effects of human-induced behavioural changes in carnivores on interspecific interactions, and especially intraguild interactions among carnivores, are still largely unknown.

1.3. Human-induced behavioural changes in carnivores

Humans are highly-skilled predators (Darimont et al. 2015), and the fear they inspire may be a significant driver of changes in carnivores behaviour (Oriol-

Cotterill et al. 2015, Clinchy et al. 2016). Humans, through their activities, can also be strong exploitative competitors, for instance, through competition for prey (e.g. Henschel et al. 2011). As both direct and indirect competitors, carnivores may need to implement the aforementioned strategies of niche partitioning to reduce the competitive pressure from humans in order to facilitate coexistence (e.g. spatiotemporal changes in habitat selection; Suraci et al. 2019b). However, alterations of the landscape for human use may, in turn, interfere with the ability of carnivores to adjust their ecological niche. For instance, movements of carnivores are likely to be strongly disrupted in areas with a high human footprint (Tucker et al. 2018, Doherty et al. 2021), preventing the effective adaptation of habitat use to reduce encounters with humans. A contrario, carnivore species that are synanthropic (Johnston 2001) may purposely stay near human settlements to benefit from anthropogenic resources (Gehrt et al. 2010), whilst maintaining the avoidance of humans on a fine spatiotemporal scale (e.g. Gehrt et al. 2009). Therefore, humans can be both competitors and resource facilitators to carnivores, illustrating the complex relationship between the two groups.

Humans, whether as predators, competitors or resource facilitators, are likely to reshape species interactions and disrupt the natural patterns of resource partitioning that have evolved over a long period of time. Consequently, there may be potential for human-induced behavioural adaptations in carnivores to create a new dynamic of interspecific competition and coexistence among terrestrial mammalian carnivores. However, our knowledge of the impact of human disturbance on competition and coexistence within carnivore guilds is limited. For

instance, we do not know if the impact of humans is uniform and disruptive in nature, or if nuances exist. Besides, it is unclear whether human disturbance affects all competing species in the same way, and how alterations of competitive interactions can affect the composition and structure of the carnivore guild. Finally, there is a need to evaluate the different spatiotemporal scales of these processes, to better understand if the impact of humans is the same globally, or if variations exist between and within landscapes.

1.4. Thesis aims, objectives and structure

Carnivores often modify their behaviour in anthropogenic landscapes, in response to human disturbance. Yet, the mechanisms through which human-induced behavioural changes in carnivores may affect niche partitioning and intraguild competition and, in turn, the structure of carnivore communities, remain poorly understood. Filling this knowledge gap is imperative to fully understand how carnivore communities may be reshaped in a world under constant anthropogenic pressures. This knowledge is paramount in order to delineate actions to improve human–wildlife coexistence in shared landscapes, by informing the beneficial or deleterious effects of a range of human activities and land uses.

Knowledge on each of the three main dimensions of niche partitioning (i.e. trophic, spatial and temporal; Schoener 1974a) is imbalanced, and the potential influence of humans has not always been recognised. Perhaps the most obvious and well-studied strategy of niche partitioning is based around what species consume (i.e. trophic partitioning). Early on, anthropogenic food resources were included in the

description of the food habits of carnivores living close to human settlements (e.g. Reig et al. 1985). The rapid evolution of the tools used to compare diets, from visual examination (e.g. McDonald & Nel 1986) to molecular and genetic techniques (Gosselin et al. 2017), will enable to characterise the human influence on trophic partitioning among species with greater precision. Similarly, understanding how species use and share the landscape has long been of interest in the study of niche partitioning. Early studies investigated species home ranges and habitat preferences on relatively large spatial scales (e.g. White et al. 1995). However, recent studies highlight the importance of fine-scale spatial analysis to fully understand species response to human disturbance (e.g. Gosselink et al. 2003), and how such fine-scale spatial adaptations may affect species interactions in human-dominated landscapes. Finally, the temporal dimension is arguably the least-known niche dimension, and the influence of humans on animals' activity pattern has seldom been addressed. However, recent evidence suggests that wildlife may globally alter their activity levels in response to human disturbance (Gaynor et al. 2018, Nix et al. 2018). Yet, the repercussion of such changes onto temporal partitioning among carnivores is still poorly understood, despite its global significance.

This thesis has two main research aims. The first is to uncover the effects of human disturbance on niche partitioning and coexistence among carnivore guilds. This investigation strives to address the research questions through a gradient of spatial scales, human disturbance types, ecosystems and carnivore communities. The second aim of this project is to contribute towards an improvement in the rigour

and harmonisation of carnivore and behavioural sciences in anthropogenic landscapes, via a critical appraisal of published literature.

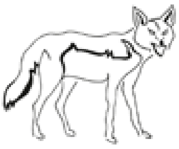
To achieve the first aim, the project seeks to achieve the following objectives, at different levels:

i. On a general and global scale, to identify the different effects of human disturbance on niche partitioning in mammalian carnivores, from the published literature.

ii. Focused on the temporal dimension and on a global scale, to quantify the influence of human disturbance on temporal partitioning in mammalian carnivores, from the published literature.

iii. On a regional scale, to quantify the fine-scale spatial interactions between two carnivores in England, using raw secondary data.

The second aim of this thesis is addressed by critically evaluating the published literature used throughout the first and second objectives, and the method used to quantify temporal niche partitioning. Additionally, recommendations and key guidelines for future studies are provided. This thesis has broad relevance for the conservation of carnivore species and carnivore communities. Recommendations on management strategies and policies are provided throughout the text, in the hope that the elements raised prompt an improvement of evidence-based wildlife management decisions and land-use planning.



To address the objectives, this thesis is divided into four data chapters and a final chapter containing an overall discussion and conclusions, as described below:

Chapter 2: Human disturbance has contrasting effects on niche partitioning within carnivore communities. This chapter reviews the existing research on niche partitioning among carnivore species globally, to extract any reported effect of human disturbance. Insights gained from this review are used to implement a theoretical framework covering the three main outcomes of the impact of humans on resource partitioning, intraguild competition and community structure.

Chapter 3: The impact of human disturbance on temporal partitioning within carnivore communities. This chapter uses data extracted from the existing literature to quantitatively evaluate the relative influence of a range of human, meteorological and ecological variables on the coefficients of temporal overlap within carnivore communities on a global scale. This chapter then discusses the importance of investigating ecological and behavioural patterns at different spatial scales to compare large-scale patterns with local variability.

Chapter 4: Coefficient of temporal overlap: evaluation of current practices and guidelines. This chapter builds on the literature extracted in chapter 3 to evaluate the methodology employed to calculate coefficients of temporal overlap and interpret results. Findings from this chapter provide key guidelines and

recommendations for future studies to develop an improved and standardised research practice.

Chapter 5: Habitat use and co-occurrence patterns of a native (Vulpes vulpes) and an invasive (Felis catus) carnivore species, in rural and suburban England. This chapter uses secondary data from a small-scale camera trap survey to uncover the patterns of habitat use and co-occurrence between native red foxes and invasive domestic cats within a rural–urban gradient in England, in relation to anthropogenic features in the landscape.

Chapter 6: Discussion and conclusion. This chapter evaluates the overall findings from the preceding data chapters. Further questions arising from the investigation are presented, and the ecological implications for terrestrial carnivore individuals, populations, communities and ecosystem functions are discussed. This chapter draws conclusions on the importance of the work in the field of carnivore ecology and improving knowledge on behavioural ecology overall during the Anthropocene.

Chapter 2

Human disturbance has contrasting effects on niche partitioning within carnivore communities

2.1. Abstract

Among species, coexistence is driven partly by the partitioning of available resources. The mechanisms of coexistence and competition among species have been a central topic within community ecology, with particular focus on mammalian carnivore community research. However, despite growing concern regarding the impact of humans on the behaviour of species, very little is known about the effect of humans on species interactions. The aim of this chapter is to establish a comprehensive framework for the impacts of human disturbance on three dimensions (spatial, temporal and trophic) of niche partitioning within carnivore communities and subsequent effects on both intraguild competition and community structure. The published literature on carnivore niche partitioning was reviewed (246 studies), and 46 reported effects of human disturbance were extracted. Evidence suggests that human disturbance impacts resource partitioning, either positively or negatively, in all three niche dimensions. The repercussions of such variations are highly heterogeneous and differ according to both the type of human disturbance and how the landscape and / or availability of resources are affected. The three main outcomes for the impacts of human disturbance on intraguild competition and carnivore community structure are presented in a theoretical framework: (a) human disturbance impedes niche partitioning, increasing intraguild competition and reducing the richness and diversity of the community; (b) human disturbance unbalances niche partitioning and intraguild competition, affecting community stability; and (c) human disturbance facilitates niche partitioning, decreasing intraguild competition and enriching the community.

Better integration of the impact of humans on carnivore communities is warranted in future research on interspecific competition.

2.2. Introduction

Traditionally, studies on interspecific competition have focused on pairs of carnivore species in their natural environment, without considering how humans could influence the different processes investigated (e.g. Creel & Creel 1996, Durant 1998). However, recent evidence suggests that beyond affecting species' behaviour (Gaynor et al. 2018, Tucker et al. 2018), human influence may be extended to how species interact (Dorresteijn et al. 2015). For example, carnivores facing negative interactions with humans can invest in antipredator behaviours in order to limit encounters with humans (Frid & Dill 2002). These behavioural adaptations may involve operating medium and fine-scale spatiotemporal avoidance of human activities (Llaneza et al. 2012, Oriol-Cotterill et al. 2015), and may interfere with competitor avoidance.

However, sensitivity to humans is not homogenous, and behavioural responses of wildlife to anthropogenic disturbance vary among species (Lowry et al. 2013, Samia et al. 2015). The most sensitive species can modify their spatiotemporal habitat use to maximise avoidance of human features and activities (e.g. Stillfried et al. 2015, Llaneza et al. 2018). For example, bobcats and coyotes inhabiting an urban nature reserve in California exhibited spatial and temporal displacement in response to human recreation, with the two species avoiding areas with higher human activity (George & Crooks 2006). Species selecting habitats with reduced human disturbance, a limited resource, could therefore face a higher risk of encountering competitors (Hayward et al. 2007, Dröge et al. 2017). Conversely, species more tolerant to humans can show a preference for human-modified environments over natural habitats (Deuel et al. 2017). Caracals —*Caracal caracal*— in South Africa have adapted their foraging behaviour to access highly available prey resources in agroecosystems, thus reducing their use of natural forest habitats (Ramesh et al. 2017). Although this behaviour comes with a higher risk of human encounters, it could decrease the probability of facing intraguild competitors which avoid these habitats (Ordeñana et al. 2010).

In addition, the attitude of humans towards carnivores is also unequal among species (Dressel et al. 2015). Lethal management is often biased towards large carnivores, mainly due to competition for food with humans (Treves & Karanth 2003, Oriol-Cotterill et al. 2015). The long-term persecution of large carnivores by humans has benefited some mesocarnivore populations by reducing competition with larger carnivores, a process known as the ‘mesopredator release’ effect (Crooks & Soulé 1999, Prugh et al. 2009), influencing in some cases the abundance and distribution of these species (Lapoint et al. 2015, Krofel et al. 2017, Newsome et al. 2017, Jiménez et al. 2019).

This chapter reviews the literature on niche partitioning among the carnivore guild, with the aim to synthesise all reported effects of human disturbance on the spatial, temporal and trophic niche dimensions, and propose a comprehensive framework investigating how these effects may impact the strength of intraguild competition, and how they could end up reshaping the structure of carnivore communities.

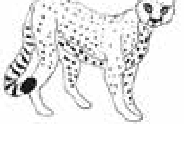
The proposed framework will be valuable to future research by highlighting gaps in the investigation of human impacts on carnivore communities and coexistence. This chapter provides additional recommendations to develop an effective and standardised research practice.

2.3. Methods

2.3.1. Literature search

A literature search was performed in October 2018, using the electronic databases Scopus (www.scopus.com) and Web of Science (www.webofknowledge.com). The following key word combination was used to search for peer-reviewed literature written in English, with no time limitation: (niche OR spatial OR temporal OR resource OR diet OR trophic) AND (partitioning OR overlap OR segregation OR separation) AND (carnivor*). The review protocol was applied following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al. 2009). This review was limited to articles published in peer-reviewed journals, leading to the omission of books, book chapters, conference proceedings, working papers, dissertations and other unpublished works. Future studies could gain additional insight by adopting a more encompassing approach, and examining grey literature.

The database search returned 1,095 records (Figure 2.1), which were subsequently screened by reading the title and abstract. To be included in the next stage, studies had to investigate the spatial, temporal and / or trophic niche of at least two sympatric mammalian terrestrial carnivore species. After this screening, 256 articles



were retained, and their full text assessed for eligibility. To be included in the final synthesis, studies had to calculate the proportion of niche overlap between two or more species or measure the relative influence of one species on another's niche utilisation (e.g. multispecies occupancy models). At this stage, 166 studies fulfilled the inclusion criteria and were retained.

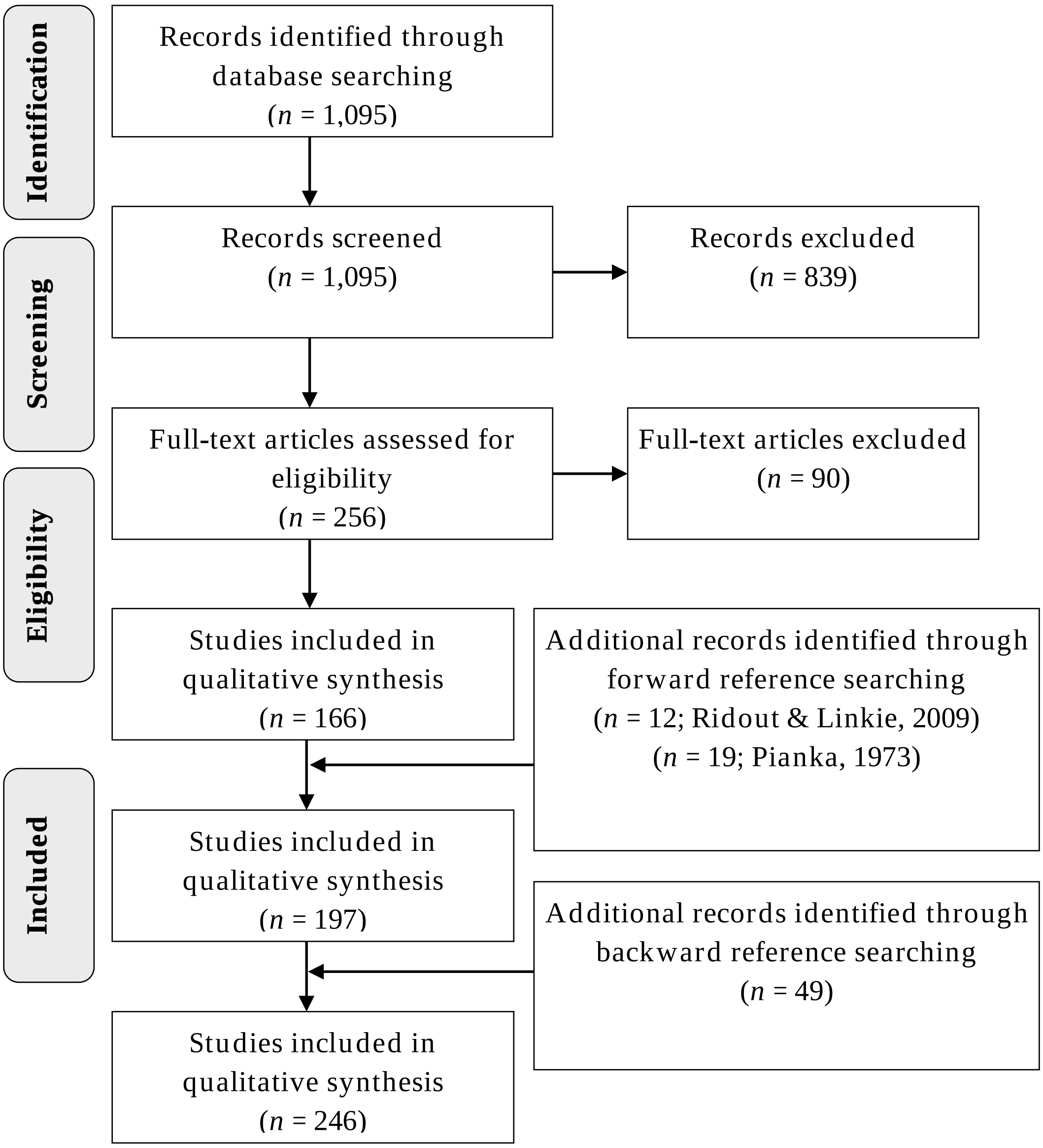


Figure 2.1. Preferred reporting items for systematic reviews and meta-analysis flowchart (Moher et al. 2009).

Although niche overlap between pairs of species was measured using a variety of methods, two methods prevailed: Pianka's overlap index (Pianka 1973), a tool used to measure the spatial, temporal and trophic niche overlap between species, which was used by 47% of the included studies (n = 78); and the coefficient of temporal overlap (Ridout & Linkie 2009), which was used by 72% of the studies investigating temporal niche partitioning (n = 38). Therefore, a second literature search was performed, using the same electronic databases, in order to identify all articles citing Pianka's overlap index or the coefficient of temporal overlap. The review protocol for these articles was repeated with the same inclusion and exclusion criteria. Following this forward reference search, 31 additional records were included, increasing the number of retained articles to 197. Finally, the reference list of each of the 197 included studies was screened to identify relevant publications (i.e. backward reference searching or 'snowballing'), adding a further 49 studies. A total of 246 articles were included in the final synthesis. As few ecosystems are undisturbed by humans, studies were included in the final synthesis whether they mentioned human disturbance at their study site or not. Using this approach allowed to identify the proportion of studies in the existing literature that incorporated human disturbance in their evaluation of niche partitioning within carnivore communities.

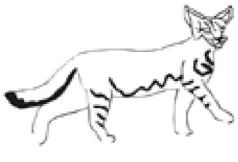
2.3.2. Data extraction

For every selected study, the following information was extracted: (1) interacting carnivore species; (2) time frame of the study (part or totality of a solar year); (3) presence / absence of seasonality in the analysis; (4) niche dimension investigated

(spatial, temporal and / or trophic); (5) experimental design (see below); and (6) presence / absence of human disturbance at the study site. The presence or absence of human disturbance was based on any information provided by the authors in the publications, commonly in the study area or discussion sections (e.g. “The study area comprises […] several public and private protected areas […] and unprotected areas, with different histories of logging and poaching”; Cruz et al. 2018; p.3).

The experimental design of each study was classified according to the definition provided in Hone (2007). Thus, studies were classified as either classical experiments (with simultaneous control, replication, and randomisation of the treatment, and statistical analyses), quasi-experiments (with simultaneous control but without replication, randomisation or analyses), pseudo-experiments (with replication, randomisation or analyses of the treatment, but lacking simultaneous control), or simple observations (none of the above).

Human disturbance was classified into two groups: top-down (i.e. relating to the direct presence of humans or human-related entities) or bottom-up (i.e. referring to modifications of the landscape for human use) disturbance. Subsequently, human disturbance was divided into seven types: top-down disturbance had four categories — lethal management of herbivores, lethal management of carnivores, non-lethal recreational activities, and presence of exotic carnivore species — whereas bottom-up disturbance had three — built environment, landscape modified for arable purposes, and landscape modified for pastoral purposes —.



When a study mentioned and analysed human disturbance, the effects on niche overlap were extracted from information provided in the results and discussion sections of the publication, and classified according to: (1) type of human disturbance; (2) direction of the effect on niche overlap (increase, decrease, or no effect found); and (3) strength of inference (statistical analysis, descriptive statistics or speculative). Speculative inference was defined as claims that are not directly measured, usually relying on the conclusions of other empirical studies to find support. To improve the accuracy of the review, any effect that was solely based on speculation was not included.

The relative strength of the effects of different types of human disturbance on values of overlap was assessed using two approaches. First, whenever possible, effect sizes from the studies demonstrating an impact of human disturbance on niche partitioning were computed by subtracting the overlap value with low disturbance from the overlap value with high disturbance (Overlap_{HD} – Overlap_{LD}). Comparing effect sizes between studies (i.e. a meta-analysis) is a powerful statistical procedure (Cohn & Becker 2003), offering support to the body of evidence found in the quantitative assessment of the literature. However, if the treatment effect is not consistent from one study to another, performing a meta-analysis may produce unreliable results (Lau et al. 1997). For this reason, the relative strength of each effect was also estimated by comparing how many times they were found in the literature.

2.4. Results and discussion

2.4.1. Description of the literature

Altogether, 246 studies published between 1986 and 2018 investigated the spatial, temporal or trophic niche partitioning between pairs of carnivore species. The most frequently studied niche dimension was the trophic (48.8%), followed by the spatial (30.4%) and temporal dimensions (20.8%). Most studies followed an observational design (n = 192, 78%), followed by pseudo-experiments (n = 39, 15.9%), and quasi-experiments (n = 15, 6.1%). None of the studies followed a classical experimental design. Over half of all studies (n = 151, 61.4%) mentioned human disturbance at their study site, but only a third (n = 72, 29.3%) incorporated human disturbance in the study design and interpretation of findings. A small proportion of studies (n = 68, 27.6%) included seasonality in their analysis (e.g. calendar seasons, breeding seasons), and most (n = 51, 75%) reported seasonal variations in the intensity of niche partitioning.

In total, 94 effects of human disturbance on carnivore niche partitioning were extracted from 72 studies. Half of these effects (n = 48, 51.1%) were founded on speculations (i.e. the effects were not directly measured), so were excluded from the synthesis. The remaining 46 effects were extracted from 34 studies and were supported by statistical analysis (n = 33, 71.7%) or descriptive statistics (n = 13, 28.3%). Most of the effects of human disturbance were extracted from pseudo-experimental (n = 28, 60.9%) and quasi-experimental (n = 16, 34.8%) studies. Only two effects were extracted from an observational design found in a single study.

A relatively small proportion of studies reporting an effect of human disturbance used an experimental design that enabled the extraction of an effect size, but nonetheless 43 effect sizes were extracted from 13 studies (Figure 2.2). The remaining 21 studies employed methodologies that did not compare coefficients of overlap between low versus high disturbance areas directly, hence preventing the extraction of comparable effect sizes. For instance, more than half of the studies investigating spatial niche partitioning (n = 11 out of 21) used multispecies occupancy models, and derived the influence of human variables based on which model was performing best. Additionally, the investigation of the different types of human disturbance on niche overlap showed a high degree of specialisation across studies, with too few replicates of each type of human disturbance among studies to conduct a reliable meta-analysis in all three niche dimensions. For instance, the effect sizes extracted show an overall increase in temporal overlap between species resulting from human disturbance, seemingly dominated by the impact of recreational activities (Figure 2.2). However, 14 of the 15 effects of recreational activities on temporal overlap were extracted from a single study (Wang et al. 2015). Similarly, 10 out of the 13 effects of agroecosystems on trophic overlaps were extracted from a single study (Palacios et al. 2012). For these reasons, effect sizes were not included in the rest of this review, and the relative importance of the different effects of human disturbance was instead estimated by comparing how many times they were found in the literature review.

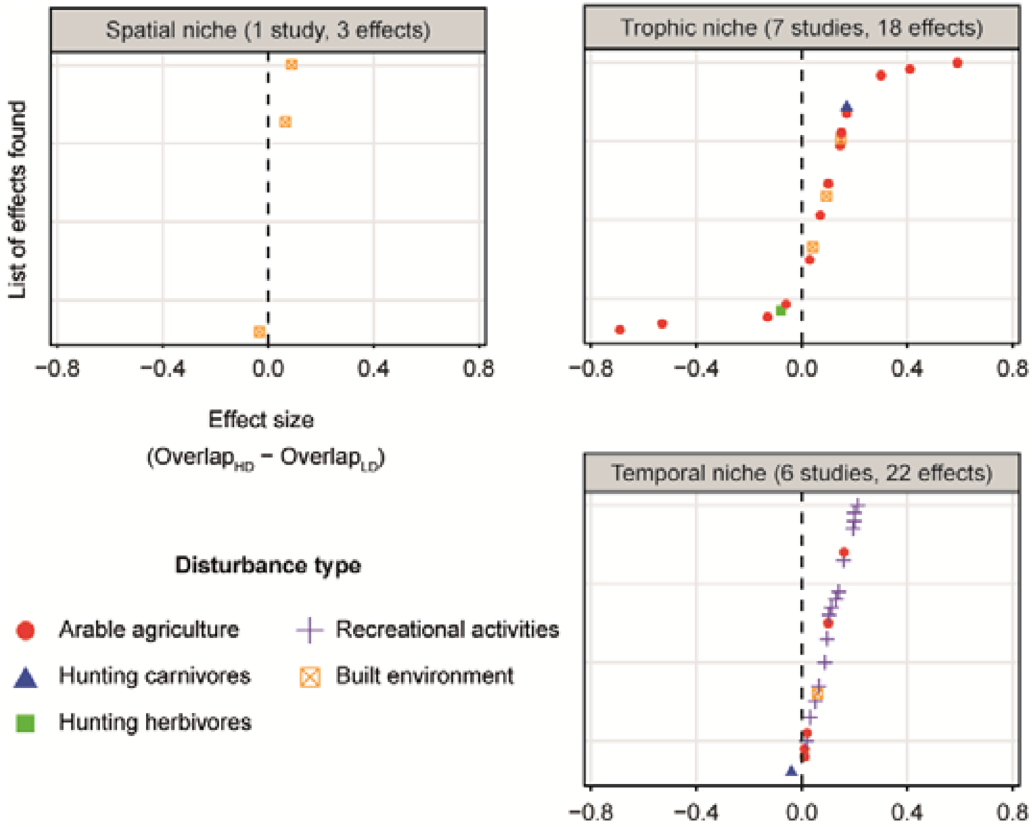


Figure 2.2. Forest plot of the extracted effect sizes of human disturbance on niche overlap between carnivore species, categorised by niche dimension and type of human disturbance. HD: high disturbance; LD: low disturbance.

2.4.2. Human influence on niche partitioning, intraguild competition, and carnivore community

Overall, the observed impact of human disturbance on niche partitioning between carnivores was not unidirectional (Figure 2.3). In fact, there was a similar number of effects reporting an increase or a decrease in niche overlap associated with human disturbance (21 and 17 effects, respectively) and, in eight studies, there was no effect of human disturbance on niche overlap (Table 2.1). More changes in niche overlap between carnivores resulted from bottom-up than top-down human disturbance (24 and 14 effects, respectively). Across niche dimensions, there were more references

to the spatial dimension (bottom-up effects: 16, top-down effects: 5), followed by trophic (bottom-up effects: 6, top-down effects: 5) and temporal dimensions (bottom-up effects: 2, top-down effects: 4).

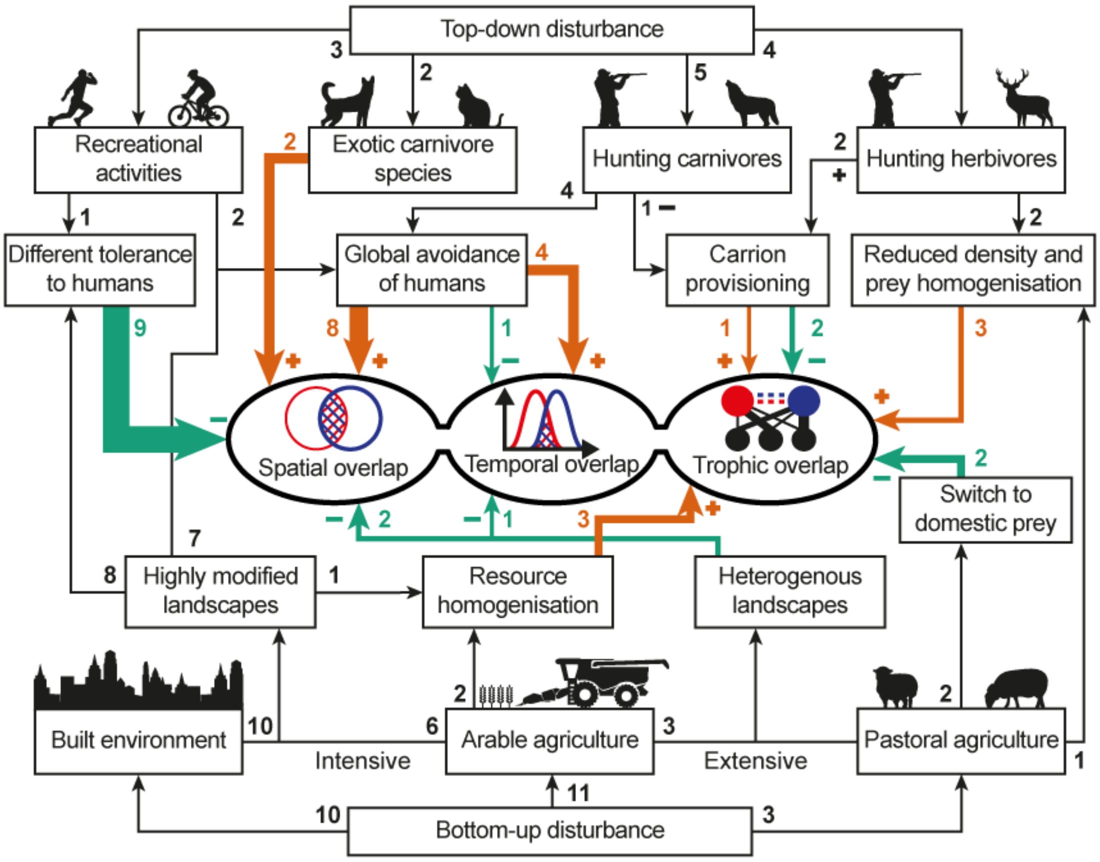


Figure 2.3. Descriptive pathways illustrating the reported evidence-based effects of human disturbance on three dimensions of niche overlap (spatial, temporal and trophic) in carnivore communities. Numbers at the start of each link correspond to the number of studies reporting that effect. Orange arrows and numbers with a + sign represent an increase in niche overlap. Green arrows and numbers with a – sign represent a decrease in niche overlap. The width of the coloured links is proportional to the number of effects on niche partitioning found in the literature search.

Table 2.1. Number and type of human disturbances extracted from the reviewed papers, and their effects on niche overlap among carnivore communities. ↗ = increase; ↘ = decrease; Ø = no impact.

	Spatial niche overlap			**Temporal niche overlap**			**Trophic niche overlap**			
Human disturbance	↗	↘	Ø	↗	↘	Ø	↗	↘	Ø	**Total**
Top-down										
Hunting carnivores	2	-	2	1	1	-	1	-	-	7
Hunting herbivores	-	-	-	-	-	-	1	3	1	5
Recreational activities	-	1	1	2	-	-	-	-	-	4
Exotic carnivore species	2	-	-	-	-	1	-	-	-	3
Bottom-up										
Arable agriculture	3	4	-	1	1	1	2	-	-	12
Pastoral agriculture	-	-	-	-	-	-	2	1	-	3
Built environment	3	6	1	-	-	1	1	-	-	12
Total top-down	4	1	3	3	1	1	2	3	1	19
Total bottom-up	6	10	1	1	1	2	5	1	-	27
Grand total	10	11	4	4	2	3	7	4	1	46

The evidence found here suggest that human disturbance can affect all three niche dimensions investigated in both directions: increasing and decreasing effects on niche overlap. Changes in niche partitioning following human disturbance are therefore not uniform and are conditional on both the type of human disturbance, and how the surrounding landscape and limiting resources are affected. Nevertheless, three predominant influences of humans on carnivore niche partitioning stand out: (a) human disturbance impedes niche partitioning, increasing intraguild competition and reducing the richness and diversity of the community; (b) human disturbance unbalances niche partitioning and intraguild competition, affecting community stability; and (c) human disturbance facilitates niche partitioning, decreasing intraguild competition and enriching the community (Figure 2.4). Despite having seemingly opposite direction, these three influences are not mutually exclusive. Many landscapes are most likely affected by more than one of these influences, and the repercussions onto the carnivore community vary depending on the relative intensity of each disturbance.

2.4.2.1. Human disturbance impedes niche partitioning

The majority of carnivore species probably perceive humans as frightening, whether they present a direct threat or not (Frid & Dill 2002, Clinchy et al. 2016), so they adapt their behaviour accordingly, at different spatiotemporal levels, to limit encounters with humans (Carter et al. 2012, Ahmadi et al. 2014, Sazatornil et al. 2016). Avoidance of humans can be achieved spatially, with carnivores seeking refuge in safer habitats to reduce risks of anthropogenic mortality (Loveridge et al. 2017, Parsons et al. 2019). Theoretically, this could increase local densities of

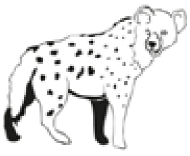
competing species and constrain spatial niche partitioning. Indeed, increased spatial overlap following avoidance of humans was the second most-reported effect, with eight studies reporting an increase in spatial overlap between carnivores in refuge habitats due to the direct avoidance of humans (Farris et al. 2017a, Sogbohossou et al. 2018) or human-related features (De Angelo et al. 2011, Pereira et al. 2012, Lewis et al. 2015, Nagy-Reis et al. 2017, Cruz et al. 2018, Smith et al. 2018). Avoidance of humans can also be achieved temporally. Similar to other mammals, carnivores have exhibited a global shift to a more nocturnal activity pattern around humans (Gaynor et al. 2018). Three studies documented carnivores that, as a consequence of human activity, were squeezed into a narrower temporal niche and faced higher levels of temporal overlap with intraguild competitors (Carter et al. 2015, Lewis et al. 2015, Wang et al. 2015, but see Sogbohossou et al. 2018).

Other causes of increases in niche overlap may be linked to the reduction in food availability following lethal wildlife management. Coexistence among large carnivores is partially enabled by their capacity to partition their prey by size (Karanth & Sunquist 1995). However, global prey depletion, and the loss of prey diversity, can render prey partitioning harder to achieve. For instance, three studies documented an increase in trophic overlap following depletion and homogenisation of the prey base (Palacios et al. 2012, Creel et al. 2018, Drouilly et al. 2018). Alternatively, two studies highlighted carnivore species diversifying their diets by including livestock (Amroun et al. 2006, Foster et al. 2010). Although this may alleviate interspecific competition for food in the short term, it can promote

human–carnivore conflicts and be detrimental to the long-term conservation of these species (e.g. Harihar et al. 2011).

In addition, predator control, when applied uniformly across the landscape, can reduce local carnivore densities (Robinson et al. 2008). However, prey carcasses attributed to kills by large carnivores can form a large part of scavenging carnivores' diets, and can potentially reduce interspecific competition among mesocarnivores (Van Dijk et al. 2008, Yarnell et al. 2013). Hence, reductions in large carnivore abundance can limit carrion provision for scavengers, weakening trophic niche partitioning between mesocarnivores. This effect, however, was only reported once, by a study comparing mesopredator diet overlap between two study areas with a large difference in grey wolf —*Canis lupus*— density due to a wolf-control program (Sivy et al. 2018). Additionally, this effect can be partially mitigated by provisioning carcasses resulting from hunting activities, as two studies documented (Barrull et al. 2014, Tsunoda et al. 2017), or livestock practices (Cortés-Avizanda et al. 2010). However, artificial disposal of carrion may inadvertently affect non-target species (e.g. Fležar et al. 2019), and does not replace the ecosystem services provided by large carnivores as carrion providers (e.g. facilitation of mesocarnivore suppression; Prugh & Sivy 2020).

Disruption of spatiotemporal niche partitioning is likely to be a common outcome of human disturbance, and could increase the frequency at which negative interactions take place among carnivores, thus increasing the potential for interference competition. Such increase in competition can have a negative impact on subordinate carnivores, further reducing the probability of survival of threatened



carnivore species (Elbroch & Kusler 2018). Similarly, the narrowing of the available trophic niche, and associated weakening of trophic partitioning, can increase exploitation competition among carnivore species (Karanth & Sunquist 1995, Creel et al. 2018). Under these circumstances, subordinate species can reduce competition with dominant species by switching to more abundant, usually smaller, prey (Randa et al. 2009, Foster et al. 2010, Drouilly et al. 2018). This mechanism is, however, unlikely to be successful if the secondary prey base is also depleted, in which case the effects of dietary overlap could also be particularly detrimental to less-competitive species (Hayward & Kerley 2008). Ultimately, increasing intraguild competition artificially among carnivores could decrease the density of subordinate species, or even exclude these species from specific habitats (Linnell & Strand 2000, Berger & Gese 2007).

2.4.2.2. Human disturbance unbalances niche partitioning

Responses of carnivores to human modification of landscapes fluctuate among species according to their degree of ecological flexibility (Lyra-Jorge et al. 2008, Caruso et al. 2016). Certain species can use modified landscapes as a shelter from competitors, which may not be as tolerant of human disturbance (Gosselink et al. 2003). Spatial overlap between carnivores is therefore reduced, advantaging more-tolerant species that can now occupy a niche with reduced competition. The reduction of spatial overlap arising out of a different tolerance to humans was found nine times in this review, in landscapes with varied intensity of human use, ranging from heavily modified urban areas (Lesmeister et al. 2015, Wang et al. 2015) and agricultural systems (De Angelo et al. 2011) to smaller villages (Prigioni et al.

2008, Farris et al. 2016). For instance, black bears —*Ursus americanus*— in North America are detected in close proximity to roads more frequently than grizzly bears —*Ursus arctos*—, their dominant competitors (Apps et al. 2006, Ladle et al. 2018). Similarly, red foxes —*Vulpes vulpes*— in North America can use areas with higher urban development as spatial refuges to limit co-occurrence with coyotes (Moll et al. 2018, Mueller et al. 2018). Although the reduction of spatial overlap following an asymmetrical avoidance of humans was the most reported effect in this review, it should be interpreted with caution as it indicates the spatial exclusion of species less tolerant to humans rather than an equal reduction in overall competition among species. Consequently, human disturbance could lead to the competitive exclusion or local extinction of species unable to adapt (Grimm et al. 2008) and a decrease in species diversity. Indeed, switches in community composition and loss of species diversity owing to human activity have been observed in other taxa (e.g. birds in urban environments; Blair 1996, small mammals in farming landscapes; Michel et al. 2006).

Species tolerant to humans can also use modified habitats to exploit highly abundant anthropogenic food resources (McKinney 2006, Bateman & Fleming 2012) or prey populations benefiting from habitat transformation (López-Bao et al. 2019). According to competition theory (Schoener 1982), the diets of competing carnivores should converge when resources are abundant (e.g. Fedriani et al. 1999). Three studies observed this pattern, wherein carnivores competing in human-dominated landscapes had high trophic overlaps owing to the homogenisation of resources and

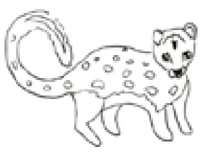
abundance of anthropogenic food resources (Barrull et al. 2014, Kauhala & Ihalainen 2014, Smith et al. 2018).

The ecological flexibility of generalist species allows them to increase their niche breadth by exploiting both natural and anthropogenic resources (Verdade et al. 2011), thereby increasing their fitness and competitive ability (Rosalino & Santos-Reis 2011, Concepción et al. 2015). This can present a double threat to specialist species, who not only are negatively impacted by anthropogenic land alterations (Fisher et al. 2003), but must now face new dominant competitors encroaching on their niche. As human land use keeps increasing (Seto et al. 2011), competitive interactions among carnivores could be destabilised, and the carnivore community reshaped into an homogenous community dominated by generalist and tolerant species (Reed & Merenlender 2008, Ordeñana et al. 2010). The paramount example of generalist predators whose competitive strength is enhanced by the use of anthropogenic resources is feral and free-ranging domestic carnivore species (e.g. dogs —*Canis domesticus*—; Vanak & Gompper 2009a). These species are commonly found at high densities in human-dominated and nearby natural habitats, and can have high niche overlaps with native carnivore species in the trophic (e.g. Glen & Dickman 2008), spatial (e.g. Vanak & Gompper 2010), and temporal (e.g. Farris et al. 2015a) niche dimensions. In addition, these species can have deleterious effects on wildlife by acting as a reservoir for diseases (e.g. cross-species transmission of the canine distemper virus; Deem et al. 2000). However, the effect of their presence on coexistence of native species has largely been understudied, and this review found

only two studies documenting an increase in spatial overlap between native species following displacement by dogs (Farris et al. 2016, 2017a).

2.4.2.3. Human disturbance facilitates niche partitioning

When kept under extensive management, agricultural landscapes can be shaped into highly heterogeneous ecosystems (Duelli 1997), facilitating fine-scale spatial segregation among species (Pereira et al. 2012, Cruz et al. 2015), a key mechanism allowing sympatry (Rosenzweig 1981). Additionally, carnivores in these communities can segregate the food resources they consume (Carvalho & Gomes 2004), and display a wide range of activity patterns by matching those of their main prey, further promoting coexistence with competitors through temporal partitioning of activity (Monterroso et al. 2014). However, only three studies reported the facilitation of spatiotemporal niche partitioning by anthropogenic heterogeneous systems, and all were undertaken in Mediterranean landscapes (Pereira et al. 2012, Monterroso et al. 2014, Cruz et al. 2015). Habitat heterogeneity and complexity at various spatial scales can benefit the entire carnivore guild (Williams et al. 2002) by reducing intraguild competition, thus nurturing rich carnivore communities. Promoting diversity in the carnivore guild is beneficial as it increases resilience to environmental stress (Sobrino et al. 2009) and overall stability of the community (e.g. Worm et al. 2006). However, if current global agricultural intensification keeps expanding, the reduction in landscape heterogeneity towards more homogenous landscapes lacking different cover and refuges (Warner 1994) could impact on the beneficial effects of extensive agroecosystems on the carnivore community (Stoate et al. 2001, Cruz et al. 2018).



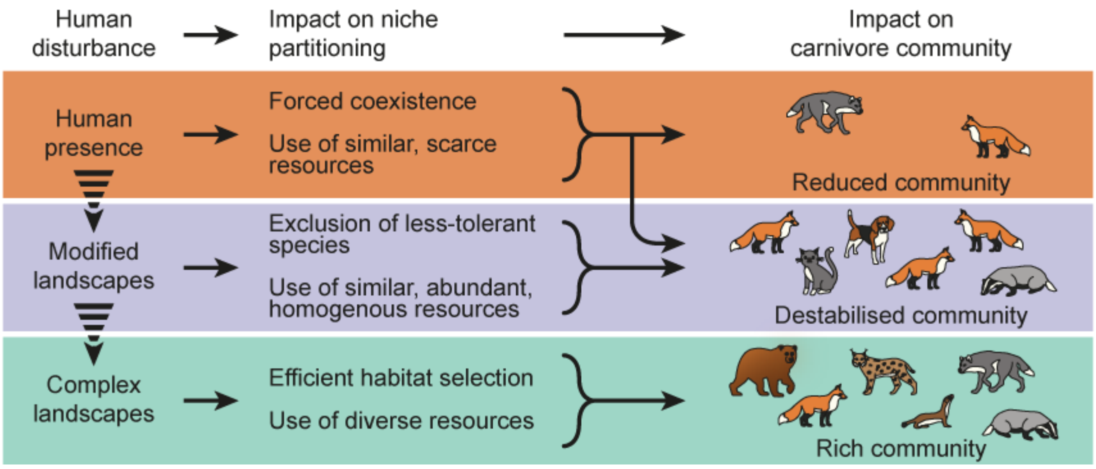


Figure 2.4. Theoretical framework of the three main impacts of human disturbance on niche partitioning and intraguild competition among carnivore species, and subsequent reorganisation of the carnivore community. Top, orange section: the omnipresence of the human apex predator forces sympatry between species seeking refuge in safer areas. Additionally, the overall reduction in diversity and abundance of wild food resources negatively affects trophic partitioning. As a result, the strength of interspecific competition is increased, which can lead to a carnivore community with poor species abundance and diversity. This can also unbalance the community, by enhancing the competitive advantage of species tolerant to human presence. Middle, blue section: human presence can trigger important modifications at the landscape level, interfering with habitat partitioning, and strongly increasing the abundance of trophic resources linked to human activities. As a result, the strength of interspecific competition is unbalanced to the advantage of species tolerant to humans and capable of using these anthropogenic resources, possibly resulting in a destabilised carnivore community. Bottom, green section: some landscape modification can, by contrast, facilitate niche partitioning in all niche dimensions, if they prioritise complex, heterogeneous landscapes (e.g. extensive agriculture). This reduces the strength of interspecific competition, and could promote a rich and diverse community.

2.4.3. Implications for conservation and future studies

This review provides a comprehensive framework that outlines the variety of impacts that humans, and their activities, have on competition among carnivores.

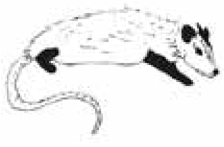
In addition, the findings emphasise the omnipresence of human influences on niche partitioning within carnivore communities, albeit having effects with diverse directions and magnitude. The patterns highlighted could be of great benefit to the conservation of carnivores in most landscapes, and especially those impacted by anthropogenic activities. Indeed, 12 species involved in this review are currently listed as globally endangered under the IUCN Red List of Threatened Species, and eight of these species were sympatric with at least one dominant competitor species. For instance, the subordinate, endangered black-footed ferret —*Mustela nigripes*— is sympatric with the American badger —*Taxidea taxus*— a dominant competitor and intraguild predator. The competitive impact of dominant carnivores on subordinate species may be driven by the outcome of the impact of human disturbance (e.g. by aggregating these competing species in particular habitats), which would add an additional stress to the conservation of threatened species. Conversely, promoting the diversity of habitats and opportunities for segregation may help reduce the intensity of interspecific competition, and be beneficial to the conservation of threatened species.

The findings presented in this chapter have important implications not only for the conservation of carnivores, but for the overall preservation of ecosystems. Indeed, carnivore species have been shown to perform important ecological roles that can affect entire ecosystems (Roemer et al. 2009, Estes et al. 2011, Ripple et al. 2014). For instance, intensive modifications of the landscape, following human activities, are typically associated with a reduction in species diversity in the carnivore community, to the benefit of highly competitive generalist species (Crooks 2002,

McKinney 2008). This decrease in species diversity may result in the loss of ecological functions when the fulfilment of this function cannot be replaced by an alternative species (i.e. functional redundancy; Flynn et al. 2009, Huijbers et al. 2015), and can have detrimental effects on the resilience of ecosystems (Mori et al. 2013). Therefore, maintaining a diversity of habitats and trophic resources in altered landscapes may help the competitive abilities of specialist species, thus restoring species diversity and ecological functions, and be beneficial to the functioning and resilience of the ecosystem.

This review also highlights understudied areas of research that will guide and encourage more experimental research to be undertaken on the anthropogenic influence of species coexistence in an ever-changing world. Using an evidence-based approach that can inform policy makers and land managers about the potential impacts of human activities on carnivore communities, and how to regulate them effectively, is a necessary step towards successful carnivore conservation (Pullin & Knight 2003).

Most of the selected studies mentioned potential effects of human disturbance at their study site, but only a fraction (72 out of 151) included these effects in the interpretation of the results. Additionally, only 13 studies used a design that compared values of overlap between low- and high-disturbance treatments, allowing the strength of the impact of human disturbance on niche partitioning to be measured (Figure 2.2). The most plausible reason for this is the high proportion of observational studies, where the effects of human disturbance were not tested, and thus relied on the conclusions of other studies. There is a lack of experimental



studies on niche partitioning within carnivore guilds, due to the ethical and logistical constraints of manipulative experiments, and the rarity of true controls in nature. The relative importance of experimental and observational studies in large carnivore science is a topic of debate (Allen et al. 2017a, Bruskotter et al. 2017). As the human footprint on natural ecosystems keeps growing, performing more manipulative studies will be necessary to measure the effects of human disturbance on species interactions accurately. In addition, some studies pooled data from multiple locations, subject to different human pressures, to calculate niche overlap (e.g. one temporal overlap value between sympatric felids in a study area combining tropical forest and oil palm plantation; Hearn et al. 2018). Although combining data from different study areas can compensate for low sample sizes (e.g. for elusive species with large spatial requirements), merging the data in such a way can mask the effects of human disturbance and produce unreliable conclusions. Nevertheless, incorporating human disturbance in the study of species interactions and competition is a productive area of research, and will improve knowledge on carnivores and community composition in general.

Likewise, a small proportion of all studies (68 out of 246) took seasonal variability into account, and most of these (51 out of 68) found seasonal variations occurring naturally in the intensity of niche partitioning (e.g. Carvalho & Gomes 2004, Vanak et al. 2013, Monterroso et al. 2014). Similarly, seasonal fluctuations in the intensity of human disturbance exist (e.g. high peaks in nature-based tourism in summer) and could potentially affect niche partitioning. For instance, Gosselink et al. (2003) observed considerable differences in the intensity of habitat partitioning between

coyotes and red foxes between summer and winter, attributed to the drastic loss of cover in an intensive row-crop agricultural system in winter. Our understanding of human influences on niche partitioning cannot be complete without incorporating natural or human-induced seasonal variations in niche partitioning, and future studies are encouraged to include such seasonal variations in their analyses.

Another limitation is the prevalence of studies investigating only one single niche dimension (180 studies out of 246). Niche partitioning is a multidimensional dynamic process, in which changes in one niche dimension may be balanced by opposing changes in other dimensions (Schoener 1974a). For instance, by increasing their nocturnal activities, some predators may increase their consumption of nocturnal prey species (Smith et al. 2018), which could indirectly increase trophic overlap with other nocturnal predators. Unidimensional studies of the influence of humans on niche partitioning are useful, but favouring investigations of multiple niche dimensions simultaneously will greatly benefit our understanding of the processes at play.

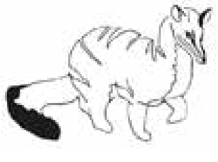
Finally, niche overlap was used as a proxy to estimate the intensity of interspecific competition, but it is not a direct measure of competition (Schoener 1982). As none of the studies included herein measured the intensity of competition directly, this review relied on the conclusions of supplementary studies to establish how changes in niche partitioning following human disturbance could impact intraguild competition and cause community structure change. Such support was found in literature that did not measure niche partitioning, focusing purely on interspecific competition or human–carnivore coexistence (e.g. Sale 1974, Bateman & Fleming

2012). Thus, future research juxtaposing niche overlap with intraguild competition intensity will improve our understanding of carnivore coexistence, and how it can be influenced by human disturbance.

2.5. Conclusions

The findings in this study reveal that human disturbance influences all three dimensions of niche partitioning in carnivore communities, with a nearly identical number of effects reported to increase and decrease niche overlap. However, variations in niche partitioning following human disturbance are not always reflected linearly on the intensity of intraguild competition. Indeed, they can have contrasting effects depending on how the surrounding landscape and the availability of resources are affected by human disturbance.

Although the trajectories of its effects can be diverse, there is no doubt that human disturbance impacts intraguild competition and community composition in carnivore guilds. By systematically including the human dimension in the analysis of interspecific competition, the scientific community will gain a better understanding of the way carnivore communities will be reshaped if human disturbance keeps increasing. Applying the systematic approach proposed herein to other animal taxa and other types of species interactions would be beneficial to research of the influence of humans on wildlife.



Chapter 3

The impact of human disturbance on temporal partitioning within carnivore communities

3.1. Abstract

Interspecific competition is an important evolutionary force, influencing interactions among species and shaping the composition of communities. In mammalian carnivores, to reduce the risks of negative encounters between competitors, species can employ a strategy of temporal partitioning, adapting activity patterns to limit synchronous activity. This strategy of non-human competitor avoidance, however, may be influenced by the expansion of human activities, which has driven wildlife towards nocturnality. Therefore, it could be hypothesised that the disruption of temporal niche partitioning by humans and their activities could increase temporal overlap between carnivores, enhancing interspecific competition. After a review of the published literature, generalized linear models were employed to quantitatively evaluate the relative influence of a range of human, meteorological and ecological variables on the coefficients of temporal overlap within carnivore communities on a global scale. None of the models investigated showed evidence of human disturbance on temporal partitioning between carnivores on a global scale. This illustrates that temporal avoidance of humans and competitors does not always follow a consistent pattern, and that its strength may be context-dependent and relative to other dimensions of niche partitioning (spatial and trophic). Similarly, the regulation of activity patterns may be under strong site-specificity, and be influenced by a combination of biotic and abiotic characteristics. Additionally, temporal avoidance of both humans and competitors may be regulated by short, reactive responses that do not impact activity patterns in the longer term. Although the global disruption of temporal

partitioning attributed to human disturbance was not detected, carnivore communities may still experience an increase in interspecific competition in other niche dimensions in human-dominated landscapes. Further research would benefit from using controlled experimental designs and investigating multiple dimensions of niche partitioning simultaneously. Finally, studies would benefit from complementing the coefficient of temporal overlap with other metrics of fine-scale spatiotemporal interactions.

3.2. Introduction

Interspecific competition is an important component regulating community structures (Schoener 1983, Wisheu 1998), and competing species must partition the resources they utilise to allow coexistence (MacArthur & Levins 1967). Resource partitioning is mostly achieved in three, often interacting, niche dimensions, being the spatial, temporal, and trophic dimensions (Schoener 1974a). Many species can, for instance, adjust their activity patterns to reduce the risk of encountering dominant non-human competitors (Carothers & Jaksić 1984, Kronfeld-Schor & Dayan 2003). In most animal communities, temporal partitioning of activity may not be the primary strategy used to limit interspecific competition (Schoener 1974a). However, carnivores could use it more than any other taxa due to the severe risks of injuries associated with interference competition (Schoener 1974a, Palomares & Caro 1999, Hunter & Caro 2008). Indeed, temporal segregation of activity between carnivores has been observed on multiple occasions (e.g. Hayward & Slotow 2009, Brook et al. 2012, Bischof et al. 2014), and could be a strategy frequently used by subordinate carnivores to reduce negative encounters with dominant counterparts, fine-tuned by a reactive response to immediate risks (e.g. Broekhuis et al. 2013).

The human apex predator (Darimont et al. 2015) produces predatory cues that are comparable to that of natural competitors or predators (e.g. human voice; Frid & Dill 2002, Clinchy et al. 2016). Human persecution has driven behavioural adaptations in most species, including both predators and prey, to limit encounters with humans and reduce human-related mortality risks (Frid & Dill 2002, Ordiz et al. 2011), being also modulated by the intensity of persecution (Sazatornil et al. 2016). Such anti-predator behaviour in response to humans can be employed regardless of the underlying threat, and even non-lethal human disturbance can drive an avoidance response (Frid & Dill 2002).

As humans are mostly diurnal, carnivores can switch their activity patterns towards more nocturnal hours to avoid potentially negative interactions (Gaynor et al. 2018). Indeed, local increases in wildlife nocturnality have been observed in direct response to variations in landscape-wide human-derived risks (e.g. during hunting season; Di Bitetti et al., 2008; Ordiz et al., 2012; Stillfried et al., 2015; but see Theuerkauf, 2009), reinforced by a lasting response to close human encounters (e.g. Ordiz et al. 2013b, Clinchy et al. 2016). The intensity with which animals adapt their circadian activity patterns to human disturbance may not be the same for all species, and depends on the behavioural plasticity and life-history characteristics (Lendrum et al. 2017). However, a recent meta-analysis by Gaynor et al. (2018) suggests that this pattern is observed globally and could be a common response from wildlife facing human disturbance. In undisturbed areas, carnivores need to

operate a trade-off between obtaining optimal resources and avoiding dominant competitors (Hayward & Slotow 2009). In human-altered habitats, carnivores may need to incorporate a third crucial element to this trade-off by avoiding humans. Therefore, since temporal partitioning is a common strategy used by carnivore species to coexist, and humans can impact on the activity patterns of species, human disturbance could interfere with the strategy of temporal partitioning between competing carnivores.

Disruption of niche partitioning can increase interspecific competition, and carry multiple ecological and community consequences. However, niche partitioning is a multidimensional dynamic process, and an increase in overlap in one niche dimension may be compensated by a decrease in another (Schoener 1974a). Therefore, interspecific competition may not necessarily be a direct result of the niche overlap in a single dimension. Similarly, not all carnivore species may be impacted equally by human disturbance, and the intensity of the avoidance response to humans may vary among species (e.g. Caruso et al. 2016). Due to direct threat, competition with humans for food, and depredation on livestock, apex carnivores typically experience most persecution (Inskip & Zimmermann 2009) and live in a landscape of fear of human-related mortality (Oriol-Cotterill et al. 2015). As a consequence, large carnivores have indeed been observed to shift their activity towards nocturnal hours (Gaynor et al. 2018). However, mesocarnivore species that are more tolerant of human disturbance (e.g. Gosselink et al. 2003) may shift their activity pattern to a lesser degree when facing human disturbance, thus maintaining temporal partitioning with dominant apex predators (Frey et al. 2020).

Unequal sensitivity to humans can induce a behavioural mesopredator release, wherein disturbance-induced alterations of activity pattern in large carnivores benefit the fitness of mesocarnivores by increasing the amount of time allocated to other activities (e.g. foraging; Brown et al. 1999). In addition, apex predators are typically found in lower densities in areas of higher human influence (Wolf & Ripple 2017), which may then limit the need for medium-sized carnivores to alter their activity pattern in response to the risk of encountering dominant competitors in disturbed landscapes.

Many carnivores now live in environments that are under human pressure, and are subject to a combination of bottom-up (e.g. modification of the landscape; Chapron et al. 2014, Venter et al. 2016) and top-down (e.g. hunting; Darimont et al. 2015, Ripple et al. 2016a) anthropogenic forces. The impact of human disturbance on a wide range of biological interactions has been widely studied (e.g. intraspecific competition; Nevin & Gilbert 2005, predator–prey interactions; Muhly et al. 2011, animal–plant interactions; Neuschulz et al. 2016). Moreover, we know that human disturbance has already reduced the niche available to animals in other dimensions (e.g. trophic, Creel et al. 2018, spatial, Tucker et al. 2018), which can result in large-scale increases in niche overlap (Manlick & Pauli 2020). However, knowledge of the influence of humans on coexistence and temporal niche partitioning between carnivores is still limited. Thus, there is a need to address this question, since not only can temporal displacements and reductions of activity carry costs that reduce species fitness (e.g. Beale & Monaghan 2004, Ciuti et al. 2012), it can also alter the way species interact, which can have cascading implications (Suraci et al. 2019a).

This chapter addresses this knowledge gap by conducting a global quantitative review of the temporal niche partitioning between terrestrial carnivores. Based on a priori knowledge of the factors influencing wildlife activity patterns, the relative influence of diverse human, meteorological and ecological factors as potential determinants of temporal partitioning within carnivore communities are investigated. Drawing on a global dataset covering a variety of ecosystems, carnivore communities and types of human disturbance, this chapter investigates whether human disturbance affects temporal niche partitioning uniformly and on a global scale. The effects of additional meteorological and ecological factors hypothesised to influence niche partitioning are also tested, either on their own or through interactions with human disturbance.

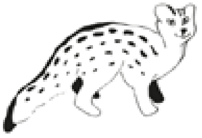
3.3. Methods

3.3.1. Literature search

To investigate temporal partitioning between carnivores, a literature search was performed in December 2019, wherein all peer-reviewed articles and grey literature citing the coefficient of temporal overlap proposed by Ridout and Linkie (2009) were examined. This method knows a growing popularity in the science of animal behaviour, illustrated by a rapidly increasing rate of citation. Hence, it has been widely accepted as one of the preferred methods to investigate temporal partitioning between animals, using camera trap data (i.e. time-stamped images of species in a known location). The coefficient of overlap uses a kernel density estimation method that ranges from 0 (no overlap) to 1 (complete overlap).

Articles citing Ridout and Linkie’s (2009) method in Scopus (cited 212 times; www.scopus.com), Web of Science (cited 195 times; www.webofknowledge.com) and Google Scholar (cited 338 times; https://scholar.google.com) were extracted. After removing duplicates, 356 articles were assessed for eligibility. Records were restricted to studies that calculated the coefficient of temporal overlap between at least one pair of sympatric carnivore species. In addition, studies were removed if one of the carnivores was an invasive species, because the recent sympatry of invasive species may not have allowed sufficient time for native species to develop a consistent strategy of temporal avoidance (e.g. Wang & Fisher 2012, Fancourt et al. 2019).

A second literature search was performed in June 2021, considering literature published up to December 2019 only, wherein all peer-reviewed articles and grey literature citing Rowcliffe et al. (2014) and the `*activity*´ package (Rowcliffe 2019) were examined. This method fits kernel density functions to animal activity data, and calculates a coefficient of temporal overlap between two activity curves using the algorithm provided by Ridout & Linkie (2009). Therefore, the coefficients of temporal overlap yielded by the `*overlap*´ package (Ridout & Linkie 2009) and `*activity*´ package (Rowcliffe 2019) are directly comparable. Articles citing Rowcliffe et al. (2014) and Rowcliffe (2009) in Scopus (cited 149 and 53 times respectively), Web of Science (cited 133 and 0 times) and Google Scholar (cited 218 and 72 times) were extracted. Studies were then assessed following the same eligibility strategy as in the first literature search, and added to the overall dataset.



Finally, species combinations which were present only once in the dataset were discarded. By doing so, the analysis focused on variations in temporal overlap within species combinations facing different anthropogenic and environmental conditions. Therefore, each species combination included in the analysis had at least two coefficients of temporal overlap, extracted from at least two different study areas. In the end, 43 studies were included in the quantitative analysis and final synthesis.

3.3.2. Data extraction

The coefficients of temporal overlap between pairs of carnivore species were extracted from the results sections of the 43 studies. For every value of temporal overlap, the following information on the interacting carnivore species was recorded: (1) species name; (2) taxonomic family; (3) average adult body mass; and (4) baseline activity pattern (Table 3.1).

To investigate the effect of anthropogenic and environmental conditions on coefficients of temporal overlap, the approximate geographic centre and size of every study area were extracted from the methodology section, when clearly stated, or through visual estimation of the maps provided in the articles. Based on a priori knowledge of factors affecting circadian activity pattern of carnivores, the following characteristics of the landscape within each study area was then averaged: (1) human density; (2) proportion of built-up environment; (3) proportion of pasture; (4) Simpson's landscape diversity index; (5) annual precipitation; (6) annual mean temperature; and (7) carnivore community richness (see Table 3.1 for detailed

methodology, source, spatial resolution and description of each variable). To ensure maximum consistency in the landscape metrics among study areas, only global databases were used. A trade-off was therefore operated between spatial resolution (finer when using the appropriate local databases for each study area) and homogeneity in the methods of calculation for each variable. This chapter did not aim to measure fine-scale temporal responses of animals to each of the variables of interest, but rather to detect a global response to human disturbance. Therefore, the analysis did not include variability in landscape characteristics within each study area, but instead focused on variability between sites. When studies indiscriminately grouped their camera trap data from more than one location, the value of each study area was averaged to create a unique value that best represents the overall conditions of the surrounding landscape. Spatial analyses were performed using a Geographical Information System (ArcGIS v10.7.1; ESRI, Redlands, California).

Table 3.1. Description, spatial resolution, range of variability and source of the variables extracted from each study areas and included in the a priori models.

Variables	**Description**	**Scale**	**Mean ± SD (range)**
Human density	Average inhabitants / km^2 in the study area during the year of data collection. For studies that span over more than one year, the first year was selected.	1km	84.5 ± 181.1 (0.1 – 886)
Built-up environment	Fractional cover (%) of built-up environment in the study area in 2015.	100m	2.9 ± 5.8 (0 – 27.3)
Pasture	Fractional cover (%) of pastures in the study area in 2000.	10km	20.8 ± 22 (0 – 91.1)
Simpson's landscape diversity index	Simpson's landscape diversity index (SIDI) in the study area calculated from a discrete land cover classification in 2015. Land cover classes comprised shrubs, herbaceous vegetation, crops, built-up, bare, wetland, closed forest and open forest.	100m	0.3 ± 0.3 (0 – 0.7)
Precipitation	Annual precipitation (mm) in the study area, averaged for the 1970-2000 period.	1km	1148.1 ± 800.8 (215 – 3149.9)
Temperature	Annual mean temperature (°C) in the study area, averaged for the 1970-2000 period.	1km	18.2 ± 6.4 (0.6 – 28.4)
Carnivore community richness	Number of mesocarnivores and large carnivores inhabiting part or all of the study area using the 2019 IUCN Red List update.	n/a	LC: 1.3 ± 2.0 (0 – 8) MC: 12.9 ± 5.5 (5 – 27)
Body mass ratio	Average body mass of larger species / Average body mass of smaller species.	n/a	7.4 ± 11.1 (1 – 73.8)
Baseline activity pattern	Species activity pattern: (1) nocturnal, (2) cathemeral or crepuscular, (3) diurnal.	n/a	(1): 18 (2): 24 (3): 1

Sources for variable: Human density: WorldPop (Lloyd et al. 2017); Built-up environment and Simpson's landscape diversity index: Copernicus 2015 global land cover database (Buchhorn et al. 2019), Fragstats v4 for calculating SIDI (McGarigal et al. 2012); Pasture: Global Agricultural Lands: Pastures, 2000 (Ramankutty et al. 2008); Precipitation and Temperature: WorldClim (Fick & Hijmans 2017); Carnivore community richness: IUCN Red List of threatened species (IUCN 2020); Body mass ratio and Baseline activity pattern: PanTHERIA database (Jones et al. 2009).

3.3.3. Data analysis

3.3.3.1. *Paired studies*

First, the findings of any studies that investigated the causal effect of human disturbance on temporal partitioning between carnivores (i.e. increase, decrease, or no effect), using an experimental or quasi-experimental design (i.e. studies with a simultaneous experimental control, Hone 2007) were qualitatively evaluated. Typically, such studies calculated and compared the coefficients of temporal overlap of similar species combinations between areas classified as under low or high human disturbance. Information of interest comprised the type of human disturbance that was investigated, and whether the authors were able to demonstrate a clear change in the coefficients of temporal overlap between the areas under low or human disturbance (i.e. when the 95% confidence intervals of the two coefficients did not overlap).

3.3.3.2. *Global models*

Using knowledge from previous studies investigating factors affecting circadian activity pattern of carnivores, ten models were explored, covering human, meteorological and ecological factors that could affect the coefficient of temporal overlap between carnivore species (Table 3.2; see justifications below). Thus, the coefficient of temporal overlap was the dependent variable, and models were fitted using Generalized Linear Mixed Models (Zuur et al. 2009), with a logit link function and beta distribution, appropriate for continuous variables restricted to an interval between 0 and 1 (Ferrari & Cribari-Neto 2004). Species combination was added as a

random effect in each model, with levels representing different locations where the species combinations were studied, and conducted model selection using AIC (Akaike 1981). Having a minimum of two replicates per species combination, and adding it as a random factor, allowed to artificially create a paired comparison design (Montgomery 2017). By doing so, the analysis could focus on the variance in coefficients of overlap explained by the different explanatory variables within species combinations, rather than testing the variance between species combinations. Two analyses were conducted in parallel:

1) The first “full” analysis used the entire dataset, and assumed that every study and coefficient of temporal overlap had similar precision. This allowed to use the entire dataset, favouring large sample size over more sophisticated models.

2) The second “weighted” analysis assigned a precision index to each value of the dependent variable. The coefficient of temporal overlap is a derived measure based on modelled activity patterns, and is associated with uncertainty (commonly provided as 95% confidence intervals). This analysis accounted for the variance associated with the dependent variable, by assigning non-null weights to the observations (with the values in weights being inversely proportional to the dispersions). Therefore, each coefficient of temporal overlap was assigned a weight equal to the inverse of the width of the 95% confidence interval. Because numerous studies included in this review did not provide the uncertainty associated with their coefficients of temporal overlap, the second “weighted” dataset was smaller than the first “full” dataset.

When no single model is clearly superior to the others in the set (e.g. typically AIC$_w$ ≥ 0.90), extracting information from single models can lead to weak inferences, and multimodel inference should be favoured (Burnham & Anderson 2002). As this was the case in this chapter (see Results), a model-averaging technique was applied to the top-ranked models with similar AIC (ΔAIC < 2), to build a full average model with 95% confidence. Spearman's rank correlation coefficients (ϱ) were calculated to investigate multicollinearity between the continuous predictors, and in case of highly correlated variables ($\varrho > 0.70$, Zar 2010), one of the variable was excluded from the average model. All modelling analyses were performed using the R packages `*glmmADMB*´ (Skaug et al. 2016), `g*lmmTMB*´ (Brooks et al. 2017) and `*MuMln*´ (Kamil 2019) in R version 3.6.1 (Team R Core 2018).

Table 3.2. A priori models testing human, meteorological and ecological continuous variables as predictors of coefficients of temporal overlap between sympatric carnivores. Hypothesis justification and support can be found in the text. SIDI = Simpson's landscape diversity index.

Variables	**Hypothesis**	**Impact on overlap**
Human density	Human presence and their diurnal activity are associated with increased nocturnality in carnivores.	Increase
Built-up environment	Human presence is higher in urban areas which leads to carnivores in urban areas being more nocturnal than in rural areas.	Increase
Pasture	Livestock depredation is a source of human–carnivore conflict. Frequent lethal management of carnivores in pastoral landscapes is associated with increased carnivore nocturnality.	Increase
Simpson’s landscape diversity index	Complex habitat mosaics nurture rich communities, and temporal partitioning is selected to facilitate stable coexistence.	Decrease
SIDI * pastures	The effects of landscape diversity are diminished in landscapes with a higher proportion of pastures.	Non-linear
Precipitation	Scarcity of spatially fixed waterpoints in dry areas forces temporal partitioning.	Increase
Temperature	Extremely high temperatures drive crepuscular or nocturnal behaviour.	Increase
Precipitation * temperature	The effects of precipitation are magnified in extremely hot areas.	Non-linear
Carnivore community richness	In richer communities, temporal partitioning is selected to facilitate stable coexistence.	Decrease
Body mass ratio	Species combinations with higher body mass ratios may invest less in temporal partitioning, and more in spatial partitioning, to improve coexistence.	Increase

3.3.4. Model justification

Carnivores have been found to increase their nocturnal activity in habitats with higher human presence (e.g. urban areas; Carter et al. 2015, Lewis et al. 2015, Wang et al. 2015), which can lead to higher temporal overlap among carnivore species

(Table 3.2; Hypotheses 1 and 2). Such temporal avoidance of humans may be especially predominant in pastoral landscapes, where human-related mortality risks are higher due to human–carnivore conflicts emerging from livestock depredations (Frank & Woodroffe 2001, Loveridge et al. 2010), therefore potentially increasing temporal overlap between carnivores even further in pastoral landscapes (Table 3.2; Hypothesis 3). Conversely, landscapes that are kept under traditional mosaic management, with a mix of natural and anthropogenic land use, can facilitate habitat selection and temporal partitioning (Monterroso et al. 2014, Curveira-Santos et al. 2017), and could reduce temporal overlap between species (Table 3.2; Hypothesis 4). Nevertheless, the reduction of temporal overlap attributed to higher landscape diversity may be diminished in landscapes with a higher proportion of areas associated with extensive grazing systems (Table 3.2; Hypothesis 5).

The daily activity patterns of animals can also be regulated by meteorological and ecological factors, which could influence the way carnivores interact with each other. For instance, in arid landscapes, where water features are a scarce and spatially-fixed resource, there is little opportunity to achieve spatial avoidance of dominant competitors (Atwood et al. 2011). Thus, subordinate species can concentrate their activity patterns at times where their dominant counterparts are less active (Atwood et al. 2011, Edwards et al. 2017), potentially reducing temporal overlap (Table 3.2; Hypothesis 6). In habitats with high daytime temperatures, shifting activity to night-time may help species reduce thermal stress (Fuller et al. 2016, Rabaiotti & Woodroffe 2019). However, this could reduce the temporal niche available to segregate with competitors (Astete et al. 2017), increasing temporal

overlap (Table 3.2; Hypothesis 7). In addition, cases of extreme thermal stress may cause most or all species to shift to nocturnal activities, rendering temporal partitioning at waterpoints unachievable. Therefore, any increase in temporal overlap through increased precipitation would be negated by higher daytime temperatures (Table 3.2; Hypothesis 8).

The strength and outcomes of species interactions is also dependent on the community composition and the interacting species (Sentis et al. 2017). In rich, and thus more complex, carnivore communities, temporal partitioning may facilitate stable coexistence between co-occurring species (Monterroso et al. 2014). Therefore, higher carnivore species richness could decrease the average temporal overlap within the community (Table 3.2; Hypothesis 9). Alternatively, the temporal overlap among some pairs of species could increase in areas with higher species richness, given that there are more species to avoid, leading to trade-offs and thus higher overlap with some species in the community (Curveira-Santos et al. 2017). Additionally, carnivore species with similar body mass have higher potential for competition, especially if they have similar diets (Wilson 1975, Dayan & Simberloff 2005). Smaller carnivores may also be at more risk of intraguild predation from larger carnivores (Woodward & Hildrew 2002). Edwards et al. (2015) observed that species combinations with higher differences in body mass used spatial partitioning to a greater extent than temporal partitioning. Conversely, species combinations with lower body mass ratios may invest in temporal partitioning to facilitate stable coexistence (Di Bitetti et al. 2010, Edwards et al. 2015). Therefore, temporal overlap may increase with high values of body mass ratios (Table 3.2; Hypothesis 10).

3.4. Results

3.4.1. Description of the literature

Altogether, 244 coefficients of temporal overlap were extracted from 43 studies (Figure 3.1). The reduced “weighted” dataset comprised 180 coefficients of temporal overlap extracted from 30 studies. The coefficients of overlap ranged from 0.12 to 0.95 (mean = 0.67 ± 0.17 SD), with a seemingly similar distribution between continents (Figure 3.2). There was a high disparity between continents, with most coefficients extracted from studies in North America (102 values from 9 studies), followed by Europe (55 values from 7 studies), Asia (42 values from 16 studies), South America (38 values from 7 studies) and, finally, Africa (5 values from 4 studies). Except for human density and built-up environment ($\varrho = 0.78$), none of the predictors extracted were highly correlated.

A total of 76 species combinations were investigated, and each species combination had on average 2.93 ± 1.93 SD (range 2 – 12) coefficients of temporal overlap. Almost half of the studies (n = 20) investigated a single species pair, whilst the other studies (n = 23) investigated 2 to 20 species pairs simultaneously (mean = 5.41 ± 4.75 SD). This review included a total of 44 species, 18 of which were strictly nocturnal, 25 were crepuscular or cathemeral, and only one species, the yellow-throated marten —*Martes flavigula*— was strictly diurnal. Felidae was the most investigated family (n = 165), followed by Mustelidae (n = 114), Mephitidae (n = 60), Canidae (n = 50), Procyonidae (n = 34), Viverridae (n = 14), Didelphidae (n = 10), Herpestidae (n = 6) and Hyaenidae (n = 6).

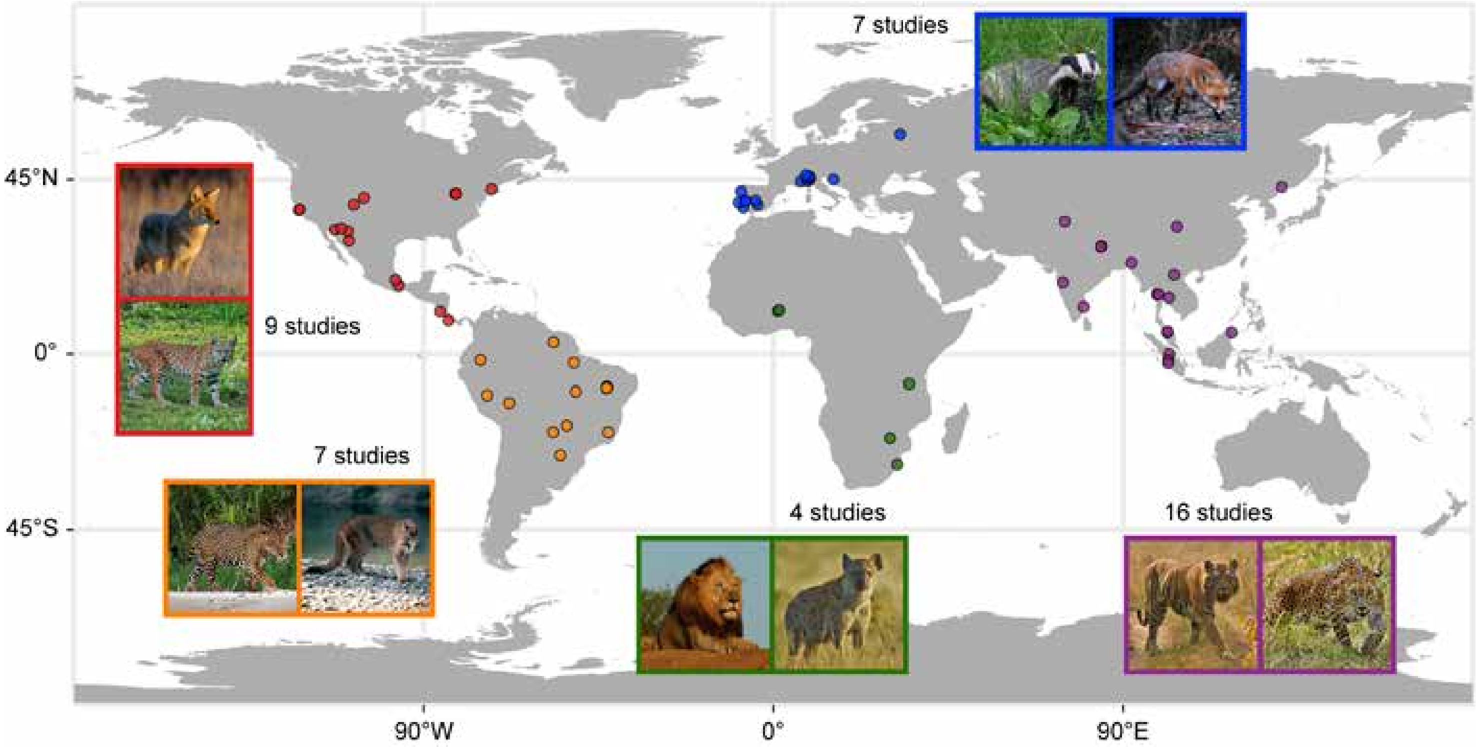


Figure 3.1. Geographical locations of the study areas included in this review, colour-coded by continent. In several cases, studies conducted research in more than one study areas. Photos show the carnivore pair that was the most studied in each continent. Red, North America: coyote and bobcat. Orange, South America: jaguar —Panthera onca— and mountain lion —Puma concolor—. Green, Africa: African lion —Panthera leo— and spotted hyena —Crocuta crocuta—. Purple, Asia: tiger —Panthera tigris— and leopard —Panthera pardus—. Blue, Europe: European badger —Meles meles— and red fox. Map design adapted from Prugh and Sivy (2020).

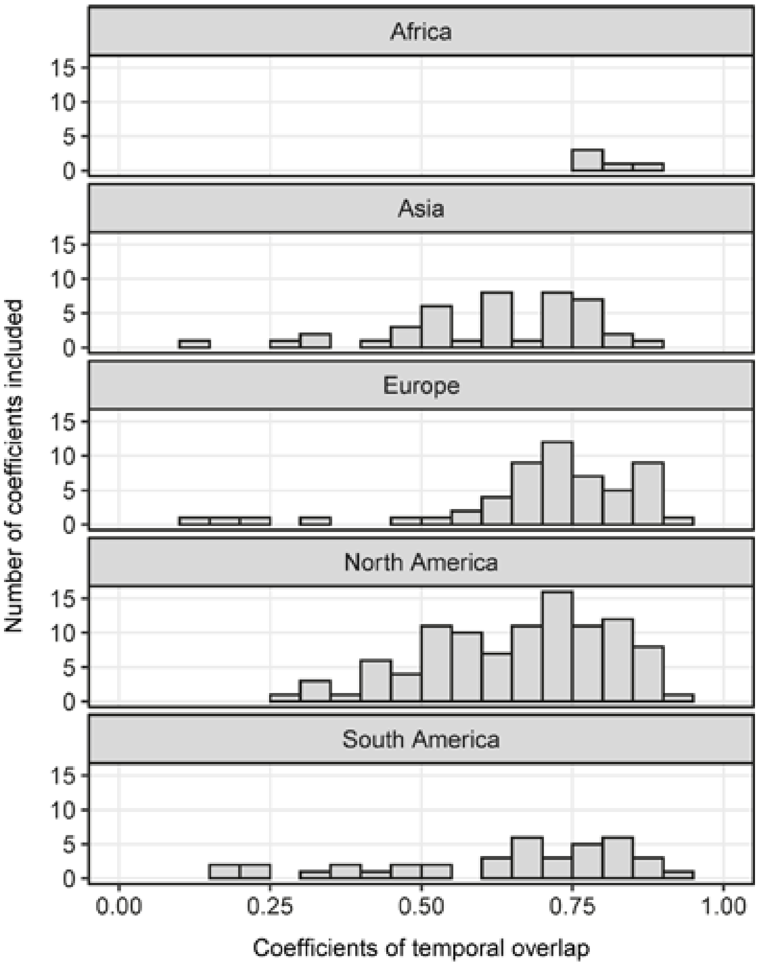


Figure 3.2. Distribution of the coefficients of temporal overlap extracted in this review, grouped by continent.

3.4.2. Paired studies

Eight studies investigated the effects of human disturbance by comparing the coefficients of temporal overlap of species pairs between areas classified as under low or high human disturbance. Of these, two studies were able to clearly demonstrate that some coefficients of temporal overlap between carnivores increased in areas under high human disturbance (e.g. the confidence intervals between low and high disturbance did not overlap; Lewis et al. 2015, Wang et al. 2015), one study reported significant reductions of temporal overlap (Baker 2016), and five found no apparent (i.e. comparison of coefficients without confidence intervals; Cruz et al. 2015) or significant change attributed to human disturbance (e.g. the confidence intervals between low and high disturbance overlapped; Carter et al. 2015, Rayan & Linkie 2016, Moll et al. 2018, Sogbohossou et al. 2018). The three studies that reported either increases or decreases in temporal overlap attributed to human disturbance in some species pairs also reported no change in other species pairs.

3.4.3. Global models

3.4.3.1. Full analysis

None of the models explored had strong support (Table 3.3). The evidence ratios (i.e. AIC_{w1} / AIC_{w2}) for the best model (Built-up environment) versus the second (interaction between Simpson's landscape diversity index and Pasture) and third (Simpson's landscape diversity index) best models were low (1.31 and 2.71, respectively), making the model selection uncertainty high. Therefore, a model-averaging technique was applied to the three top-ranked models with similar AIC ($\Delta AIC < 2$), "Built-up environment", "Simpson's landscape diversity index * Pasture" and "Simpson's landscape diversity index", to build the full average model with 95% confidence.

Table 3.3. Results of the a priori model selection (full dataset) for predictors of coefficients of temporal overlap between sympatric carnivores, with models ranked based on their AIC. Species combination was added as a random factor in each model. The "" sign indicates an interaction. Models in bold were selected to build the full model average.*

Models	**AIC**	**ΔAIC**	**AIC$_w$**
Built-up environment	**-282.66**	**0.00**	**0.38**
Simpson's landscape diversity index * Pasture	**-282.15**	**0.52**	**0.29**
Simpson's landscape diversity index	**-280.69**	**1.97**	**0.14**
Temperature	-278.81	3.86	0.05
Null (Intercept only)	-278.22	4.44	0.04
Pasture	-276.72	5.94	0.02
Precipitation	-276.68	5.98	0.02
Human density	-276.34	6.32	0.02
Body mass ratio	-276.27	6.39	0.02
Precipitation * Temperature	-276.25	6.41	0.02
Carnivore community richness	-274.96	7.71	0.01

None of the variables included in the full average model were significant predictors of coefficients of temporal overlap between carnivores (Table 3.4). Additionally, the standard errors of the estimate for pasture, Simpson's landscape diversity index and the interaction between Simpson's landscape diversity index and proportion of pasture overlapped with zero, further indicating weak relationships. The Simpson's landscape diversity index and proportion of built-up environment were positively associated with temporal overlap, whilst the proportion of pasture showed a negative relationship with temporal overlap (Table 3.4; Figure 3.3). The lack of statistical significance and weak relationships found suggest that no human, environmental or meteorological variables are global predictors of carnivore temporal overlap.

Table 3.4. Full model average (full dataset) of the three best a priori models ($\Delta AIC < 2$), with 95% confidence. Species combination was added as a random factor. All explanatory variables were standardised for comparison purposes. SE = Standard Error.

Variable	**Estimate**	**SE**	**z value**	**p-value**
(Intercept)	0.633	0.079	7.941	< 0.005
Pasture	-0.006	0.034	0.170	0.865
Simpson’s landscape diversity index	0.048	0.048	0.985	0.325
Built-up environment	0.073	0.054	1.336	0.181
Simpson’s landscape diversity index * Pasture	0.038	0.052	0.740	0.459

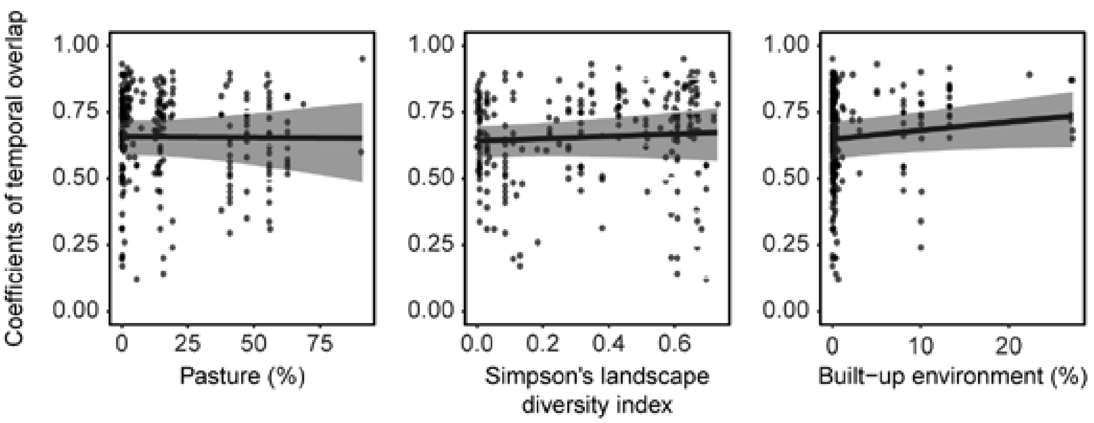


Figure 3.3. Predicted effects of the explanatory variables included in the full model average on coefficients of temporal overlap (full dataset). The grey ribbon represents the 95% confidence intervals.

3.4.3.2. Weighted analysis

None of the models explored had strong support (Table 3.5). The evidence ratios (i.e. AIC_{w1} / AIC_{w2}) for the best model (interaction between Simpson’s landscape diversity index and Pasture) versus the second model (Built-up environment) was low (1.70), making the model selection uncertainty high. The other models had really poor weight ($AIC_w < 0.001$). Therefore, a model-averaging technique was applied to the two top-ranked models with similar AIC (ΔAIC < 2), "Simpson's landscape diversity index * Pasture" and "Built-up environment", to build the full average model with 95% confidence.

Table 3.5. Results of the a priori model selection (weighted dataset) for predictors of coefficients of temporal overlap between sympatric carnivores, with models ranked based on their AIC. Species combination was added as a random factor in each model. The "" sign indicates an interaction. Models in bold were selected to build the full model average.*

Models	**AIC**	**ΔAIC**	**AIC$_w$**
Simpson's landscape diversity index * Pasture	**-2741.71**	**0.00**	**0.63**
Built-up environment	**-2740.63**	**1.08**	**0.37**
Pasture	-2717.92	23.79	0.00
Precipitation * Temperature	-2699.30	42.42	0.00
Simpson's landscape diversity index	-2692.40	49.31	0.00
Temperature	-2687.40	54.31	0.00
Carnivore community richness	-2686.29	55.42	0.00
Human density	-2670.16	71.55	0.00
Null (Intercept only)	-2642.40	99.31	0.00
Precipitation	-2641.86	99.85	0.00
Body mass ratio	-2640.58	101.13	0.00

As was the case in the "full" analysis, the Simpson's landscape diversity index and proportion of built-up environment were positively associated with temporal overlap, whilst the proportion of pasture showed a negative relationship with temporal overlap (Table 3.6, Figure 3.4). The observed pattern was stronger than in the "full" analysis, with lower standard errors and higher z values for each predictor. However, the "weighted" model suffered strong underdispersion, with a dispersion parameter of 0.005 (where values < 1 indicate underdispersion, and values > 1 indicate overdispersion), weakening the reliability of the findings. A comparative visual examination of Figure 3.3 and Figure 3.4 shows no apparent difference in the predicted effects of the three explanatory variables between the two models (i.e. full and weighted), further indicating that no human, environmental or meteorological variables were global predictors of carnivore temporal overlap.

Table 3.6. Full model average (weighted dataset) of the two best a priori models (ΔAIC < 2), with 95% confidence. Species combination was added as a random factor. All explanatory variables were standardised for comparison purposes. SE = Standard Error.

Variable	**Estimate**	**SE**	**z value**	**p-value**
(Intercept)	0.652	0.089	7.297	< 0.005
Pasture	-0.077	0.020	3.719	< 0.005
Simpson's landscape diversity index	0.054	0.020	2.734	0.006
Built-up environment	0.097	0.025	3.933	< 0.005
Simpson's landscape diversity index * Pasture	0.005	0.012	0.365	0.715

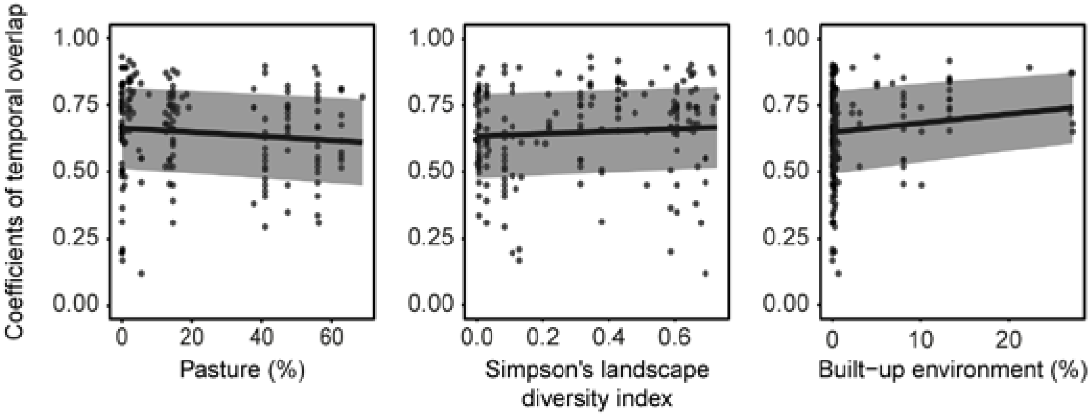


Figure 3.4. Predicted effects of the explanatory variables included in the full model average on coefficients of temporal overlap (weighted dataset). The grey ribbon represents the standard error.

3.5. Discussion

Although accumulating evidence suggests that human disturbance increases nocturnal activity in wildlife (Gaynor et al. 2018, Nix et al. 2018), there was no evidence at a global scale for an impact of the selected human, environmental or meteorological variables on temporal partitioning between carnivores. However, it cannot be said that human disturbance has no impact on temporal partitioning. Rather, the effects of human disturbance are diverse and probably context-dependent, as illustrated by the findings from the eight studies that compared temporal overlap between low and high human disturbance treatments. As hypothesised, in two of these studies, some species, but not all, increased nocturnal activity in response to higher urbanisation, which increased temporal overlap between competitors (Lewis et al. 2015, Wang et al. 2015). Conversely, Baker (2016) documented that, although human disturbance — a combination of paved roads and hiking trails — induced an increase in wildlife nocturnality, most temporal overlaps between species were lower in more disturbed areas. This is because species within disturbed landscapes might co-occur in safe areas to a greater extent, and subordinate species can fine-scale their temporal partitioning with dominant competitors by narrowing or displacing their peaks of activity. Indeed, maintaining temporal partitioning with competitors in a reduced, nocturnal, temporal window can be a strategy adopted to ensure avoidance of both humans and competitors simultaneously (e.g. Sogbohossou et al. 2018). Such fine-scale adaptations may not be detected by diel measurements of temporal overlap, and could be one of the reasons behind the lack of a significant trend in these results. Similarly, it is possible

that, despite an increased nocturnality caused by human disturbance, carnivores could adjust their activity patterns on a fine temporal scale to simultaneously avoid both humans and competitors, therefore not increasing the temporal overlap among carnivores. This could explain why the remaining five studies reported relatively similar coefficients of temporal overlap in areas under low and high human disturbance (e.g. human presence; Carter et al., 2015; Sogbohossou et al., 2018; plantations and reduction in landscape diversity; Cruz et al., 2015; Rayan & Linkie, 2016; built-up environment; Moll et al., 2018). In addition, the lower density of large carnivore populations in high human density areas (Woodroffe 2000), coupled with a high anthropogenic resource availability, could relax competition among carnivores able to adapt to human disturbance (Ruscoe et al. 2011, Wolf & Ripple 2017), thus reducing the importance of temporal partitioning in promoting stable species coexistence. Another possible explanation could be that the baseline activity pattern of species included in the analysis (i.e. diurnal, nocturnal, or crepuscular / cathemeral) may influence the findings. An effect of human disturbance on overlap may be less likely between nocturnal–nocturnal pairs, but could be expected in diurnal–crepuscular pairs. However, due to a strong dearth of diurnal species in the studies included in the analysis, which created a severe unbalance between groups and low sample size for species pairs with a diurnal carnivore, the baseline activity patterns of species could not be included in the analysis.

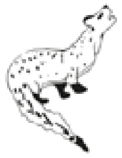
None of the ecological or meteorological factors were significant predictors of coefficients of temporal overlap. Although temporal overlap increased with the Simpson's landscape diversity index, contrary to the hypothesis, the relationship

was weak. Temporal overlap was hypothesised to decrease with higher landscape diversity, as complex habitats enable fine-scale habitat segregation and promotes species richness (Rosenzweig 1981, Pereira et al. 2012). However, this hypothesis was not supported by the models. Although previous studies observed that temporal segregation was indeed likely to play a role in complex communities (Monterroso et al. 2014), it is possible that, in the dataset used in this study, higher landscape diversity did not increase species richness systematically, due to other external factors (e.g. habitat fragmentation; Rybicki et al. 2020). Another possibility is that species richness did indeed increase with landscape complexity, but that temporal partitioning was not selected as a primary mechanism allowing coexistence with competitors. In the latter case, species-specific temporal preferences may reflect strategies unrelated to competitive interactions (e.g. foraging strategies; Curveira-Santos et al. 2017).

Indeed, internally, the circadian rhythm is governed by each species' biological clock, an endogenous program that dictates the timing of many behaviours (Pittendrigh 1981). Externally, this is regulated by biotic (e.g. predators matching their preys' activity; Gantchoff & Belant 2016) and abiotic factors (e.g. daytime temperature; Rabaiotti & Woodroffe 2019). As competitor avoidance is just one the many factors regulating activity pattern, it may not be selected in systems where other factors are more limiting to the species' fitness (Schoener 1974b). For instance, this is seen in systems with harsh environmental conditions or low prey availability (Cozzi et al. 2012, Broekhuis et al. 2014, Astete et al. 2017). In other systems, where none of the governing factors exert an extreme pressure on the individuals' fitness, activity pattern can be governed by a combination of several interacting factors (e.g. moonlight and prey activity; Mukherjee et al. 2009, Penteriani et al. 2013, Penido et al. 2017). Thus, the relative strength of each external factor regulating circadian activity pattern may be strongly related to the biotic and abiotic conditions of the surrounding landscape. This site-specificity renders the investigation of temporal partitioning on a global scale ineffective, by yielding incomplete results that cannot be applied locally.

3.6. Limitations

There are two main limitations to this chapter that could explain the weak relationships found between the predictors investigated and coefficients of temporal overlap. First, the data collected may be too coarse to analyse processes happening at much smaller spatial and temporal scales. Concerns over spatial scaling and perception bias in ecology have been raised before (Wiens 1989, Levin 1992). As characteristics of the landscape change with spatial scale (Turner et al. 1989), it is possible that some environmental variables have an influence on activity pattern and temporal partitioning among carnivores, albeit on a different spatial grain than what was used in this analysis. This chapter favoured the use of standardised variables by using the same large-scale indices for all studies. Although doing so meant using a coarser spatial grain, with reduced precision, it ensured a complete comparability between study sites. For instance, several studies measured the levels of human activity as the average number of photographs of people at camera trap sites (e.g. Wang et al. 2015, Moll et al. 2018). Such fine-scale spatiotemporal metric cannot be determined a posteriori, and was therefore not



applicable to all studies included in this review. To address this issue, future surveys should favour well-designed data collection that record the characteristics of the surrounding landscape systematically whilst deploying cameras in the field, enabling the investigation of ecological processes on different spatial scales simultaneously (e.g. Wilmers et al. 2013). In this study, human density was used as a proxy for the probability of encountering humans, but this relationship may not always be true (e.g. some natural parks may experience peaks of human visitations on a regular basis, but have a low recorded human density due to the lack of habitations). Although measuring human activity on camera can prove ethically challenging (Brittain et al. 2020, Sharma et al. 2020), it may be needed to fully comprehend the fine-scale temporal responses of animals to human presence.

Secondly, the coefficient of temporal overlap, which is based on the daily activity patterns of species, may not be the best-fitting tool to investigate temporal partitioning. Daily activity patterns are typically calculated by indiscriminately grouping data spanning several days, months or years into a 24h window. Evaluating temporal partitioning in such a way assumes that competitor avoidance is a predictive process, with long-lasting and consistent effects. Instead, competitor avoidance may often be a reactive response, in which subordinate species adapt their use of landscape to the nearby presence of competitors in temporal scales that are too small to have lasting effects on the circadian activity pattern (Broekhuis et al. 2013, López-Bao et al. 2016). Likewise, although human's influence on wildlife behaviour may exceed that of natural predators (Ciuti et al. 2012, Clinchy et al. 2016), it is likely that the broad-scale nocturnal adaptations of carnivores to humans

and human features works in combination with finer-scale immediate responses to human stimuli (e.g. Ordiz et al. 2013b, Moll et al. 2018). Alone, the coefficient of temporal overlap portrays a broad picture of temporal segregation, and is best paired with an ecological interpretation of the activity curves (where the peaks are, how narrow etc), or other metrics of fine-scale temporal interactions, such as time-to-event analysis (e.g. Prat-Guitart et al. 2020). Similarly, combining metrics of temporal association with spatial displacement metrics (e.g. multispecies occupancy models; Mackenzie et al. 2004, Rota et al. 2016), or spatiotemporal models (e.g. co-detection modelling; Cusack et al. 2017, time-dependent observation modelling; Ait Kaci Azzou et al. 2021), can yield a more complete picture of fine-scale avoidance of competitors, and how human disturbance might be mediating these interactions. In this regard, the coefficient of temporal overlap is a useful tool in measuring the average temporal overlap between species and large-scale responses to human disturbance but can overlook fine-scale interactions that are essential to allow coexistence. In addition, studies that indiscriminately group data over long periods of time may overlook seasonal variations in behaviour (e.g. Monterroso et al. 2014, Caravaggi et al. 2018), especially if they do not account for the variation in daylength throughout the year in their analysis (i.e. by using solar time instead of clock time; Nouvellet et al. 2012, Vazquez et al. 2019). These studies are thus at risk of recording faulty behavioural timings, which can lead to erroneous conclusions on the way species share time. Similarly, camera trap surveys focusing on calculating activity pattern and temporal partitioning do so by grouping the data from the different stations within their study area. However, there may be consequential

variations in human disturbance or habitat features across individual camera stations which could impact on species behaviour on a fine-scale. Finally, the coefficient of temporal overlap is a pairwise approach to evaluating temporal partitioning. Interspecific competition and niche partitioning are complex systems, with many species involved. Restricting the investigation of temporal partitioning to two species, without considering the impact of the presence and activity of other species forming the community, essentially distils complex patterns of multispecies partitioning into dyads. For all these reasons, it is in the best interest of studies that employ camera traps to avoid overinterpreting the coefficients of temporal overlap to investigate the potential for competition among sympatric species.

3.7. Conclusions

Undoubtedly, humans impact on the activity patterns of wildlife, but this chapter found no evidence that this process could impact temporal overlap between carnivores consistently on a global scale. Instead, the influence of humans on temporal partitioning could be diverse and context-specific, and thus requires further investigation due to the theoretical implications for community structure. Similarly, this chapter found no strong evidence that the ecological and meteorological factors investigated were significant predictors of temporal partitioning globally. Therefore, temporal avoidance of competitors may be regulated by multiple factors simultaneously, with the relative strength of each factor varying with the biotic and abiotic conditions of the landscape.

Large-scale analysis, such as this one, can yield valuable and statistically powerful results. Conducting such investigations on a global scale allows the inclusion of a large range of human activities and landscape transformation, providing valuable insights into the role of humans on species coexistence in animal communities. However, they can also mask the local variability in the response of the processes investigated. Similarly, the investigation of human disturbance on temporal partitioning among carnivores suffered a lack of controlled studies, a common issue in carnivore science (Allen et al. 2017a, Bruskotter et al. 2017). Complete experiments with carnivores can rarely, if ever, be executed excellently in the field. Future studies would benefit from adopting controlled experimental designs whenever possible, for instance by contrasting temporal overlap in a given species pair between ecologically-similar sites with low and high disturbance (e.g. Frey et al. 2020), or across a gradient of human disturbance (e.g. Lewis et al. 2015). Choosing the right factors to control, with the right species, would eliminate some of the biases that are introduced by pooling temporal data across days and sites, and could be pivotal in detecting the effects of human disturbance on activity overlap between co-occurring species.

Carnivore communities, where temporal partitioning is not negatively affected by humans, may still experience an increase in interspecific competition following human disturbance. Indeed, increases in nocturnality can affect other dimensions of niche partitioning (e.g. increased trophic competition for nocturnal preys; Smith et al. 2018). For this reason, future studies would benefit from investigating multiple dimensions of niche partitioning simultaneously (i.e. spatial, temporal, and trophic),

in order to fully understand how human-induced changes in carnivore activity affect interspecific competition.

This chapter reinforces the importance of elucidating context-dependent spatiotemporal responses of carnivores to the combined influences of human activities and dominant competitors, to better inform wildlife management strategies and land-use planning. Evidence-based decision making should benefit both animal and human communities, and aim to promote human–wildlife coexistence. However, the temporal adaptation of wildlife to humans is still a neglected aspect of management regulations. In areas where restricting human access can be difficult to achieve spatially (e.g. national parks with high tourist frequentation), limiting human activity to a reduced window in time could help widen the “safe” temporal niche available to carnivores, and promote coexistence with competitors. This could be achieved, for instance, by restricting public access to hours outside of high animal activity (e.g. temporal closure during night and crepuscular hours; Wittington et al. 2019). Time is an important component of species interaction and coexistence, that ought to be included with careful examination into conservation programs and management implementations.

Chapter 4

The coefficient of temporal overlap: evaluation of current practices and guidelines

4.1. Abstract

The number of studies investigating animal activity patterns and temporal partitioning among species is growing rapidly, thanks to the increasing popularity and accessibility of remote-sensing camera traps. Recently developed methods can estimate activity levels by fitting diel activity pattern as a continuous distribution, and can be employed to compute coefficients of temporal overlap between two species. However, the implementation of this coefficient in the scientific literature is not homogenous, and currently faces uncertainties and irregularities. Given the importance of temporal partitioning as one of the three main niche dimensions regulating species interactions and community structure, there is an urgent need to highlight the limitations and consideration of the tools used by researchers. In this chapter, three common methodological issues are discussed: (a) accuracy and precision of the estimates; (b) inclusion of seasonality in the analysis; and (c) interpretation of the findings. Overall, studies showcased a good level of transparency when presenting their findings, but a high proportion may suffer from lower accuracy and precision after modelling the activity curve estimates of species with too few detections. Similarly, most surveys did not account for variations in daylight length throughout the year, or seasonal adjustments of diel activity pattern, and may have missed important patterns of temporal partitioning. Finally, the majority of authors subjectively classified the degree of temporal overlap as being either “low” or “high”, which can lead to irregularities between studies. Authors are encouraged to maintain good levels of transparency by systematically providing the confidence intervals, and should be explicitly cautious when

interpreting coefficients modelled from fewer than 100 species detections. The use of solar time should be favoured over clock time, as it is more ecologically meaningful. The decision to incorporate seasonality in the analysis should be contingent on the total number of detections and the goal of the study. Additionally, authors should present their findings in a purely descriptively manner, or classify each coefficient with respect to the overall distribution of coefficients in the study. Finally, complementing the coefficients of overlap with befitting statistical tests may be the most effective way to uncover the patterns at play.

4.2. Introduction

Understanding how animals use time as a resource is essential to know the ecological niche that species occupy (Hutchinson 1957). The diel activity pattern, a measure of how species distribute activity over the day, is primarily regulated by each species' endogenous biological clock (Pittendrigh 1981), and can be partially adjusted in response to exogenous factors such as weather (Brivio et al. 2016), food availability (Masi et al. 2009) or human disturbance (Ordiz et al. 2012). In addition, most species can adapt their activity pattern in response to the presence of other species, whether to reduce predation risk (Lima & Dill 1990), improve predation success (Lima 2002), or ease competitive interactions (Di Bitetti et al. 2010). Temporal partitioning, the process where different species segregate time as a limited resource, is, therefore, a prevalent mechanism facilitating stable coexistence between sympatric species (Schoener 1974a, Kronfeld-Schor & Dayan 2003). Indeed, time is one of the three main niche dimensions, along with the trophic and spatial

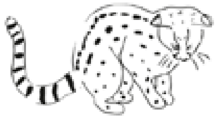
dimensions, that competitors can partition to facilitate stable coexistence (Schoener 1974a).

A range of methods has been used to quantify animal activity levels, each presenting their own advantages and disadvantages (Zimmermann et al. 2016). Direct observations in the animal’s natural environment or in artificial conditions are time-demanding and can be difficult to achieve for cryptic species (Duckworth 1998). Indirect observations can ease these issues by monitoring animal behaviour remotely. For instance, fitting animals with tracking devices, such as Very High Frequency (VHF) or Global Positioning System (GPS) collars, enables animal activity to be recorded with great precision. However, VHF and GPS telemetry investigations are limited by the number of species and individuals that can be fitted and monitored throughout the study period. On the other hand, using time-stamped cameras to monitor animal behaviour does not require the direct presence of the observer, and facilitates multi-taxa surveys by allowing the monitoring of several species from the same community simultaneously (Caravaggi et al. 2017).

Camera traps are increasingly being used in the fields of conservation and ecology because they offer a relatively affordable and time-effective monitoring tool, whilst inflicting minimal disturbance (Rowcliffe & Carbone 2008, Burton et al. 2015, Caravaggi et al. 2017). Consequently, the use of time-stamped camera trap data has enabled to further the investigation of animal activity patterns and temporal partitioning (Bridges & Noss 2011, Caravaggi et al. 2017, Frey et al. 2017). At first, studies using diel activity patterns from camera traps commonly assigned behaviours to discrete categories (e.g. night, day and crepuscular periods; Van

Schaik & Griffiths 1996). Data were then analysed using traditional tools to measure niche similarity, such as Pianka's overlap index (Pianka 1973) and Renkonen similarity index (Krebs 1989). Although these tools are still currently used for other niche dimensions (e.g. trophic; Yarnell et al. 2013), they may not represent the most precise option to measure temporal overlap, as they require classifications of activity data into discrete blocks of time.

Recent methods have improved the insight gained from camera trap data by fitting diel activity pattern as a continuous distribution over a 24h period, using nonparametric circular kernel density functions (e.g. Ridout & Linkie 2009, Oliveira-Santos et al. 2013, Rowcliffe et al. 2014). To apply these methods, species capture times are treated as a random sample from an underlying distribution (i.e. 24h period), with kernel density functions generating a continuous measure of the density of data points along this distribution. This method can be further employed to evaluate temporal partitioning between two species by measuring the proportion of the day that the two species are active simultaneously. The coefficient of temporal overlap (Δ), proposed by Ridout and Linkie (2009), is an innovative method capable of measuring the degree of similarity between two kernel density curves (i.e. two activity curves). This coefficient is defined as the area lying under both density curves, and ranges from 0 (no overlap) to 1 (complete overlap). In their simulation study, Ridout and Linkie (2009) proposed two different parameterisations of the coefficient of overlap, and recommended to use the Δ_4 estimator if the smaller sample of the two species has more than 75 observations, and the Δ_1 estimator for smaller sample sizes (Meredith & Ridout 2014a, b).



The coefficient of temporal overlap is usually provided alongside an indication of its precision, in the form of the lower and upper bounds of the confidence intervals (commonly 95% CI), that can be estimated via bootstrapping techniques. This approach has achieved rapidly-growing popularity in the evaluation of camera trap data (Figure 4.1) and is one of the preferred methods for estimating temporal partitioning among species. As such, it has been utilised in a variety of animal taxa across a range of ecological processes (e.g. sexual segregation in ungulates; Pratas-Santiago et al. 2016, predator–prey interactions; Biggerstaff et al. 2017, influence of human activity on wildlife; Oberosler et al. 2017). In addition, the conditional circular kernel density functions proposed by Oliveira-Santos et al. (2013) allow to differentiate between the activity range overlap (95% overlap of active periods) and core overlap (50% overlap) of active periods of the studied species.

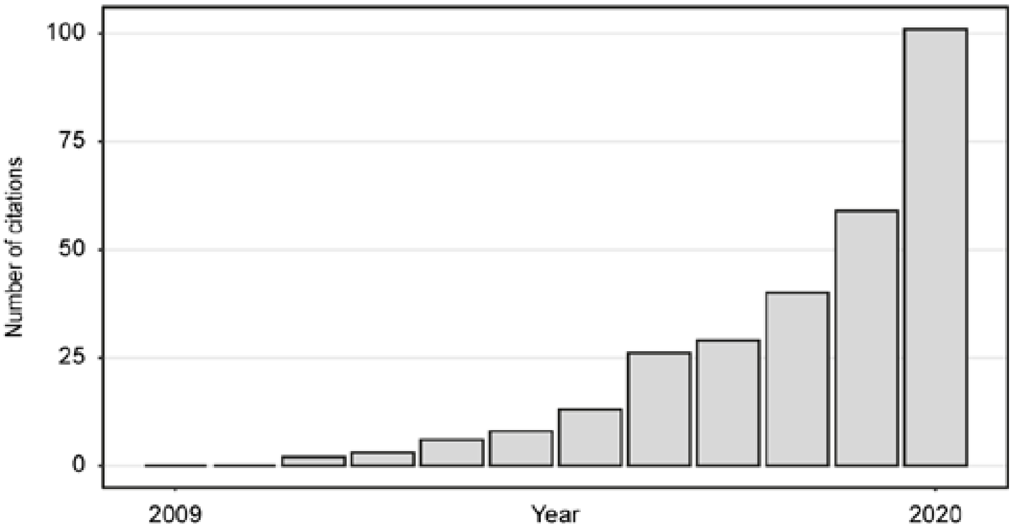


Figure 4.1. Number of citations per year from 2009 to 2020 for the article by Ridout and Linkie (2009), based on the Springer citation tool (https://citations.springernature.com).

Like most fast-growing methods, the implementation of the coefficient of temporal overlap in the scientific literature may face uncertainty and irregularity in its early stage. This chapter critically evaluates the three following aspects relating to the use of the coefficient of temporal overlap in the literature:

(1) Accuracy and precision of the results: the number of animal detections may impact on the reliability of the activity curves, and thus on the coefficient of temporal overlap (Rowcliffe et al. 2014). Recently, Lashley et al. (2018) compared the activity curves of four species with different sample sizes, ranging from 10 to 500 detections per species, and were able to detect two thresholds. Using Watson's U2 statistic (Zar 2010) and correlation tests, Lashley et al. (2018) found that the activity curves simulated using sub-samples with as few as 10 detections were not significantly different from the overall dataset for each species. However, they also demonstrated that mean overlap increased and associated estimates of error (i.e. 95% confidence intervals) decreased rapidly as sample sizes increased until an asymptote near 100 detections was reached, which they recommended as the minimum sample size.

(2) Inclusion of seasonality parameters: numerous species adjust their activity to light intensity (Kavanau & Ramos 1975) or ambient temperature (e.g. Hetem et al. 2012, Rabaiotti & Woodroffe 2019), both of which are directly related to the sun's actual position in the sky. Solar time is a metric referring to the position of the sun in the sky, relative to known reference points (e.g. sunrise, zenith or sunset). This measure incorporates the variation in daylight length throughout the year originating from Earth's titled axis and elliptical orbit around the sun, as opposed to the classical 24-hours clock time. Thus, using clock time can result in erroneous assumptions about behaviour, and solar time may often be better suited to

investigate animal diel behaviours (Nouvellet et al. 2012). Earth's titled axis and elliptical orbit around the sun are also responsible for seasons. Seasonal changes in environmental conditions and natural annual cycle of species can affect activity patterns (e.g. Ordiz et al. 2017, Caravaggi et al. 2018) and, consequently, impact temporal partitioning between species (e.g. Monterroso et al. 2014).

(3) Interpretation of the findings: defining what constitutes a "low" or "high" coefficient of temporal overlap between two activity patterns is largely subjective. The lack of objective thresholds can create disparities in the literature, as has been observed in other areas of ecology (e.g. Thomas & Taylor 2006), which may, in turn, prevent the comparability of findings between studies. Moreover, since the coefficient of overlap is purely descriptive in nature, the complementary use of statistical tests is necessary to determine if two activity curves significantly differ (e.g. Gerber et al. 2012).

This chapter critically reviews existing literature that uses coefficients of temporal overlap to measure temporal partitioning between species, with the goal to identify any common issues and limitations. Furthermore, this chapter discusses the implications of each of the limitations raised for the reliability of the reviewed studies' findings, and provides key guidelines for future studies to improve the investigation of temporal partitioning in animal behaviour studies.

4.3. Methods

A literature search was performed in December 2020, wherein all peer-reviewed articles citing Ridout and Linkie's (2009) method from Scopus (321 citations;

www.scopus.com) and Web of Science (282 citations; www.webofknowledge.com) were extracted. As the literature search was operated in conjunction with chapter 3, only studies that calculated the coefficient of temporal overlap between at least two terrestrial carnivore species were retained. Nonetheless, this search returned a total of 89 studies, and this subset is considered large enough to be a reasonable representation of the literature available currently using the coefficient of temporal overlap to investigate species activity pattern and temporal partitioning. A second literature search was performed in June 2021, wherein all peer-reviewed articles using the *'activity'* package from Rowcliffe et al. (2014) / Rowcliffe (2019) and papers using the *'circular'* package from Oliveira-Santos (2013) / Agostinelli & Lund (2017) to calculate temporal overlap between pairs of carnivores were added to the dataset. Both methods use kernel density functions on circular time data, and allow to calculate a coefficient of overlap between two curves. This second search yielded five relevant articles, resulting in a total of 94 included studies.

The primary goal of this chapter was to critically evaluate studies that have been published following a process of peer-review. The scope of the review was restricted to these studies as peer review is currently the gold standard for the dissemination of scientific research (Goodman et al. 1994; Ware 2008). Even though some reports (grey literature) are produced to the same high standards and requirements expected of publications in the primary literature, these were not included in the scope of the review as much of the grey literature does not meet these high standards. Furthermore, there is no quality metric that can be used to assess grey literature, meaning that reports would have to be assessed based on

parameters that would be set subjectively, introducing an inevitable bias. Clearly, the peer review process is imperfect (Smith 2006), so biases are unavoidable, but evaluating unpublished work with the same criteria and severity as peer-reviewed articles would yield further biases and inequitable results, and would be unfair to both published and non-published work. Furthermore, it is not uncommon for highly-cited published literature reviews to solely incorporate peer-reviewed studies (e.g. Burton et al. 2015; Hunter et al. 2018; Prugh & Sivy 2020). For these reasons, this chapter did not incorporate grey literature, and focused solely on peer-reviewed articles. To evaluate the use of the coefficient of temporal overlap by each study, methodological information was extracted on the accuracy and precision of the results, whether seasonality parameters were considered, and how the authors interpreted their findings (Table 4.1).

Firstly, to assess the accuracy and precision of the studies, the number of detections of each species used to calculate the coefficients of temporal overlap was extracted. Additionally, studies were classified based on whether indicators of precision had been calculated and reported. Secondly, studies were classified as using either clock or solar time to estimate activity patterns. Recently, Vazquez et al. (2019) demonstrated that a transformation from clock to solar time might not be necessary at latitudes below 20°, or in studies with a duration of less than a month below 40° latitude, where the difference between clock and solar time could be too small to be impactful. Therefore, studies were grouped by approximate latitude and survey duration. Survey duration relates to the number of calendar months of the year that were monitored, with a maximum value of 12 (e.g. studies that monitored from

January to March for five years consecutively were assigned a study duration of three months). Furthermore, studies that calculated coefficients of temporal overlap for each season separately were identified, be it dry versus wet seasons, reproductive season, or the four seasons based on the Gregorian calendar. Finally, each study was evaluated on the interpretation of their findings. Each study's threshold values for "low" and "high" activity overlap was recorded, and the justification behind this choice explored. Studies were also examined to assess whether complementary statistical tests were run to identify significant differences between the activity curves of the two species.

Table 4.1. Description of the criteria extracted and evaluated during the literature review process.

Criteria evaluated	**Information extracted**
Accuracy and precision	
+ Number of detections of each species used to calculate the coefficient of temporal overlap	< 10; 10 – 100; > 100
+ Calculated and reported indicators of precision	Yes / No
Seasonality	
+ Transformation from clock to solar time	Yes / No
+ Survey duration	< 4; 4 – 9; > 9 months
+ Latitude of the study area	< 20°; 20 – 40°; > 40°
+ Provided different coefficients of temporal overlap per season	Yes / No
Interpretation	
+ Threshold values for " low" and "high" activity overlap, and justification	In-text description
+ Use of a statistical test to identify significant differences between the two activity patterns	Yes (and which) / No

4.4. Results and discussion

4.4.1. Accuracy and precision

The majority of studies (n = 78, 83%) reported the number of detections of each species used to calculate the coefficients of temporal overlap (Table 4.2). Sample sizes ranged from as few as 4 detections for domestic cats —*Felis catus*— (Fancourt et al. 2015, Horn et al. 2020), to a maximum of 9939 detections for the American marten —*Martes americana*— (Frey et al. 2020). Five studies, three of which were published after the recommendations by Lashley et al. (2018), calculated at least one activity curve using fewer than 10 detections (yielding 13 activity curves in total), whilst more than half of the studies used 10 – 100 detections (259 activity curves) or over 100 detections (153 activity curves). Eight studies reported the number of detections recorded during the entire survey, but calculated separate species activity curves and coefficients of overlap (e.g. for different sites or seasons), thus making it impossible to know the exact number of detections used in the analyses. Finally, eight studies did not report the number of detections, for any species.

Similarly, most studies (n = 72, 77%) calculated and reported indicators of precision (Table 4.2). Of them, 68 studies reported the confidence intervals alongside the coefficient of temporal overlap (e.g. Δ = 0.52 [95% CI 0.31 – 0.65]), using 500 to 10,000 bootstrap samples, whilst 4 studies reported the standard deviation or standard error instead (e.g. Δ = 0.52 ± 0.08 SD). Finally, 8 studies mentioned calculation of 95% CI but did not report them, and 14 studies did not calculate

indicators of precision, with all 22 studies producing the coefficient of temporal overlap as a stand-alone value.

Table 4.2. Summary of the accuracy and precision criteria, assessed from 94 studies. The number of detections used to calculate the species activity curves, and subsequent coefficients of temporal overlap, was classified according to the three thresholds mentioned by Lashley et al. (2018). Studies with sample sizes falling in more than one threshold were counted several times. "Curves" refer to the number of activity curves that were estimated with the corresponding number of detections threshold.

Number of studies reporting the number of detections used to calculate curves		**Number of detections reported**	**Number of studies (curves produced)**
Reported number of detections used	78	< 10	5 (13)
Did not report number of detections	16	10 – 100	63 (259)
		> 100	63 (153)
Number of studies calculating and reporting indicators of precision			
Calculated and reported	72		
Calculated but not reported	8		
Not calculated or reported	14		

Overall, the studies reviewed showcased a good level of transparency, both with regard to reporting sample size and confidence intervals. However, more than half of the studies used fewer detections than the minimum recommended by Rowcliffe et al. (2014) and Lashley et al. (2018) to produce the activity curves (n > 100 detections). The importance of an adequate sample size is a recurrent topic of discussion in ecology (e.g. Bissonette 1999, Pearson et al. 2007). Indeed, limited sample sizes may negatively affect the accuracy and precision of the activity curve estimates, and the subsequent coefficients of overlap. Thus, studies with low sample size are at risk of obtaining confidence intervals too large to guarantee a reliable

coefficient overlap. For instance, Horn et al. (2020) found Δ = 0.48 (95% CI 0.04 – 0.75) between domestic cats (n=4 detections) and margay —*Leopardus wiedii*—(n=6). Although the yielded coefficient Δ = 0.48 indicates medium temporal overlap between the two species, the confidence intervals suggest that the actual coefficient may be anywhere from Δ = 0.04 (almost no overlap) to Δ = 0.75 (relatively high overlap). Similarly, Comley et al. (2020) found Δ = 0.31 (95% CI 0.06 – 0.57) between serval —*Leptailurus serval*— (n = 8) and caracal (n = 9). Hence, interpreting coefficients of temporal overlap with low sample sizes needs extreme caution, especially if the number of detections for one species, or both species, is close to 10 (Lashley et al. 2018). In circumstances when obtaining 100 detections is difficult (e.g. for elusive species), particular care should be taken when interpreting the resulting activity curves and coefficients of overlap. This may be especially relevant if the two species included in the pairwise comparison have a small sample size, as this may lead to cumulative errors in the coefficient. The fact that smaller sample sizes yield larger estimates of error, coupled with the concern that numerous studies used fewer detections than recommended, highlights the importance of calculating and reporting the coefficient's confidence intervals. These error estimates can also be used to evaluate how external factors influence temporal partitioning, by contrasting the mean overlap coefficient of species pairs between treatment groups, and overlaying their confidence intervals (Frey et al. 2017). If the confidence intervals between the two treatments do not overlap (e.g. natural forest Δ = 0.85 [95% CI 0.79 – 0.87] versus urban habitat Δ = 0.93 [95% CI 0.89 – 0.96]), one could reasonably postulate that there is an effect of the treatment on temporal overlap.

Studies reporting standard errors or standard deviations in lieu of the 95% confidence intervals are, although not incorrect, unable to operate such treatment comparison. For instance, Shankar et al. (2020) reported both the standard deviation and 95% confidence intervals of the coefficients of temporal overlap they calculated, which presented differences between the lower and upper bounds of the distribution (e.g. $\Delta = 0.61 \pm 0.08$ SD and $\Delta = 0.61$ [95% CI 0.43 – 0.76] between the jungle cat —*Felis chaus*— and golden jackal —*Canis aureus*—).

4.4.2. Seasonality

Long-term studies were predominant, with 49 studies having a duration > 9 months, 32 studies lasting 4 to 9 months, and 13 studies undertaken for < 4 months (Figure 4.2). None of the studies extracted lasted less than one month. Latitude was more evenly distributed, with 37 studies located at latitudes < 20°, 36 studies between 20° and 40°, and 22 studies between 40° and 60°. Very few studies (n = 15, 16%) transformed their activity recordings to solar time, irrespective of latitude or duration. Of the 57 studies that would benefit from such transformation (i.e. studies longer than a month and above 20°; Vazquez et al. 2019), only 10 (18%) converted their data to solar time.

The review found 16 studies that compared coefficients of temporal overlap between seasons, whilst the other 78 studies calculated a unique coefficient for either a portion of a year (43 studies) or more than a year (35 studies).

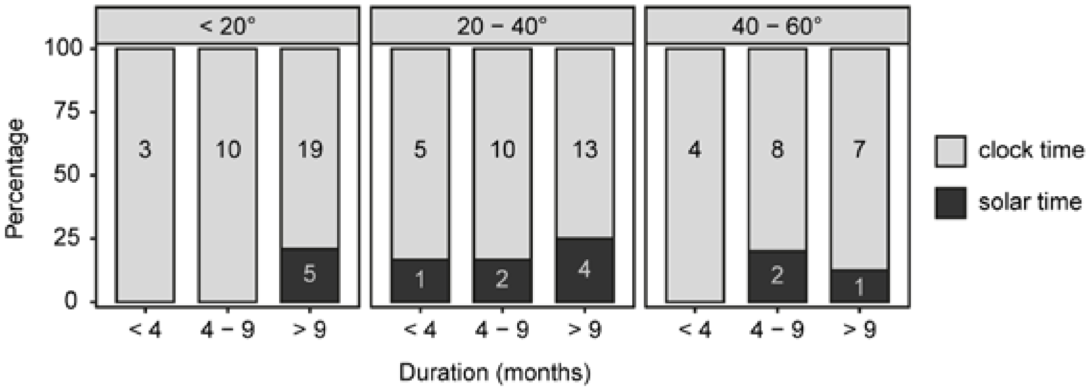


Figure 4.2. Percentage and number of studies using either clock time or solar time, according to their latitude and duration.

Similar to the review of field studies by Nouvellet et al. (2012), a high proportion of the studies extracted here did not take into account the variations of daylight length throughout the year. Therefore, as animals often adjust their activity to the variation in daylength (Daan & Aschoff 1975), these studies may be at risk of having recorded faulty behavioural timings, especially around sunset and sunrise, and may have reached imprecise conclusions on animal activity patterns and species interactions. This flaw may particularly influence pairwise comparisons in which one or both species are crepuscular, typically displaying two activity peaks at dusk and dawn. For instance, the solar time analysis of African wild dog —*Lycaon pictus*— hunting behaviour undertaken by Nouvellet et al. (2012), revealed species-specific predation time windows for three prey species. However, analysing the same dataset with clock time instead suggested that all three prey species were killed within the same time window, thus revealing a false pattern. The transformation from clock to solar time increases the workload needed to complete data analysis, but the recent average anchoring method proposed by Vazquez et al. (2019) in the R package ‘*activity*’ (Rowcliffe 2019) greatly simplifies its implementation. Vazquez et al. (2019)

also specified that studies with variation in day length too small to produce important biases might not need time transformation (e.g. tropical studies < 20° latitude). Nonetheless, solar time is more ecologically meaningful than clock time and should therefore be seen as a preferred metric to investigate animal behaviour in relation to time.

Seasonal adjustments of diel activity pattern and temporal partitioning between species can also be influenced by other factors such as changes in the natural annual cycle of species (e.g. Caravaggi et al. 2018), food availability (e.g. Bu et al. 2016), or human disturbance (e.g. Nix et al. 2018). Yet, this review revealed that the majority of studies (n = 78, 93%) did not contrast coefficients of temporal overlap between different seasons. Some studies grouped all the year's detections indiscriminately and, as such, are at risk of missing important information on animal activity patterns and species interactions. Other studies focused their survey around a fraction of the year only (e.g. Gantchoff & Belant 2016), thus minimising seasonal variation. However, if findings are derived from a partial temporal window, they may not be applicable to the entirety of a year's pattern of species interactions. The importance of seasonality has been raised in other fields of ecology (e.g. predator–prey spatiotemporal dynamics; Furey et al. 2018, Broekhuis et al. 2021), yet it is still often overlooked in empirical studies (White & Hastings 2020). Incorporating season in the pairwise comparisons of activity curves can be challenging, since it requires the division of species detections among the different categories forming the seasons, and can greatly reduce the sample size used to calculate each coefficient. This can also lead to unbalanced sample sizes between seasons if species are more active during certain periods of the year (e.g. Torretta et al. 2016).

4.4.3. Interpretation

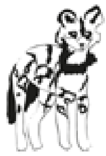
Half of the studies classified the degree of temporal overlap subjectively, with no justification for their choice (Table 4.3). The range of low overlap classifications from these studies ranged from $\Delta = 0.07$ to $\Delta = 0.63$, and high overlap ranged from $\Delta = 0.46$ to $\Delta = 0.96$. Six studies chose their threshold values with respect to the overall distribution of coefficients of temporal overlap from their study: originally, Monterroso et al. (2014) defined Δ values $\leq$ 50th percentile of their sample as low overlap ($\Delta < 0.66$), and Δ values > 75th percentile as high overlap ($\Delta > 0.76$); four subsequent studies applied these same percentile thresholds to their own data, and one study used the 5th and 95th percentiles to identify low and high overlap, respectively. Nine studies referenced another study to justify their threshold values. Of these, five studies referenced Monterroso et al. (2014): two studies used the same threshold values (i.e. $\Delta < 0.66$ and $\Delta > 0.76$) but disregarded the overall coefficients from their own study; two studies confused percentiles with coefficients of overlap, and thus defined low overlap as $\Delta < 0.50$ and high overlap as $\Delta > 0.75$; and one study chose threshold values intermediate to those of Massara et al. (2018) and Monterroso et al. (2014). The four other studies employed the threshold values proposed by Lynam et al. (2013), in which $\Delta < 0.35$ was considered low overlap and $\Delta > 0.80$ high overlap, themselves not providing any justification for this choice. Finally, 34 studies were descriptive only, providing the coefficients of overlap as

they were, or alongside within-study comparisons (e.g. coefficient A was higher or lower than coefficient B).

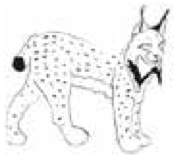
Most of the studies (n = 62, 66%) did not run a statistical test to identify significant differences between activity patterns (Table 4.3). Studies that did run statistical tests favoured the Mardia–Watson–Wheeler test (Batschelet 1981) and Watson's two-sample test of homogeneity (Zar 2010), being used in 13 and 11 studies, respectively. Eight other tests were used in ten studies: ANOVA for circular data (used in two studies), Fisher's exact test, Kolmogorov–Smirnov test, Log-likelihood ratio test (although test outputs do not appear in the results section), one-tailed t-test with Rosario algorithm, randomisation test using bootstrap samples from the R package *'activity'* (Rowcliffe 2019; used in two studies), Spearman's rank correlation test (used in two studies), and Wr (a uniform score statistic using circular ranks; Fisher 1993).

Table 4.3. Summary of the interpretation of the findings, assessed from 94 studies. Studies that ran more than one type of statistical test to identify significant differences between the two activity patterns were counted several times. "Other" tests included: ANOVA for circular data; Fisher's exact test; Kolmogorov–Smirnov test; Log-likelihood ratio test; one-tailed t-test; randomisation test using bootstrap samples; Spearman's rank correlation test; and the uniform score statistic Wr.

Number of studies using threshold values for "low" and "high" overlap		**Number of studies running complementary statistical test**	
No justification	45	Mardia–Watson–Wheeler	13
Percentiles of the distribution	6	Watson's two-sample test for homogeneity	11
Based on another study's findings	9		
Descriptive only	34	Other	10
		None	62



Studies subjectively classifying low versus high temporal overlap may use inconsistent thresholds, which can lead to misleading interpretation and subsequent conclusions. For instance, Singh et al. (2017) classified the coefficient of overlap $\Delta = 0.63$ between clouded leopard —*Neofelis nebulosa*— and marbled cat —*Pardofelis marmorata*— as "low", whilst Zhao et al. (2020) included $\Delta = 0.46$ between red fox and leopard in a list of "high" coefficients of overlap. Subjectivity and inconsistency in science can lead to discrepancies between studies. For instance, the notion of trophic cascades is prevalent in the study of predator–prey interactions, yet the term long suffered from a lack of explicit definition, leading to inconsistencies in its use and loss of meaning (Polis et al. 2000, Schmitz et al. 2000, Ripple et al. 2016c). Classifying low and high overlap with respect to the overall distribution of coefficients of temporal overlap performed in the study can help standardise the choice of threshold, but this method also has limitations. First, it requires monitoring of numerous species in order to obtain a reliable estimate of the coefficient's distribution in the community, and accurately estimate the percentiles (Schoonjans et al. 2011). Even then, the thresholds obtained, although statistically accurate, may lack ecological relevance. For instance, the thresholds calculated by Torretta et al. (2017) yielded a very small contrast between low overlap (50th percentile, $\Delta < 0.79$) and high overlap (75th percentile, $\Delta > 0.83$). One solution could be to use the tails of distribution as percentiles (e.g. 5th and 95th percentiles; Hearn et al. 2018), but this requires an even larger sample size. Alternatively, studies using thresholds based on another study's distribution and percentiles can be a valid approach, but only when monitoring the same animal community, in similar



conditions. For instance, Curveira-Santos et al. (2017) re-used the threshold values proposed by Monterroso et al. (2014) because both studies were investigating the same Iberian mesocarnivore community.

Statistical tests can complement the coefficient of overlap and help interpret the differences between two activity curves. However, most studies did not run complementary statistical tests, and solely used the coefficient of temporal overlap to evaluate niche partitioning and differences in activity patterns between species. Statistical tests can be especially useful for evaluating the effects of specific variables on a species' diel activity pattern, such as contrasting activity patterns between areas under low and high human landscape disturbance (Frey et al. 2020). However, studies should not rely solely on p-values to determine whether the activity curves of two species are "statistically different" or not, considering that the use and mis-use of statistical significance and p-values is at the heart of a scientific debate (Halsey 2019, Kuffner & Walker 2019). Behavioural scientists should not aim to answer whether two activity curves are "statistically different" or not, but rather "how" and "how much" these curves differ. For instance, Marinho et al. (2020) defined the coefficient of temporal overlap between the ocelot —*Leopardus pardalis*— and the northern tiger cat —*Leopardus tigrinus*— as "high" (Δ = 0.77 [95% CI 0.70 – 0.84]), and complemented their analysis by highlighting that the two species nonetheless showed a separation of their peaks of higher activity, thus potentially displaying fine-scale temporal avoidance.

4.5. Summary of recommendations

For species having been detected less than 10 times during a survey, activity curves should not be calculated, and therefore not included in any pairwise comparison with another species, as their accuracy and precision cannot be guaranteed. In the eventuality of species having been detected 10 to 100 times, authors should acknowledge this limitation explicitly, and be cautious when interpreting results. Thus, for full transparency, authors should systematically provide the sample size used to calculate the activity curves and the 95% confidence intervals alongside the coefficients of temporal overlap.

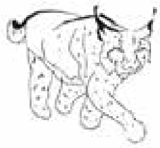
Researchers should use solar time as the standard method, independently of study duration and latitude. Whenever possible, activity curves and pairwise comparisons should be calculated separately and compared between seasons. However, this splits each species' detections into separate groups, and causes a trade-off between incorporating seasonality into the analysis and maintaining a sufficient sample size. Thus, researchers should make their decision contingent on the number of detections and the goal of the study.

Finally, researchers should remain as objective as possible when presenting findings, and remove any personal perception of what may constitute a low or high temporal overlap. To do so, the results can be kept purely descriptive, by supplying the coefficients of temporal overlap as they are. Alternatively, the coefficients of overlap can be compared to the overall pairwise comparisons of the study (e.g. by defining thresholds for low and high overlap using percentiles calculated with the

overall distribution of the coefficients of temporal overlap in the study), or of previous studies conducted in similar sites and conditions. The best way to investigate partitioning of time among species may be through the complementary use of the coefficient of overlap, befitting statistical tests, and an ecological interpretation of the activity curves.

4.6. Conclusions

The number of studies investigating species activity patterns and temporal partitioning is rapidly increasing, largely due to the growing popularity and accessibility of remote-sensing camera traps (Burton et al. 2015, Caravaggi et al. 2017). The coefficient of temporal overlap allows quantification of the proportion of time that two species spend active simultaneously, and is a powerful metric to investigate predator–prey interactions and niche partitioning among competitors. However, the current application in the scientific literature is undermined by recurrent flaws and limitations. It is hoped that the issues raised in this chapter, and the recommendations provided, prompt an improvement in the rigour of animal behaviour studies, and promote coherence and comparability among studies investigating animal activity patterns and temporal niche partitioning.



Chapter 5

Habitat use and co-occurrence patterns of a native (Vulpes Vulpes) and an invasive (Felis catus) carnivore species, in rural and suburban England

5.1. Abstract

Competitive interactions between domestic and native carnivores are poorly known in human-modified landscapes, where human activities may affect competing species disparately. In England, red foxes and free-ranging domestic cats are the most abundant and widely distributed mesocarnivore species. Both generalist predators, their patterns of landscape use may reflect a segregation of spatial niche, with the intent to reduce intraguild competition between them. To address this, the influence of landscape variables on habitat use and patterns of co-occurrence of red foxes and free-ranging cats were examined in an urban–rural gradient in Southern England. Cat occupancy increased with proximity to densely built human settlements, thus displaying dependence on human housing and anthropogenic food sources. In contrast, foxes displayed no preference in their habitat use. These findings suggest that co-occurrence and interactions between the two species may be relatively rare in suburban and areas of England, although this could not be statistically verified. Spatial distribution of cats and rural foxes may be dependent on human land use and resource provisioning to a greater extent than interspecific interactions.

5.2. Introduction

The proliferation of free-ranging domestic and feral carnivore species in the wild is a problematic issue for conservation, as these species can exert an important predation pressure on native wildlife (Loss et al. 2013), have a high potential for hybridisation (Daniels et al. 2001, Godinho et al. 2011), and act as a reservoir for

transmissible diseases (Deem et al. 2000, Gerhold & Jessup 2013). In addition, invasive carnivores can enhance intraguild competition with their native counterparts, either via interference competition (e.g. Vanak & Gompper 2010) or exploitation competition (e.g. due to high trophic overlap, although the effects on interspecific competition still need experimental validation; Castañeda et al. 2020). Free-ranging domestic and, to a lower extent, feral carnivores, can benefit from the use of abundant human-derived resources, thus increasing their fitness and gaining a competitive edge over native carnivores who are not as tolerant to humans and not able to use anthropogenic resources (Vanak et al. 2015). This could be especially threatening to native carnivores in regions where these species are already threatened by human activities (e.g. Farris et al. 2017a).

In the United Kingdom (UK), there are 10.9 million estimated domestic cats, of which 73% (i.e. approximately 8 million cats) live either indoors and outdoors, or outdoors only (PDSA 2019). Free-ranging cats exert an important predation pressure on birds, rodents, reptiles and amphibians (Woods et al. 2003, Thomas et al. 2012). No accurate estimates exist for the number of unowned cats (i.e. feral) in the UK, but their negative effect on native wildlife in other continents is of great concern (Jessup 2004, Loss et al. 2013). The UK also hosts a high abundance of red foxes (Harris & Yalden 2008), largely attributable to the past eradication of apex predators (i.e. mesopredator release, Prugh et al. 2009, Pasanen-Mortensen et al. 2013) and the increase in landscape surface devoted to urban areas and intensive agriculture (Webbon et al. 2004). Foxes share multiple prey species with domestic cats (Meckstroth et al. 2007, Castañeda et al. 2020), and it is possible that the cumulative predation pressure from the two species strongly limit the prey populations (Roos et al. 2018). However, very few studies have investigated niche partitioning between the two species in human-influenced landscapes (e.g. spatiotemporal partitioning; Krauze-Gryz et al. 2012, trophic overlap; Castañeda et al. 2020), and little is known about how they interact.

Foxes, as native predators, could theoretically be negatively affected by competition with cats, a recently introduced carnivore. However, foxes thrive in urbanised landscapes, where they strongly benefit from anthropogenic food supply (Contesse et al. 2004, Soulsbury et al. 2010). This perennial source of food may, in turn, alleviate competition with other species (Wiens 1993). It seems therefore unlikely that foxes can be negatively affected by the presence of cats as intraguild competitors. However, the same cannot be said for the inverse situation. Foxes (~6 kg, Jones et al. 2009) present a physical threat to cats (~3 kg) and kittens (e.g. Molsher 1999). Foxes could therefore affect the movements and habitat use of cats, as has been observed in other countries (e.g. in Australia, Molsher et al. 2017).

The first aim of this chapter is to identify what natural and anthropologically-modified environmental features influence the use of the landscape by cats and foxes. Based on existing knowledge found in the literature, the probability of occurrence of both cats and foxes is predicted to increase in proximity to human habitats. The second aim is to investigate if co-occurrence between the two species and conditional occupancy (i.e. the probability of one species occupying a site given the presence or absence of a second species) is moderated by human attributes of the landscape. Interactions between cats and foxes are predicted to have no

influence on the distribution of each species in the landscape, due to the abundance of anthropogenic resource near human-dominated habitats.

5.3. Methods

5.3.1. Study areas and camera trapping

The data used in this study was originally collected for a different project, investigating the density of West European hedgehogs —*Erinaceus europaeus*— in rural and suburban landscapes across England (Schaus et al. 2020). Eight study areas were surveyed in England between 2016 and 2018 (Figure 5.1). Study areas were selected to represent a gradient of urbanisation in England, ranging from the countryside at Brackenhurst campus (dominated by a mixture of arable and pastural lands, with some woodlands, grasslands and wetlands), to the residential areas of Ipswich (consisting mostly of houses, developed surface and private gardens).

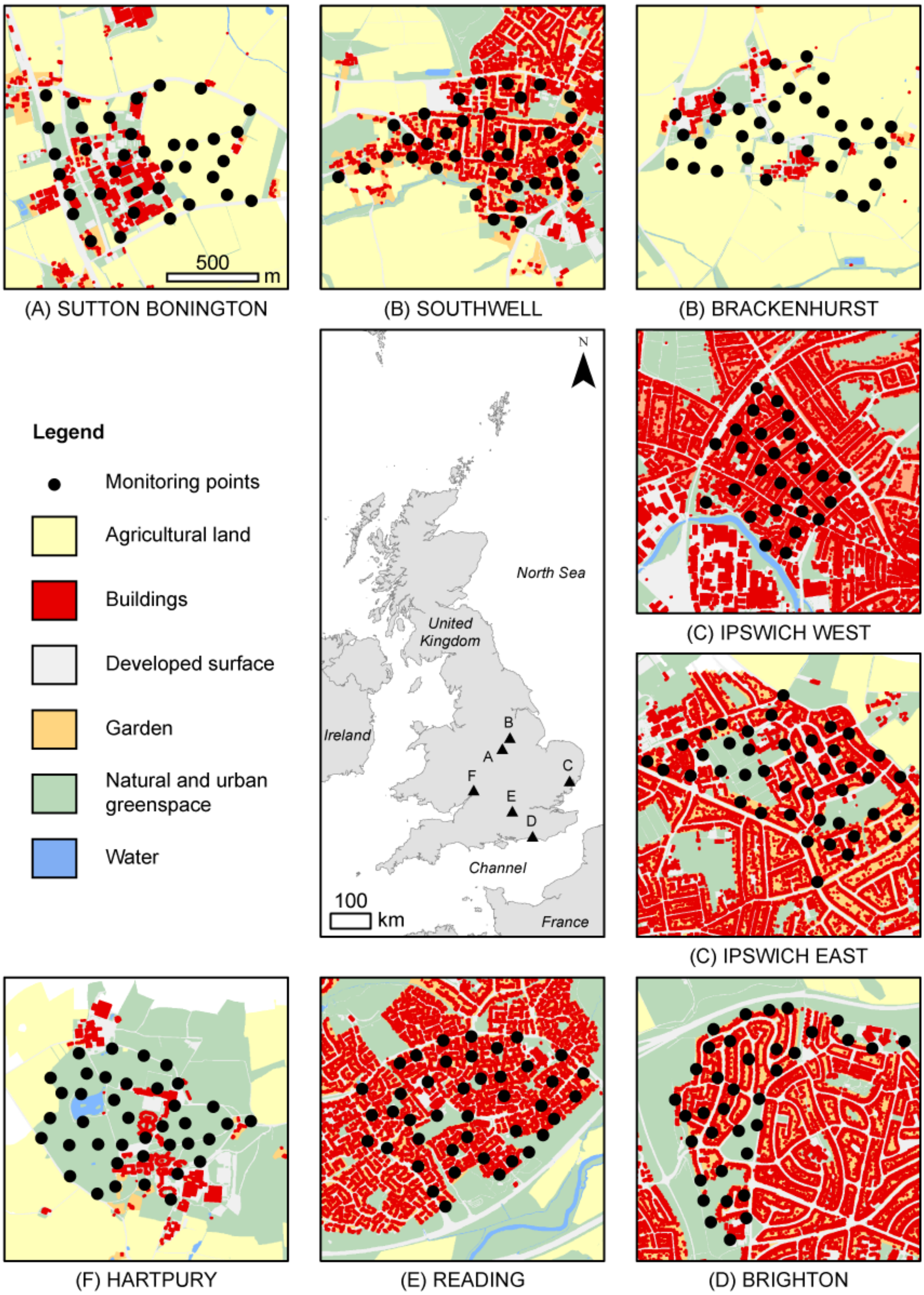


Figure 5.1. Maps of study areas with camera locations, marked with black dots, and environmental variables. Inset map shows the location of the eight study areas in England, UK.

In the original study by Schaus et al. (2020), 30 cameras (Bushnell 119537 Trophy Cam 8MP Night Vision; Bushnell Outdoor Products, Overland Park, KS, USA) were deployed simultaneously within each study site for a minimum of five consecutive nights. Cameras were then transferred to 30 different random locations within the same study site for another minimum of five consecutive nights (i.e. a one-week cycle). Each site was monitored during four weekly cycles, totalling 120 camera stations per study site. Cameras were only active during night-time (i.e. from dusk to dawn), as the focus of the original study was on hedgehogs, which are nocturnal. All data were collected under licence from Natural England (2018-36011-SCI-SCI); ethical approval was granted by Nottingham Trent University's Animal, Rural and Environmental Science Ethical Review Group (code: ARES520).

To investigate hedgehogs' densities, camera stations were considered temporally independent from one week cycle to another and could therefore be located very close to each other spatially. However, this assumption cannot be made for this study, since occupancy models are more effective when the assumption of spatial independence between camera stations is met (Kendall & White 2009, Hines et al. 2010), or at least when a minimum distance between stations is respected to avoid counting the same environmental variables twice. Therefore, all camera stations within each study site were pooled, regardless of temporality (i.e. cameras from the four week cycles were joined), and subsequently sub-sampled to retain the maximum number of camera stations possible whilst ensuring a minimum distance of 100m between cameras (Table 5.1). Thus, a trade-off was performed between the spatial dependency of stations and the total number of stations included in the

analysis. Spatial autocorrelation in occupancy probability between camera stations was assessed using Moran's I index (Moran 1950; see methodology below).

Table 5.1. Camera trapping surveys in the eight study areas of England, UK.

Study area	**Survey period**	**Centroid**	**Area (km²)**	**Stations**	**Trap nights**
Brackenhurst	Apr.– May 2016	53°03′45″N 00°57′21″W	0.65	32	193
Brighton	May – June 2018	50°51′03″N 00°12′00″W	0.86	36	226
Hartpury	July 2017	51°54′26″N 02°18′33″W	0.65	39	213
Ipswich West	Apr.– May 2017	52°03′58″N 01°07′59″E	0.41	27	163
Ipswich East	Apr.– May 2018	52°04′08″N 01°11′26″E	0.80	42	280
Reading	Sept.– Oct. 2016	51°25′41″N 00°54′41″W	0.74	42	220
Southwell	May – June 2016	53°04′32″N 00°57′52″W	0.68	38	265
Sutton Bonington	July – Aug. 2018	52°49′54″N 01°14′54″W	0.77	36	275

5.3.2. Environmental variables

Based on a priori knowledge found in the literature, environmental variables that were found to affect fox and cat habitat use were extracted. Domestic cats living in urban and suburban areas rely on humans for food and shelter (Széles et al. 2018, Crowley et al. 2020), and are typically found close to houses and farms (Germain et al. 2008, Webster et al. 2019, Vanek et al. 2020). Greenspaces and gardens that are available nearby can also be used, sometimes more extensively than urban habitats (Thomas et al. 2014). Similarly, red foxes are generalist mesocarnivores that can

exploit and benefit strongly from anthropogenic resources, and readily associate with human-modified and urban habitats (Gosselink et al. 2003, Lesmeister et al. 2015). Foxes can also select row-crop fields in summer, where small mammals can be found in high densities (Gosselink et al. 2003), and woodlands, which offer suitable habitat for denning (Uraguchi & Takahashi 1998).

Based on this knowledge, the following environmental variables were calculated within a 50m circular buffer zone around each camera station to quantify the conditions of the surrounding habitat: 1) building density (number of buildings); 2) proportion of greenspace (natural and urban); 3) proportion of gardens; 4) proportion of agricultural lands (row-crop fields); 5) linear distance from each camera station to the nearest building; and 6) linear distance to the nearest patch of woodland. All environmental variables were extracted from the Ordnance Survey MasterMap Topography layer (© Crown copyright and database rights, 2020, Ordnance Survey, 100025252), using a Geographical Information System (ArcGIS v10.7.1; ESRI, Redlands, California).

5.3.3. Occupancy modelling

To investigate interactions between cats and foxes, a two-stage modelling approach was used. First, single-season, single-species occupancy models (MacKenzie et al. 2002) were used to investigate which of the environmental variables best predicted the occupancy of domestic cats (ΨA) and red foxes (ΨB) separately. The relative abundance of cats and foxes on a landscape scale was calculated as the number of photos taken at each station divided by the number of trapping days, averaged within each study area. Cat and fox relative abundances were added as variables influencing detection probability and occupancy, to account for variations in abundance between study areas (e.g. the probability to detect a fox was assumed to be higher in areas with higher fox abundance). Since cameras were systematically placed facing an open field to increase the chances of detecting hedgehogs (Schaus et al. 2020), detection probability should be comparable between stations. Models were ranked separately for each species using the '*AICcmodavg*' package (Mazerolle 2020) in R 4.0.2 (Team R Core 2018), which features functions to calculate a second-order variant of the quasi Akaike Information Criterion (QAICc) that include an additional bias-correction term for small sample sizes. Models with QAICc < 2 were considered to have "substantial empirical support" (Burnham & Anderson 2002). Models with uninformative parameters were discarded (Arnold 2010). Habitat variables were normalized using a log + 1 transformation, to improve model convergence. Finally, the effects of spatial autocorrelation in occupancy probability of the top single-species occupancy models (QAICc < 2) were assessed using Moran's I index (Moran 1950). The pseudo occupancy residuals were computed at each station by subtracting the generated posterior predictive distribution of the best models (ΨA and ΨB) to a theoretical independent and constant posterior predictive distribution (i.e. with constant occupancy and detection at all stations). The pseudo occupancy residual values were then assigned at each station, and Moran's I statistic was used to measure the overall spatial autocorrelation of the models' pseudo residuals at a regional (i.e. between study areas) and local (i.e. within each study area) scale. Due to their close proximities, the study areas of

Brackenhurst and Southwell, and Ipswich East and Ipswich West, were grouped to evaluate spatial autocorrelation. Threshold distances at the local scale were calculated as the minimum distance to ensure every station had at least one neighbouring station, whilst the threshold distance for the regional scale was chosen to ensure that stations from different study areas were separated.

Using the best predictors for the occupancy of domestic cats (ΨA) and occupancy of red foxes (ΨB), multispecies models were built to test how building density and distance to the nearest building influence cat and fox interactions ($\Psi A:B$ and $\Psi B:A$). To investigate interactions between the two species, single-season, multispecies occupancy models developed by Rota et al. (2016) were employed. The Rota et al. (2016) parameterization allows to model detection and occurrence probabilities of interacting species as a function of covariates via a multinomial logit link function. In addition, the latent occupancy state is a multivariate Bernoulli random variable that does not require the a priori assumption that one species is dominant over the other. Models that did not incorporate interactions (i.e. $\Psi A:B = \Psi B:A = 0$) or that assumed species interactions as independent from environmental covariates (i.e. $\Psi A:B = \Psi B:A = 1$) were also included in model selection. Single-species and multispecies models were fitted using the '*unmarked*' package (Fiske & Chandler 2011) in R 4.0.2 (Team R Core 2018), and candidate models were compared with QAICc, where models with QAICc < 2 were considered to have "substantial empirical support" (Burnham & Anderson 2002).

5.4. Results

5.4.1. Camera trapping

Cats and foxes were detected in all study areas, with important variations in the number of detections for each species among study areas (Table 5.2). At the station level, cats were detected at 76 stations, foxes at 57 stations, and the two species co-occurred at 9 stations only. Distance to the nearest building ranged from 0 to 388 meters (mean: 36.8 ± 62 SD), and there was on average 15.2 ± 15.5 individual buildings in the 50m circular buffer zone around each camera. The most common habitat type was greenspace, covering on average 24.6 ± 29.6% of the buffer zone, followed by agricultural land (14.3 ± 30.3%). Proportion of garden was excluded from the analysis, due to high correlation with building density (Spearman's rank correlation coefficients $\varrho = 0.75$; Zar 2010).

Table 5.2. Number of records for red foxes and domestic cats in the eight study areas. Naïve occupancy was calculated as the number of locations where a species was detected divided by the total number of stations within each study area.

Study area	**Number of detections**		**Naïve Occupancy**	
	Cat	Fox	Cat	Fox
Brackenhurst	1	9	0.03	0.28
Brighton	16	85	0.22	0.53
Hartpury	3	20	0.05	0.26
Ipswich West	163	1	0.81	0.04
Ipswich East	31	17	0.38	0.10
Reading	35	4	0.31	0.10
Southwell	20	49	0.29	0.18
Sutton Bonington	6	4	0.08	0.08

5.4.2. Occupancy modelling

5.4.2.1. Single-species occupancy modelling

For cats, substantial support was found for two occupancy sub-models: Ψ(Cat relative abundance + Building density + Distance to nearest building) and Ψ(Cat relative abundance + Building density + Distance to nearest building + Proportion of greenspace). The top two models had a cumulative weight of 0.76 (Table 5.3). Since the two models had similar AIC (ΔAIC < 2), "proportion of greenspace" was considered an uninformative parameter (i.e. it did not explain enough variation, Arnold 2010), and was therefore discarded. Cat occupancy increased with building density (β_{BDE} = 0.57 ± 0.23 SE; Figure 5.2a) and decreased with distance to the nearest building (β_{DNB} = -0.40 ± 0.18 SE; Figure 5.2b). Cat relative abundance positively affected the probability of detection (β_{CRA} = 2.82 ± 0.39 SE) and occupancy (β_{CRA} = 2.15 ± 1.05 SE) of cats.

For red foxes, substantial support was found for six occupancy sub-models (Table 5.3). However, no parameter was consistently present in each of the top sub-models, and all parameters could be considered uninformative. Therefore, none of the variables investigated seemed to affect fox occupancy. Fox relative abundance positively affected the probability of detection (β_{FRA} = 5.60 ± 1.10 SE) and occupancy (β_{FRA} = 5.05 ± 1.59 SE) of foxes substantially.

*Table 5.3. Full model set used to evaluate occupancy (Ψ) for domestic cats and red foxes. Detection probability (p) of cats and foxes were predicted to vary with cat and fox relative abundance, respectively, in each of the model evaluated. The top-ranked models are bolded. a CRA = cat relative abundance; FRA = fox relative abundance; BDE = building density; DNB = distance to nearest building; DNW = distance to nearest woodland; PGR = proportion of greenspace; PAG = proportion of agricultural land. b number of model parameters. c difference in Quasi Akaike's Information Criterion between current model and the best model. d Quasi Log Likelihood. e model weight. f cumulative model weight. * model with uninformative parameter.*

Species	**Model** ^{a}	**K** ^{b}	**QAIC$_c$**	**ΔQAIC$_c$** ^{c}	**QLL** ^{d}	**w_i** ^{e}	**Cum. w_i** ^{f}
Domestic cat	**p (CRA), Ψ (CRA + BDE + DNB)**	**6**	**889.19**	**0.00**	**-438.45**	**0.48**	**0.48**
	p (CRA), Ψ (CRA + BDE + DNB + PGR) *	**7**	**890.24**	**1.05**	**-437.92**	**0.28**	**0.76**
	p (CRA), Ψ (CRA + BDE)	5	892.13	2.94	-440.96	0.11	0.87
	p (CRA), Ψ (CRA + BDE + PGR)	6	893.01	3.82	-440.36	0.07	0.94
	p (CRA), Ψ (CRA + DNB)	5	894.12	4.93	-441.96	0.04	0.98
	p (CRA), Ψ (CRA + DNB + PGR)	6	896.12	6.93	-441.91	0.02	1.00
	p (CRA), Ψ (CRA)	4	914.17	24.98	-453.02	0.00	1.00
	p (CRA), Ψ (CRA + PGR)	5	914.97	25.78	-452.38	0.00	1.00
Red fox	**p (FRA), Ψ (FRA + BDE + DNW) ***	**6**	**687.52**	**0.00**	**-337.61**	**0.19**	**0.19**
	p (FRA), Ψ (FRA + DNW) *	**5**	**688.31**	**0.79**	**-339.05**	**0.13**	**0.32**
	p (FRA), Ψ (FRA + PAG + DNW) *	**6**	**688.75**	**1.22**	**-338.23**	**0.10**	**0.42**
	p (FRA), Ψ (FRA + BDE) *	**5**	**688.77**	**1.24**	**-339.28**	**0.10**	**0.53**
	p (FRA), Ψ (FRA + DNB + DNW) *	**6**	**688.78**	**1.25**	**-338.24**	**0.10**	**0.63**
	p (FRA), Ψ (FRA + BDE + PAG + DNW) *	**7**	**689.52**	**1.99**	**-337.56**	**0.07**	**0.70**
	p (FRA), Ψ (FRA + BDE + DNB + DNW)	7	689.62	2.10	-337.61	0.07	0.77
	p (FRA), Ψ (FRA + DNB + PAG + DNW)	7	690.28	2.75	-337.94	0.05	0.82
	p (FRA), Ψ (FRA + DNB)	5	690.81	3.28	-340.30	0.04	0.85
	p (FRA), Ψ (FRA + BDE + DNB)	6	690.85	3.32	-339.28	0.04	0.89
	p (FRA), Ψ (FRA + BDE + PAG)	6	690.85	3.33	-339.28	0.04	0.93
	p (FRA), Ψ (FRA)	4	691.62	4.09	-341.74	0.02	0.95
	p (FRA), Ψ (FRA + PAG)	5	691.94	4.41	-340.86	0.02	0.97
	p (FRA), Ψ (FRA + DNB + PAG)	6	692.53	5.01	-340.12	0.02	0.99
	p (FRA), Ψ (FRA + BDE + DNB + PAG)	7	692.95	5.42	-339.28	0.01	1.00

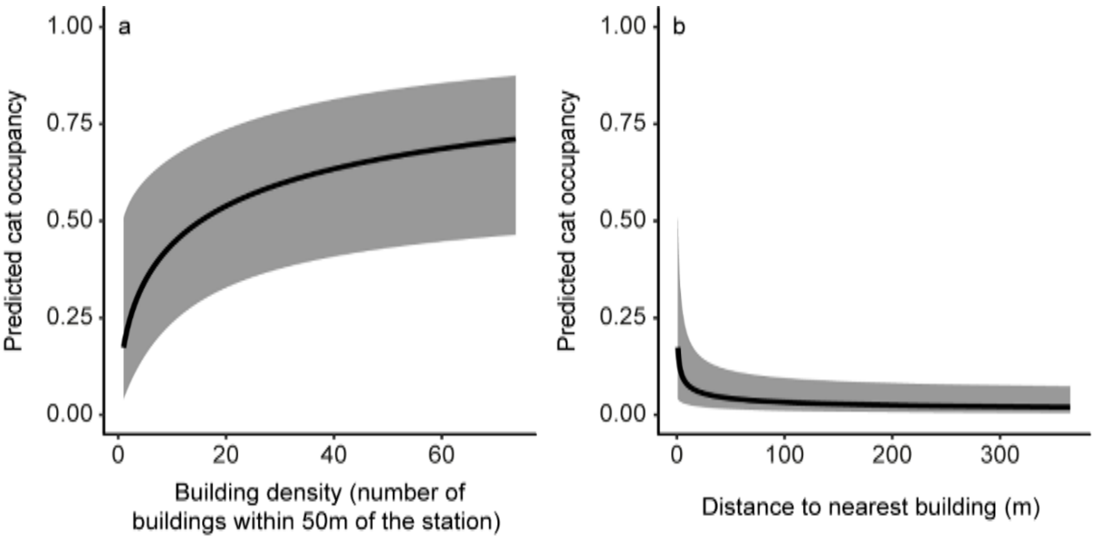


Figure 5.2. Domestic cat occupancy increased with the number of buildings within a 50m buffer of each station (a), and decreased with the distance to the nearest building (b). The grey ribbon represents the 95% confidence intervals.

The best cat occupancy model showed strong spatial autocorrelation on a regional scale (i.e. between study areas; Table 5.4), and the spatial distribution of higher and/or lower observed occupancy compared to model predictions was more spatially clustered than would be expected if underlying spatial processes were random. This pattern was also observed at the local scale in certain study areas (Table 5.4), suggesting that nearby camera stations were not always independent. Due to the lack of a top model for fox occupancy, spatial autocorrelation could not be measured for the fox dataset. However, given the larger daily movement rate of foxes (Macdonald 1987), spatial autocorrelation could be reasonably expected as well.

Table 5.4. Moran's I index (spatial autocorrelation) and z-score values for the pseudo occupancy residuals of the top model for cat occupancy: Ψ(Cat relative abundance + Building density + Distance to nearest building).

	Threshold distance (m)	Moran's I index	z-score	p-value
Global	5,000	0.480	32.753	<0.001
Brackenhurst and Southwell	170	0.685	6.647	<0.001
Brighton	180	0.302	2.446	0.014
Hartpury	171	0.415	0.767	<0.001
Ipswich East and West	216	0.524	6.981	<0.001
Reading	161	0.029	0.383	0.701
Sutton Bonington	226	0.307	3.118	0.002

5.4.2.2. Multispecies occupancy modelling

Substantial support was found for three models (Table 5.5). However, some of the top-ranked models are contradictory, and thus none of them can be considered as better. The output of model selection, in this case, does not provide a suite of models that could be averaged to extract relevant information, but shows instead that none of these models can explain interactions between cats and foxes. It should be noted that this was a small dataset, and the frequency of co-detections was low.

Table 5.5. Full multispecies model set evaluating symmetrical interactions (ΨAB) between cats and foxes. Multispecies occupancy models included: ΨA (cat relative abundance + building density + distance to the nearest building); ΨB (fox relative abundance); pA (cat relative abundance); pB(fox relative abundance). Top-ranked models are bolded. BDE = building density; DNB = distance to nearest building. b number of model parameters. c difference in Quasi Akaike's Information Criterion between current model and the best model. d Quasi Log Likelihood. e model weight. f cumulative model weight.

Model [a]	**K** [b]	**$QAIC_c$**	**$\Delta QAIC_c$** [c]	**QLL** [d]	**w_i** [e]	**Cum. w_i** [f]
ΨAB (BDE + DNB)	**13**	**1577.48**	**0.00**	**-775.09**	**0.39**	**0.39**
ΨAB (BDE)	**12**	**1577.70**	**0.22**	**-776.29**	**0.35**	**0.73**
ΨAB (Constant)	**11**	**1579.32**	**1.83**	**-778.19**	**0.15**	**0.89**
ΨAB (No interaction)	10	1581.16	3.67	-780.19	0.06	0.95
ΨAB (DNB)	12	1581.48	3.99	-778.18	0.05	1.00

5.5. Discussion

Camera trap data were analysed to explore the spatial ecology of red foxes and domestic cats in rural and suburban England. Cat occupancy was found to increase with proximity to nearest building and with higher building densities, which was partly in accordance with the first hypothesis that probability of occurrence of cats and foxes was predicted to increase in proximity to human habitats. A multispecies investigation of conditional occupancy and co-occurrence of the two species could not be properly tested due to a small dataset and the rarity of co-detections.

The single-species occupancy models yielded in this chapter suffered from spatial autocorrelation, likely because the original camera trap survey was designed for an animal with smaller daily movements than cats or foxes. Studies often aim to maintain independence of station-level information by basing the spacing between

cameras on the size of an animal’s home range (e.g. Karanth 1995, O’Connell & Bailey 2011; but see MacKenzie et al. 2017). When the area covered by the cameras is too small compared to the species home range, as was the case in this chapter, spatial autocorrelation may affect species detection and introduce bias in the identification of key ecological factors influencing occupancy (Maffei & Noss 2007, Kolowski et al. 2021). Whilst recent statistical analysis have been developed to account for such spatial autocorrelation (e.g. Johnson et al. 2013, Bardos et al. 2015), they still present challenges and difficulties (Guillera-Arroita 2016). Adopting a mix of survey-design strategies, and including these design features into the modelling framework, will facilitate multi-species camera-trap studies (Iannarilli et al. 2021).

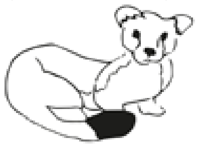
5.5.1. Occupancy and habitat use of cats and foxes

Previous research shows that urban and suburban areas can foster large cat populations (e.g. Flockhart et al. 2016, Vanek et al. 2020). Within these areas, cat abundance is typically higher in residential areas with high building density, owing to the reliance of cats on humans for food and shelter (Flockhart et al. 2016, Vanek et al. 2020). Similarly, free-ranging cat occupancy in rural landscapes has been observed to increase with density and proximity to anthropogenic features (Krauze-Gryz et al. 2012, Morin et al. 2018). Dependence on human features was found in this chapter too, suggesting that most free-ranging cats within the urban and sub-urban areas monitored were not feral cats (i.e. living independently of humans), but were more likely to be domestic cats with a regular access to human housing.

Red foxes are highly adaptable medium-sized carnivores, and are increasingly colonising urban areas worldwide (e.g. Harris & Rayner 1986, Gloor et al. 2001, Janko et al. 2012). Previous studies in the UK suggested that fox distribution was correlated with housing density in a suburban area (Macdonald 1981), whilst other studies found that foxes preferred areas with lower housing density (Harris & Rayner 1986, Odell & Knight 2001), or did not find an effect of housing density on urban fox distribution (Harris 1981a). This heterogeneity of results may reflect different strategies used by populations of urban versus rural foxes. Urban and rural foxes develop distinct spatial behaviours, illustrated by dissimilar home range sizes (Janko et al. 2012), habitat selection (e.g. Gosselink et al. 2003), and even genetic differentiation (Atterby et al. 2015). Therefore, it is likely that the majority of foxes caught on camera for this study were rural foxes showing a preference for natural habitats (e.g. Cavallini & Lovari 1994), as opposed to urban foxes that select gardens in dense residential areas (Harris 1981b).

5.5.2. Patterns of spatial co-occurrence between cats and foxes

Little is known about the spatial interaction between cats and foxes in human-dominated landscapes, but comparisons can be drawn from other species or types of landscapes. For instance, in cities of North America, domestic cats can select areas with higher building densities, to avoid another urban-thriving canid, the coyote, who prefers to occupy urban parks and forests (Gehrt et al. 2013, Kays et al. 2015). Therefore, the habitat use of cats within the urban landscape can be partly regulated by the presence of a larger competitor, and a similar pattern could hypothetically be observed between cats and urban foxes in the UK. In relatively



less disturbed landscapes, feral cats have been observed to avoid areas with high fox density (Ferreira et al. 2011) and adapt their habitat use to the presence of fox (Molsher et al. 2017; but see Šálek et al. 2014), suggesting a potential for interspecific competition between the two species.

Despite being subordinate, and spatially restricted by foxes, cats may have an indirect negative impact on foxes, for instance through competition for prey. In natural and semi-natural habitats, high levels of trophic overlap have been found between the two species (e.g. Glen et al. 2011, Woinarski et al. 2018), and the presence of fox influences the feeding behaviour of cats (Molsher et al. 2017). In human-dominated landscapes, high trophic overlaps between these two species have also been observed, indicating a potential for trophic competition (Castañeda et al. 2020). This competition could, however, be eased by the generalist feeding behaviour of the two species, and the abundance of anthropogenic food resources. In addition, Kays et al. (2020) found that domestic cats have remarkably small home ranges (average of 0.036 km^2), centred around their homes. Thus, the ecological impact of cats on native wildlife (either through predation or intraguild competition) may be severe, but spatially limited to landscapes that are already highly disturbed by humans.

5.6. Conclusions

Feral and free-ranging domestic carnivores can intensify intraguild competition and be a threat to native carnivores. This study found that free-ranging cats occurred mostly in the vicinity of densely built human housing, whilst foxes preferred

natural habitats further away from human settlements. These findings suggest that co-occurrence and interactions between the two species may be relatively rare in suburban and rural areas of the UK, although this could not be statistically verified.

Future studies should differentiate between the spatial behaviour of feral versus free-ranging cats, and urban versus rural foxes, as they display strong differences in habitat selection. Whilst the negative impact of domestic cats is likely to be constrained within areas adjacent to human settlements, the same cannot be said for feral cats, whose larger home ranges and preference for natural habitats may cause substantial harm to native wildlife.

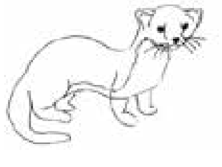
Chapter 6

General discussion and conclusions

6.1. Overview of thesis

This thesis aimed to characterise and quantify the effects of human disturbance on spatial, temporal and trophic niche partitioning among carnivores. The novelty of this work resides in its shift of focus from the direct impact of humans on species and species behaviour towards less-studied effects of humans on species interactions and natural patterns of interspecific competition, which can constitute an additional pressure on these species. This research gap was addressed innovatively by investigating global patterns whilst simultaneously considering local variability, all through the use of diverse methods ranging from the review of existing literature to the analysis of raw data.

Human disturbance was found to impact resource partitioning in all three niche dimensions proposed by Schoener (1974a). However, the findings highlighted contrasting outcomes across dimensions and carnivore species, and human disturbance has to potential to either increase, decrease, or destabilise niche partitioning and interspecific competition among carnivore communities (Chapter 2). Indeed, carnivore adaptations to both humans and competitors were found to be strongly dependent on the biotic and abiotic characteristics of the landscape, and the type of human disturbance considered (Chapter 3). Similarly, human disturbance may not affect all species equally. For instance, anthropogenic resource provisioning can affect the spatial distribution of species tolerant to humans to a greater extent than interspecific interactions, illustrating the disruptive effect of human disturbance on intraguild competition (Chapter 5). This study also



evaluated the published literature used throughout the chapters, by providing a critical appraisal of the strengths and weaknesses of the procedures used and reported findings. Specifically, this thesis focused on an in-depth evaluation of the method used to quantify the coefficient of temporal overlap between species, and key guidelines were provided to benefit further research (Chapter 4).

6.2. The future of carnivore communities

Carnivore communities in anthropogenic biomes face multiple threats. Top-down threats can directly affect carnivore populations through the legal or illegal killing of carnivores, either for commercial use (e.g. Gratwicke et al. 2008) or as an attempt to reduce conflicts with human interests (Treves & Karanth 2003), and through human-induced depletion of trophic resources (Wolf & Ripple 2016). Top-down anthropogenic pressures can also have indirect deleterious effects on carnivores via behavioural responses, such as the increase of physiological stress resulting from non-lethal human activities (e.g. Piñeiro et al. 2012). Similarly, bottom-up disturbances, referring to changes in land use for human purposes, can negatively affect carnivores by removing species' natural habitats (Gálvez et al. 2013), increasing habitat fragmentations (Crooks 2002), and changing the availability, spatial distribution and nature of trophic resources (Murray et al. 2015). These threats are likely to impact and modify the rules of intraguild competition and species coexistence within carnivore communities. In this regard, findings from chapter 2 show that, as a result, carnivore guilds may be reshaped in three different ways.

First, intraguild competition may be exacerbated, thus increasing the frequency and intensity of species interactions and having an overall negative effect on species richness and abundance in the community. This situation could occur if all species saw the fundamental niche they occupy reduced by human activities, and were forced to shift towards resources already used by other species. However, this scenario remains mostly theoretical, and is unlikely to happen in nature. In reality, the decrease in the abundance of native species is typically concurrent with the proliferation of species unaffected, or benefiting from, human activities (e.g. Farris et al. 2015b, Wearn et al. 2017).

Indeed, the second way in which human disturbance can affect intraguild competition is by providing a competitive advantage to species tolerant of humans and capable of using anthropogenic resources. Biotic homogenisation has been observed in plants and animals inhabiting anthropogenic biomes (McKinney 2008, van Rensburg et al. 2009). In such cases, species richness and diversity carry on being negatively impacted at regional and global scales (i.e. gamma diversity; Whittaker 1960, McKinney & Lockwood 1999, Smart et al. 2006), while the overall species abundance, conversely, increases. In addition, the replacement of endemic species with already widespread species benefiting from human activities can reduce spatial diversity among carnivore communities (i.e. reduced Beta diversity; Whittaker 1960, Harrison 1993). In this scenario, the new homogenous carnivores communities can be dominated by two types of species: (a) native medium-size carnivores may be released from top-down control by large carnivores, leading to mesopredator outbreaks and spatial expansion (Prugh et al. 2009).

Such mesopredators commonly have a flexible diet and habitat selection, and can thrive in human-dominated landscapes (e.g. Krofel et al. 2017). (b) exotic carnivores (i.e. introduced species, free-ranging and feral domestic species) are increasing worldwide in number and range (e.g. Hughes & Macdonald 2013), and represent a major threat to global biodiversity through predation, competition and disease transmission (Doherty et al. 2016). Although the outcome of interactions between exotic and native carnivores depends on the relative position of the two species in the interference hierarchy, exotic species may often act as a new, dangerous competitor (Heim et al. 2019). As such, exotic carnivores can exclude native species from their natural habitats (Vanak et al. 2015), or even contribute to local species extinctions (Glen & Dickman 2005, Fillios et al. 2012).

Finally, besides promoting human–wildlife coexistence (Rosenzweig 2003), redesigning human habitats can prove beneficial to carnivore communities. Promoting mosaic landscapes in human-dominated areas that include patches of habitats suitable for all native species can diminish the likelihood of interference interactions, and facilitate stable coexistence. In addition, ensuring a high availability and accessibility of trophic resources in these habitats can alleviate competition for food, and allow the sympatry of species within the same trophic level (Levin 1974). Therefore, it is possible to promote rich and diverse carnivore communities in human-dominated landscapes, comprised of small / medium (Pereira et al. 2012) and large carnivores (May et al. 2008) alike.

6.3. Conservation implications and importance of study

The IUCN Red List of Threatened Species (global assessment data and range data; IUCN 2020) reports 256 terrestrial species belonging to the order Carnivora. Of these, 40 (15.6%) are listed as Vulnerable; 24 (9.4%) as Endangered; and 4 (1.6%) as Critically Endangered. As human pressures on the environment are likely to continue increasing globally, the number of threatened carnivores could grow rapidly. Many carnivore populations are now in decline, but this phenomenon is primarily attributed to the direct impact of human persecution and land use changes (Ripple et al. 2014, 2016b, Marneweck et al. 2021). This thesis illustrates new ways in which humans can constitute an additional pressure on these species, by interfering with the natural patterns of interspecific competition. Thus, understanding how human disturbance may affect the way species interact with each other is of high conservation value, especially considering how the outcomes of interspecific interactions shape animal communities.

Altering carnivore communities can have cascading effects on lower trophic levels, and on the structure of the ecosystem, although the exact effects can be difficult to predict due to the complexity of food webs. Furthermore, the loss of native species, and the invasion by exotic species, can alter ecosystem processes (Loreau et al. 2001, Hooper et al. 2005). For instance, this is observed in vertebrate scavenger communities, where the reduction in species richness resulting from human activities (Sebastián-González et al. 2019) can lead to the redistribution of resources to lower trophic levels (Cunningham et al. 2018), or to a complete loss of carrion-

removal ecosystem services (Huijbers et al. 2015, DeVault et al. 2016, Mateo-Tomás et al. 2017).

Findings from this thesis highlight the urgent need to adapt land-use planning, wildlife management, and human activities to limit the negative impact on carnivore communities. First and foremost, any practice reducing the diversity of resources available to carnivores (i.e. their niche breadth) for human gains should be swiftly reassessed. Current estimates predict that species may lose up to 58% of their natural habitat by 2100 (Jantz et al. 2015, Beyer & Manica 2020), which would contribute to large-scale faunal extinctions (Pereira et al. 2010, Pimm et al. 2014). Active restoration targeting habitat diversity across spatial scales (e.g. by restoring areas to varying stages of ecological succession; Lengyel et al. 2020) provides a larger variety of microhabitats and trophic resources, which facilitates resource partitioning between species (Vander Zanden et al. 2016). Secondly, there is an urgent need to address management of invasive carnivore species, not only because of the impact they have on native prey populations, but also with regard to the additional competitive pressure they enforce onto native carnivore species. The importance of controlling introduced predators has recently gained recognition, and large-scale programs of predator control and/or eradication are emerging (e.g. Aotearoa’s Predator Free 2050 project). The first step towards successful removal of invasive carnivores must involve a change in the regulation of domestic animals ownership laws, coupled with thorough programs of public education to raise awareness. Such legislation may include the mandatory identification and neutering of owned pets (e.g. Belgium became the first country to require almost all of the domestic cats to be spayed or neutered before the age of 6 months); severe fines for illegal ownership and abandonments of animals; and restricted access to the outdoors (spatially and/or temporally). In addition, Trap-Neuter-Release or “catch and kill” programs can be implemented to decrease the stray and feral populations, although their effectiveness is strongly reduced if immigration is not controlled simultaneously (e.g. by reducing the rate of abandonment of domestic animals; Natoli et al. 2006, Lohr et al. 2013). Finally, limiting access to human-provided food resources (e.g. by improving waste management in public spaces, or raising awareness of the impact of feeding animals directly) would help manage populations of free-ranging domestic carnivores (Bhalla et al. 2021). Unfortunately, enforcing legislation on domestic animal ownership and performing lethal control of stray and feral animals still face strong public reproval and controversy, which present another set of challenges that should be addressed through social sciences.

6.4. Limitations of work and avenues for further research

There are several limitations identified in this thesis, and to the overall science of species coexistence, that should be considered when drawing conclusions.

Firstly, exploring the different processes involved in the behavioural adaptation to humans, and subsequent consequences on species interactions and niche partitioning, may suffer from a lack of precision if undertaken solely on a global scale. Large-scale studies can yield good information on the global effect of humans on species behaviour (e.g. Gaynor et al. 2018, Manlick & Pauli 2020, Doherty et al. 2021). However, as chapter 3 illustrates, these global patterns may often be

overridden by fine-scale specificities of the landscape and animal communities. The large-scale indices used to quantify human, meteorological or ecological factors are probably too coarse to detect the processes at play. Understanding the spatial and temporal scales at which species adapt to humans and intraguild competitors is critical to evaluate how interspecific interactions may be reshaped by human interference. Future investigations will benefit from combining large-scale indices (e.g. remote sensing imagery to estimate land use) and in situ measurements of characteristics of the landscape (e.g. daily variations in human presence). Incorporating multi-scale perspectives into conservation and management plans can help address the global challenge of human–wildlife coexistence (Carter et al. 2012, Wilmers et al. 2013).

A further limitation in the current literature is the lack of experimental studies, either natural or manipulative, on behavioural adaptations to humans. Studies that evaluate the influence of external variables on niche partitioning by monitoring two or more treatment groups (e.g. Lewis et al. 2015, Wang et al. 2015) are still scarce, despite yielding highly inferential results. One solution lies in the coordinated distributed experiments collaborative approach promoted by Fraser et al. (2013), in which standardised experiments are used to control spatial and temporal scales across a wide geographic range. Coordinated distributed experiments may help uncover global patterns, whilst retaining fine-scale experimental control and precision. Similarly, chapter 4 highlights the importance of robust research methodology, careful presentation and meaningful interpretation of the data in promoting coherence and comparability among studies. Ultimately, adopting a

rigorous, evidence-based approach will help obtain a better understanding of the effects of human disturbance on animal communities (Pullin & Knight 2003).

The conclusions presented in this thesis are mostly built upon the findings from studies published in peer-reviewed journals. Through a critical appraisal of the currently available literature, this thesis provides guidelines and recommendations that will lead to an improvement in the scientific rigour, and promote harmonisation among studies. The main recommendations are as follow:

i. Multidimensional investigations of niche partitioning should be favoured. Approaches measuring the combined spatial and temporal niche dimensions yield more robust inferences on the processes underlying species interactions and niche partitioning (Cusack et al. 2017). A variety of tools are now available to operate such spatiotemporal analysis (e.g. Cusack et al. 2017, Ait Kaci Azzou et al. 2021). Dietary niche breadth and overlap among competing carnivores are also important components of resource partitioning, and can be successfully integrated within spatiotemporal studies (e.g. Gantchoff & Belant 2016, Monterroso et al. 2016, Osorio et al. 2020). Simultaneously investigating the three main dimensions of niche partitioning will yield the most detailed picture of the processes at play, and be beneficial to our understanding of the impact of human disturbance on interspecific interactions (e.g. Smith et al. 2018).

ii. Increased attention should be given towards small and medium carnivores, since the current research is largely biased towards large carnivores (Brooke et al. 2014, Marneweck et al. 2021). As smaller carnivores adapt their behaviour in response to

human activities in a similar extent to large carnivores (Bateman & Fleming 2012, Clinchy et al. 2016), they can also affect interactions with other species (e.g. Nagy-Reis et al. 2017). In addition, small carnivores can play important ecological roles in the ecosystem (Roemer et al. 2009), and more research on their behaviour and demographics is warranted to ensure their successful conservation.

iii. Similarly, there is an urgent need to improve our understand of the impact of exotic species on native carnivores. Invasive species may put additional pressure on threatened carnivore populations through competition for resources (Vanak et al. 2015) or predation (Ritchie et al. 2014). Findings from chapter 5 suggest that domestic carnivores with regular access to human resources could be excluding native species from human-modified habitats, as was found in other studies (Vanak & Gompper 2009b). As anthropogenic biomes expand, the extirpation of native carnivores and recolonisation by exotic carnivores could pose a grave threat to native carnivore populations (Farris et al. 2017b).

6.5. Conclusion

The findings of this thesis provide a novel insight into the effects of human disturbance on resource partitioning and coexistence among carnivores. The findings have demonstrated that the human influence is diverse, and can affect niche partitioning in three contrasting ways. As such, human disturbance can either disrupt niche partitioning (thus increasing intraguild competition), unbalance niche partitioning and intraguild competition, or facilitate niche partitioning (hence decreasing intraguild competition). In addition, the global analysis of temporal

overlap among carnivores and local investigation of spatial co-occurrence between red foxes and domestic cats highlights the importance of considering fine-scale patterns interspecific interactions and behavioural adaptations to humans. To do so, further research would benefit from conducting more experimental studies, although the difficulty of running experimental studies at the spatial scale where carnivores operate is at the heart of heated debates (Allen et al. 2017a, b, Bruskotter et al. 2017), and should aim to harmonise the methods used to ensure the best methodological rigour and inference on their results.

This study highlights that the impacts of human pressures on niche partitioning can deregulate intraguild competitive interactions and threaten stable coexistence among species, which will eventually end up reshaping the structure of carnivore communities. Anthropogenic biomes and human pressures are expanding globally, yet the full impact of changes in carnivore community structure on other ecological guilds and trophic levels has rarely been addressed. There is an urgent need to better understand the cascading effects that human-induced changes in niche partitioning and intraguild competition within carnivore communities can have on terrestrial ecosystem structure and function. Ultimately, research and conservation attention is required to slow or reverse the current deleterious effects of humans, and promote the beneficial ones.

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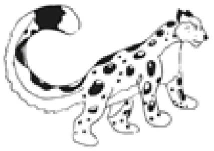

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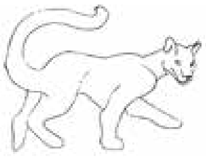

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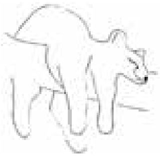

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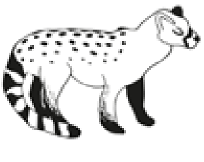

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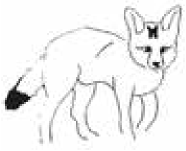

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Appendix I: Sévêque A, Gentle LK, López-Bao JV, Yarnell RW, Uzal A (2020) Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biological Reviews 95: 1689–1705.

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Human disturbance has contrasting effects on niche partitioning within carnivore communities

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ABSTRACT

Among species, coexistence is driven partly by the partitioning of available resources. The mechanisms of coexistence and competition among species have been a central topic within community ecology, with particular focus on mammalian carnivore community research. However, despite growing concern regarding the impact of humans on the behaviour of species, very little is known about the effect of humans on species interactions. The aim of this review is to establish a comprehensive framework for the impacts of human disturbance on three dimensions (spatial, temporal and trophic) of niche partitioning within carnivore communities and subsequent effects on both intraguild competition and community structure. We conducted a systematic review of the literature on carnivore niche partitioning (246 studies) and extracted 46 reported effects of human disturbance. We found evidence that human disturbance impacts resource partitioning, either positively or negatively, in all three niche dimensions. The repercussions of such variations are highly heterogeneous and differ according to both the type of human disturbance and how the landscape and/or availability of resources are affected. We propose a theoretical framework of the three main outcomes for the impacts of human disturbance on intraguild competition and carnivore community structure: (*i*) human disturbance impedes niche partitioning, increasing intraguild competition and reducing the richness and diversity of the community; (*ii*) human disturbance unbalances niche partitioning and intraguild competition, affecting community stability; and (*iii*) human disturbance facilitates niche partitioning, decreasing intraguild competition and enriching the community. We call for better integration of the impact of humans on carnivore communities in future research on interspecific competition.

Key words: Carnivora, coexistence, competition, spatial partitioning, species interactions, temporal partitioning, trophic partitioning

CONTENTS

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I. INTRODUCTION

The competitive exclusion principle (Gause, 1934; Hardin, 1960) states that two interacting species occupying similar ecological niches (Hutchinson, 1957), and therefore competing for the same resources, cannot co-exist in the long term. However, the limiting similarity theory of MacArthur & Levins (1967) highlights the existence of a threshold in niche similarity under which stable coexistence is possible. Thus, to achieve coexistence, competing species must segregate one or more dimensions of their ecological niche, a process commonly referred to as resource partitioning (Schoener, 1974). Consequently, interspecific competition and resource partitioning regulate the strength of interactions between species, and are significant forces shaping community structures (Schoener, 1983; Wisheu, 1998).

Over the last 20 years, interspecific competition has been identified as a key mechanism structuring mammalian carnivore guilds (e.g. Linnell & Strand, 2000; Caro & Stoner, 2003; Hunter & Caro, 2008). Dominant predators can reduce the fitness of subordinate species (Jiménez *et al.*, 2019), commonly smaller species, through exploitation competition (e.g. consumption of similar prey species; Hayward & Kerley, 2008) or interference competition (e.g. intraguild predation; Palomares & Caro, 1999). Subordinate species can diminish this deleterious impact by partitioning resources from their competitors, and typically do so through a combination of three niche dimensions (Schoener, 1974): spatially, subordinate species can adjust their habitat use to limit sympatry with dominant predators (e.g. Durant, 1998; Viota *et al.*, 2012); temporally, competitors can alter their activity pattern to reduce the amount of time where species are active simultaneously (e.g. Hayward & Slotow, 2009); and trophically, competitors can segregate their diets by using different food resources (e.g. Karanth & Sunquist, 1995).

Accumulating evidence, however, has reported high values of niche overlap within different competing carnivore guilds worldwide (e.g. Mitchell & Banks, 2005; Glen & Dickman, 2008; Cozzi *et al.*, 2012; Davis *et al.*, 2018), suggesting that niche segregation alone is not the fundamental mechanism driving coexistence, and may be the outcome of more complex processes (Vanak *et al.*, 2013). For example, risk avoidance may often be a reactive, rather than predictive, process (Broekhuis *et al.*, 2013; López-Bao *et al.*, 2016). In this case, carnivore species can maintain awareness of their nearest competitors at all times and adapt their use of space and time to prevent risky encounters. As such, competing species live in a landscape in which contrasting habitats result in different levels of risk of interference competition [i.e. the landscape of fear (Laundré, Hernández & Altendorf, 2001; Ritchie & Johnson, 2009)].

Traditionally, studies on interspecific competition have focused on pairs of carnivore species in their natural environment, without considering how humans could influence the different processes investigated (e.g. Creel & Creel, 1996; Durant, 1998). However, recent evidence suggests that beyond affecting species' behaviour (Gaynor *et al.*, 2018; Tucker *et al.*, 2018), human influence may be extended to how species interact (Dorresteijn *et al.*, 2015). For example, carnivores facing negative interactions with humans can invest in antipredator behaviours in order to limit encounters with humans (Frid & Dill, 2002). These behavioural adaptations may involve operating medium and fine-scale spatiotemporal avoidance of human activities (Llaneza, López-Bao & Sazatornil, 2012; Oriol-Cotterill *et al.*, 2015), and may interfere with competitor avoidance.

However, sensitivity to humans is not homogenous, and behavioural responses of wildlife to anthropogenic disturbance vary among species (Lowry, Lill & Wong, 2013; Samia *et al.*, 2015). The most sensitive species can modify their spatiotemporal habitat use to maximise avoidance of human features and activities (e.g. Stillfried *et al.*, 2015; Llaneza, Sazatornil & López-Bao, 2018). For example, bobcats, *Lynx rufus*, and coyotes, *Canis latrans*, inhabiting an urban nature reserve in California exhibited spatial and temporal displacement in response to human recreation, with the two species avoiding areas with higher human activity (George & Crooks, 2006). Species selecting habitats with reduced human disturbance, a limited resource, could therefore face a higher risk of encountering competitors (Dröge *et al.*, 2017; Hayward, O'Brien & Kerley, 2007). Conversely, species more tolerant to humans can show a preference for human-modified environments over natural habitats (Deuel *et al.*, 2017). Caracals, *Caracal caracal*, in South Africa have adapted their foraging behaviour to access highly available prey resources in agroecosystems, thus reducing their use of natural forest habitats (Ramesh, Kalle & Downs, 2017*a*). Although this behaviour comes with a higher risk of human encounters, it could decrease the probability of facing intraguild competitors which avoid these habitats (Ordeñana *et al.*, 2010).

In addition, the attitude of humans towards carnivores is also unequal among species (Dressel, Sandström & Ericsson, 2015). Lethal management is often biased towards large carnivores, mainly due to competition for food with humans (Treves & Karanth, 2003; Oriol-Cotterill *et al.*, 2015). The long-term persecution of large carnivores by humans has benefited some mesocarnivore populations by reducing competition with larger carnivores, a process known as the 'mesopredator release' effect (Crooks & Soulé, 1999; Prugh *et al.*, 2009), influencing in some cases the abundance and distribution of these species (Lapoint, Belant & Kays, 2015; Krofel *et al.*, 2017; Newsome *et al.*, 2017; Jiménez *et al.*, 2019).

Human encroachment into natural ecosystems is increasing at an alarming rate (Watson *et al.*, 2016), so it is critical to understand how anthropogenic perturbations impact communities and species interactions. There is extensive literature on the impact of humans on predator–prey dynamics (e.g. Berger, 2007; Muhly *et al.*, 2011), plant–herbivore interactions (e.g. Young *et al.*, 2013; Atkins *et al.*, 2019) and mutualist interactions (e.g. Wright, Hernandéz & Condit, 2007; Toby Kiers *et al.*, 2010). Still, there is an important gap in knowledge on the impact of human disturbance on competition and coexistence within animal guilds, such as among carnivores.

To address this knowledge gap, we review the literature on niche partitioning among the carnivore guild, with the aim to: (*i*) synthesise all reported effects of human disturbance on the spatial, temporal and trophic niche dimensions; and (*ii*) propose a comprehensive framework investigating how these effects may impact the strength of intraguild competition, and how they could end up reshaping the structure of carnivore communities. The proposed framework will be valuable to future research by highlighting gaps in the investigation of human impacts on carnivore communities and coexistence. We provide additional recommendations to develop an effective and standardised research practice.

II. MATERIALS AND METHODS

(1) Literature search

We performed a literature search in October 2018, using the electronic databases *Scopus* (https://www.scopus.com) and *Web of Science* (https://www.webofknowledge.com). We used the following key word combination to search for peer-reviewed literature written in English, with no time limitation: (niche OR spatial OR temporal OR resource OR diet OR trophic) AND (partitioning OR overlap OR segregation OR separation) AND (carnivor*). The review protocol was applied following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher *et al.*, 2009).

The database search returned 1,095 records (Fig. 1), which were subsequently screened by reading the title and abstract. To be included in the next stage, studies had to investigate the spatial, temporal and/or trophic niche of at least two sympatric terrestrial vertebrate carnivore species. After this screening, 256 articles were retained, and their full text assessed for eligibility. To be included in the final synthesis, studies had to calculate the proportion of niche overlap between two or more species or measure the relative influence of one species on another's niche utilisation (e.g. multispecies occupancy models). At this stage, 166 studies fulfilled the inclusion criteria and were retained.

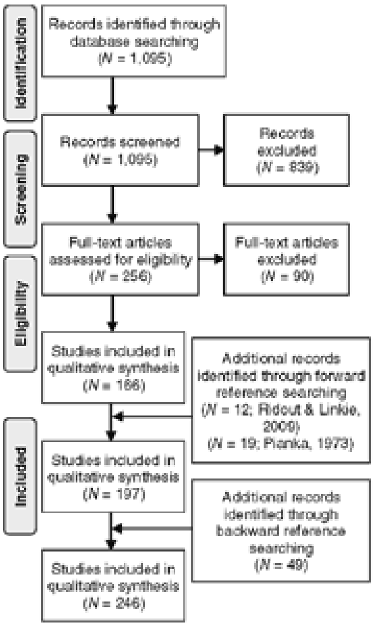

Fig 1. Preferred reporting items for systematic reviews and meta-analysis flowchart (Moher *et al.*, 2009).

Although niche overlap between pairs of species was measured using a variety of methods, two methods prevailed: Pianka's overlap index (Pianka, 1973), which measures the spatial, temporal and trophic niche overlap between species, which was used by 47% of the included studies ($N = 78$); and the coefficient of temporal overlap (Ridout & Linkie, 2009), which was used by 72% of the studies investigating temporal niche partitioning ($N = 38$). We performed a second literature search, using the same electronic databases, in order to identify all articles citing Pianka's overlap index or the coefficient of temporal overlap. The review protocol for these articles was repeated with the same inclusion and exclusion criteria. Following this forward reference search, 31 additional records were included, increasing the number of retained articles to 197. Finally, we screened the reference list of each of the 197 included studies to identify relevant publications (i.e. backward reference searching or 'snowballing'), adding a further 49 studies. A total of 246 articles were included in the final synthesis (see online supporting information Appendix S1 for a full reference list of included studies). As few ecosystems are undisturbed by humans, studies were included in the final synthesis whether they mentioned human disturbance at their study site or not. Using this approach allowed us to identify the proportion of studies in the existing literature that incorporated human disturbance in their evaluation of niche partitioning within carnivore communities.

(2) Data extraction

For every selected study, we extracted the following information: (1) interacting carnivore species; (2) time frame of the study (part or totality of a solar year); (3) presence/absence of seasonality in the analysis; (4) niche dimension investigated (spatial, temporal and/or trophic); (5) experimental design (see below); and (6) presence/absence of human disturbance at the study site. The presence or absence of human disturbance was based on any information provided by the authors in the publications, commonly in the study area or discussion sections [e.g. "The study area comprises [...] several public and private protected areas [...] and unprotected areas, with different histories of logging and poaching" (Cruz *et al.*, 2018, p. 3)].

The experimental design of each study was classified according to the definition provided in Hone (2007). Thus, studies were classified either as classical experiments (with simultaneous control, replication, and randomisation of the treatment, and statistical analyses), quasi-experiments (with simultaneous control but without replication, randomisation or analyses), pseudo-experiments (with replication, randomisation or analyses of the treatment, but lacking simultaneous control), or simple observations (none of the above).

Human disturbance was classified into two groups: top-down (i.e. relating to the direct presence of humans or human-related entities) or bottom-up (i.e. referring to modifications of the landscape for human use) disturbance. Subsequently, human disturbance was divided into seven types: top-down disturbance had four categories lethal management of herbivores, lethal management of carnivores, non-lethal recreational activities, and presence of exotic carnivore species whereas bottom-up disturbance had three built environment, landscape modified for arable purposes, and landscape modified for pastoral purposes.

When a study mentioned and analysed human disturbance, the effects on niche overlap were extracted from information provided in the results and discussion sections of the publication, and classified according to: (1) type of human disturbance; (2) direction of the effect on niche overlap (increase, decrease, or no effect found); and (3) strength of inference (statistical analysis, descriptive statistics or speculative). We defined speculative inference as claims that are not directly measured, usually relying on the conclusions of other empirical studies to find support. To improve the accuracy of the review, any effect that was solely based on speculation was not included.

The relative strength of the effects of different types of human disturbance on values of overlap was assessed using two approaches. First, whenever possible, we extracted effect sizes from the studies demonstrating an impact of human disturbance on niche partitioning by subtracting the overlap value with low disturbance from the overlap value with high disturbance ($\text{Overlap}_{\text{HD}}$ $\text{Overlap}_{\text{LD}}$). Comparing effect sizes among studies (i.e. a meta-analysis) is a powerful statistical procedure (Cohn & Becker, 2003), offering support to the body of evidence found in the quantitative assessment of the literature. However, if the treatment effect is not consistent from one study to another, performing a meta-analysis may produce unreliable results (Lau, Ioannidis & Schmid, 1997). For this reason, we also estimated the relative strength of each effect by comparing how many times they were found in the literature.

III. RESULTS AND DISCUSSION

(1) Description of the literature

We found 246 studies published between 1986 and 2018 that investigated the spatial, temporal or trophic niche partitioning between pairs of carnivore species (Appendix S1). The most frequently studied niche dimension was the trophic (48.8%), followed by the spatial (30.4%) and temporal dimensions (20.8%). Most studies followed an observational design (78%, N = 192), followed by pseudo-experiments (15.9%, N = 39), and quasi-experiments (6.1%, N = 15). None of the studies followed a classical experimental design. Over half of all studies (61.4%, N = 151) mentioned human disturbance at their study site, but only a third (30.1%, N = 74) incorporated human disturbance in the study design and interpretation of findings. A small proportion of studies (27.6%, N = 68) included seasonality in their analysis (e.g. calendar seasons, breeding seasons), and most (75%, N = 51) reported seasonal variations in the intensity of niche partitioning.

In total, 94 effects of human disturbance on carnivore niche partitioning were extracted from 72 studies. Half of these effects (51.1%, N = 48) were founded on speculations (i.e. the effects were not directly measured), so were excluded from the synthesis. The remaining 46 effects were extracted from 34 studies (Appendix S2) and were supported by statistical analysis (71.7%, N = 33) or descriptive statistics (28.3%, N = 13). Most of the effects of human disturbance were extracted from pseudo-experimental (60.9%, N = 28) and quasi-experimental (34.8%, N = 16) studies. Only two effects were extracted from an observational design found in a single study.

A relatively small proportion of studies reporting an effect of human disturbance used an experimental design that enabled the extraction of an effect size, but we were able to extract 43 effect sizes from 13 studies (Fig. 2). The remaining 21 studies employed methodologies that did not compare coefficients of overlap between low *versus* high disturbance areas directly, hence preventing the extraction of comparable effect sizes. For instance, more than half of the studies investigating spatial niche partitioning (N = 11 out of 21) used multi-species occupancy models, and derived the

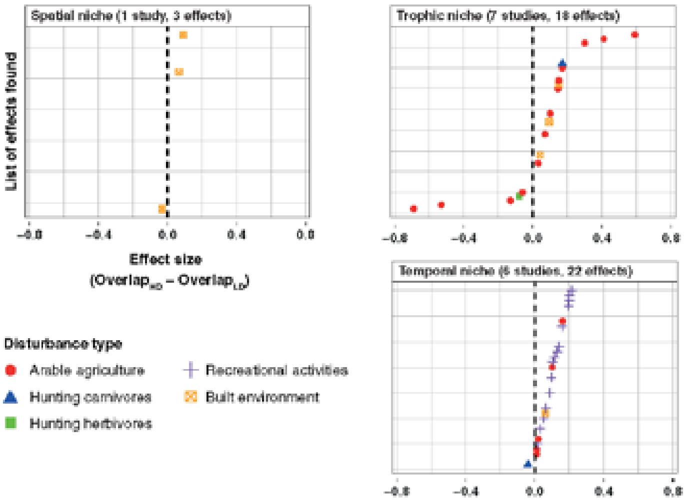

Fig 2. Forest plot of the extracted effect sizes of human disturbance on niche overlap between carnivore species, categorised by niche dimension and type of human disturbance. HD, high disturbance; LD, low disturbance.

influence of human variables based on which model was performing best. Additionally, the investigation of the different types of human disturbance on niche overlap showed a high degree of specialisation across studies, with too few replicates of each type of human disturbance among studies to conduct a reliable meta-analysis in all three niche dimensions. For instance, the effect sizes extracted show an overall increase in temporal overlap between species resulting from human disturbance, seemingly dominated by the impact of recreational activities (Fig. 2). However, 14 of the 15 effects of recreational activities on temporal overlap were extracted from a single study (Wang, Allen & Wilmers, 2015). Similarly, 10 out of the 13 effects of agroecosystems on trophic overlaps were extracted from a single study (Palacios, Walker & Novaro, 2012). For these reasons, we decided not to include effect sizes in the rest of this review, instead estimating the relative importance of the different effects of human disturbance by comparing how many times they were found in the literature review.

(2) Human influence on niche partitioning, intraguild competition, and carnivore community

The aim of our study was to establish a comprehensive framework of human disturbance impacts on niche partitioning within carnivore communities and their subsequent effect on intraguild competition and community structure. Overall, the observed impact of human disturbance on niche partitioning between carnivores was not unidirectional (Fig. 3, see Appendix S3 for a specific example). In fact, we found a similar number of effects reporting an increase or a decrease in niche overlap associated with human disturbance (21 and 17 effects, respectively) and, in eight studies, there was no effect of human disturbance on niche overlap (Table 1). We found more changes in niche overlap between carnivores resulting from bottom-up than top-down human disturbance (24 and 14 effects, respectively). Across niche dimensions, there were more references to the spatial dimension (bottom-up effects: 16, top-down effects: 5), followed by trophic (bottom-up effects: 6, top-down effects: 5) and temporal dimensions (bottom-up effects: 2, top-down effects: 4).

We found evidence that human disturbance can affect all three niche dimensions investigated in both directions: increasing and decreasing effects on niche overlap. Changes in niche partitioning following human disturbance are therefore not uniform and are conditional on both the type of human disturbance, and how the surrounding landscape and limiting resources are affected. Nevertheless, we found three predominant influences of humans on carnivore niche partitioning: (*a*) human disturbance impedes niche partitioning, increasing intraguild competition and reducing the richness and diversity of the community; (*b*) human disturbance unbalances niche partitioning and intraguild competition, affecting community stability; and (*c*) human disturbance facilitates niche partitioning, decreasing intraguild competition and enriching the community (Fig. 4). Despite having seemingly opposite direction, these three influences are not mutually exclusive. Many landscapes are most likely affected

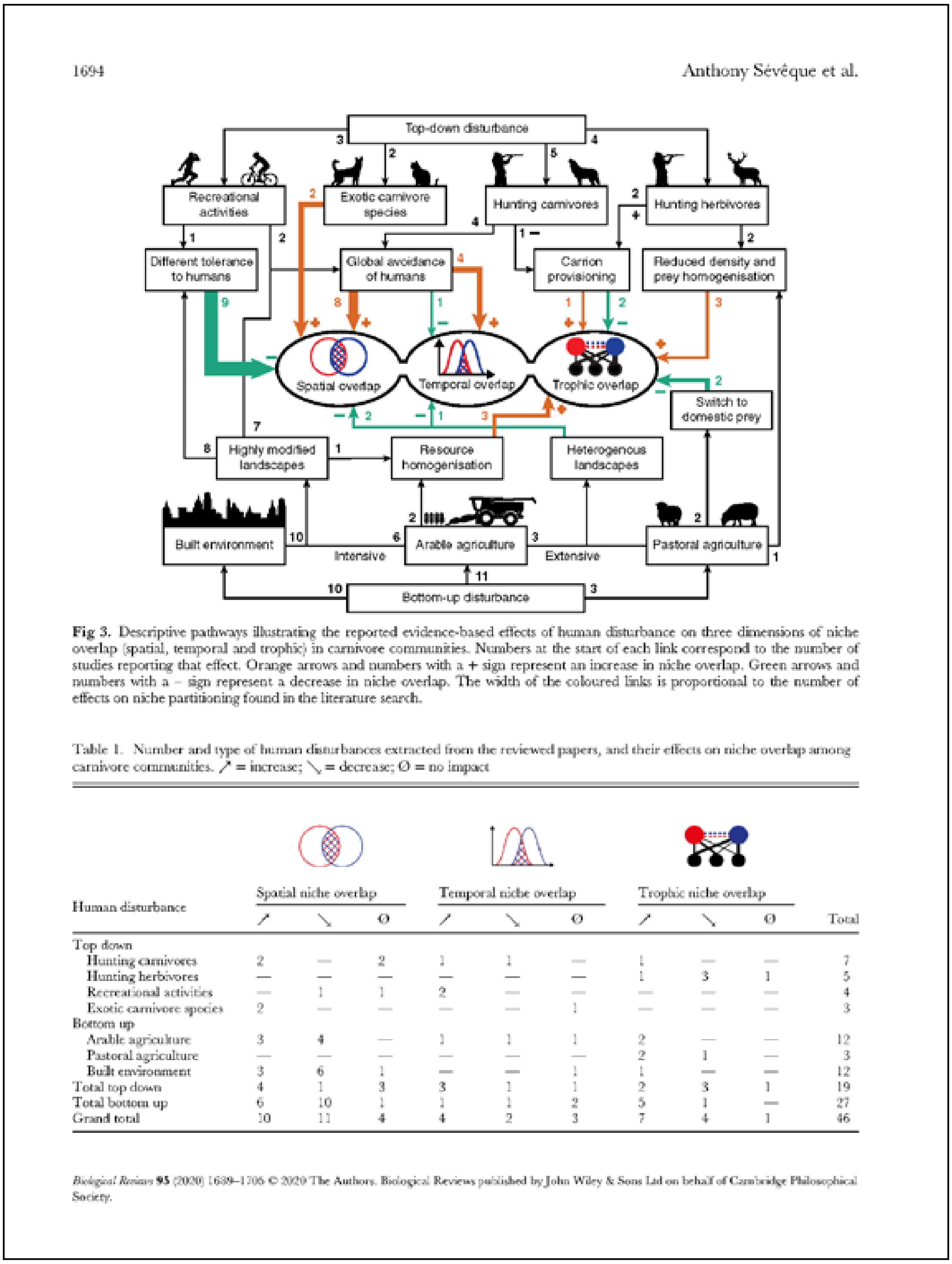

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Fig 3. Descriptive pathways illustrating the reported evidence-based effects of human disturbance on three dimensions of niche overlap (spatial, temporal and trophic) in carnivore communities. Numbers at the start of each link correspond to the number of studies reporting that effect. Orange arrows and numbers with a + sign represent an increase in niche overlap. Green arrows and numbers with a – sign represent a decrease in niche overlap. The width of the coloured links is proportional to the number of effects on niche partitioning found in the literature search.

Table 1. Number and type of human disturbances extracted from the reviewed papers, and their effects on niche overlap among carnivore communities. ↗ = increase; ↘ = decrease; Ø = no impact

Human disturbance	Spatial niche overlap			Temporal niche overlap			Trophic niche overlap			Total
	↗	↘	Ø	↗	↘	Ø	↗	↘	Ø	
Top down										
Hunting carnivores	2	—	2	1	1	—	1	—	—	7
Hunting herbivores	—	—	—	—	—	—	1	3	1	5
Recreational activities	—	1	1	2	—	—	—	—	—	4
Exotic carnivore species	2	—	—	—	—	1	—	—	—	3
Bottom up										
Arable agriculture	3	4	—	1	1	1	2	—	—	12
Pastoral agriculture	—	—	—	—	—	—	2	1	—	3
Built environment	3	6	1	—	—	1	1	—	—	12
Total top down	4	1	3	3	1	1	2	3	1	19
Total bottom up	6	10	1	1	1	2	5	1	—	27
Grand total	10	11	4	4	2	3	7	4	1	46

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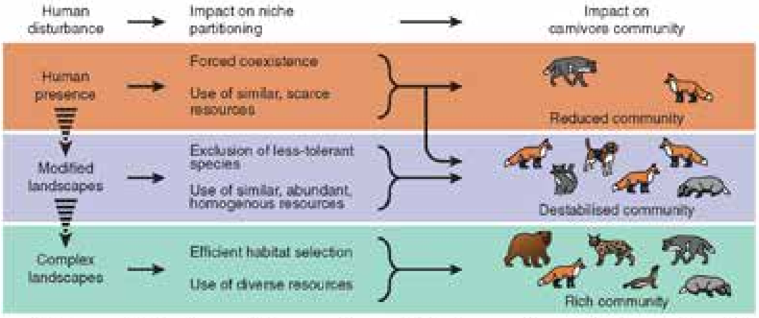

Fig 4. Theoretical framework of the three main impacts of human disturbance on niche partitioning and intraguild competition among carnivore species, and subsequent reorganisation of the carnivore community. Top, orange section: the omnipresence of the human superpredator forces sympatry between species seeking refuge in safer areas. Additionally, the overall reduction in diversity and abundance of wild food resources negatively affects trophic partitioning. As a result, the strength of interspecific competition is increased, which can lead to a carnivore community with poor species abundance and diversity. This can also unbalance the community, by enhancing the competitive advantage of species tolerant to human presence. Middle, blue section: human presence can trigger important modifications at the landscape level, interfering with habitat partitioning, and strongly increasing the abundance of trophic resources linked to human activities. As a result, the strength of interspecific competition is unbalanced to the advantage of species tolerant to humans and capable of using these anthropogenic resources, possibly resulting in a destabilised carnivore community. Bottom, green section: some landscape modification can, by contrast, facilitate niche partitioning in all niche dimensions, if they prioritise complex, heterogeneous landscapes (e.g. extensive agriculture). This reduces the strength of interspecific competition, and could promote a rich and diverse community.

by more than one of these influences, and the repercussions onto the carnivore community vary depending on the relative intensity of each disturbance.

(a) *Human disturbance impedes niche partitioning*

The majority of carnivore species probably perceive humans as frightening, whether they present a direct threat or not (Frid & Dill, 2002; Clinchy *et al.*, 2016), so they adapt their behaviour accordingly, at different spatiotemporal levels, to limit encounters with humans (Carter *et al.*, 2012; Ahmadi, López-Bao & Kaboli, 2014; Sazatornil *et al.*, 2016). Avoidance of humans can be achieved spatially, with carnivores seeking refuge in safer habitats to reduce risks of anthropogenic mortality (Loveridge *et al.*, 2017; Parsons *et al.*, 2019). Theoretically, this could increase local densities of competing species and constrain spatial niche partitioning. Indeed, we found that increased spatial overlap following avoidance of humans was the second most-reported effect, with eight studies reporting an increase in spatial overlap between carnivores in refuge habitats due to the direct avoidance of humans (Farris *et al.*, 2017; Sogbohossou *et al.*, 2018) or human-related features (De Angelo, Paviolo & Di Bitetti, 2011; Pereira *et al.*, 2012; Lewis *et al.*, 2015; Nagy-Reis *et al.*, 2017; Cruz *et al.*, 2018; Smith *et al.*, 2018). Avoidance of humans can also be achieved temporally. Similar to other mammals, carnivores have exhibited a global shift to a more nocturnal activity pattern around humans (Gaynor *et al.*, 2018). We found three studies documenting carnivores that, as a consequence of human activity, were squeezed into a narrower temporal niche and faced higher levels of temporal overlap with intraguild competitors (Carter *et al.*, 2015; Lewis *et al.*, 2015; Wang *et al.*, 2015; but see Sogbohossou *et al.*, 2018).

Other causes of increases in niche overlap may be linked to the reduction in food availability following lethal wildlife management. Coexistence among large carnivores is partially enabled by their capacity to partition their prey by size (Karanth & Sunquist, 1995). However, global prey depletion, and the loss of prey diversity, can render prey partitioning harder to achieve. For instance, three studies documented an increase in trophic overlap following depletion and homogenisation of the prey base (Palacios *et al.*, 2012; Creel *et al.*, 2018; Drouilly, Nattrass & O'Riain, 2018). Alternatively, two studies highlighted carnivore species diversifying their diets by including livestock (Amroun, Giraudoux & Delattre, 2006; Foster *et al.*, 2010). Although this may alleviate interspecific competition for food in the short term, it can promote human–carnivore conflicts and be detrimental to the long-term conservation of these species (e.g. Harihar, Pandav & Goyal, 2011).

In addition, predator control, when applied uniformly across the landscape, can reduce local carnivore densities (Robinson *et al.*, 2008). However, prey carcasses attributed to kills by large carnivores can form a large part of scavenging carnivores' diets, and can potentially reduce interspecific competition among mesocarnivores (Van Dijk *et al.*, 2008; Yarnell *et al.*, 2013). Hence, reductions in large carnivore abundance can limit carrion provision for scavengers, weakening trophic niche partitioning between mesocarnivores. This effect, however, was only reported once in our literature search by a study comparing mesopredator diet overlap between two study areas with a large difference in grey wolf, *Canis lupus*, density due to a wolf-control program (Sivy *et al.*, 2017). Additionally, this effect can be partially mitigated by provisioning carcasses resulting from hunting activities, as we found in two studies (Barrull *et al.*, 2014; Tsunoda *et al.*, 2017), or livestock practices (Cortés-Avizanda, Carrete & Donázar, 2010). However, artificial disposal of carrion may inadvertently affect non-target species (e.g. Fležar *et al.*, 2019), and does not replace the ecosystem services provided by large carnivores as carrion providers (e.g. facilitation of mesocarnivore suppression; Prugh & Sivy, 2020).

Disruption of spatiotemporal niche partitioning is likely to be a common outcome of human disturbance, and could increase the frequency at which negative interactions take place among carnivores, thus increasing the potential for interference competition. Such increase in competition can have a negative impact on subordinate carnivores, further reducing the probability of survival of threatened carnivore species (Elbroch & Kusler, 2018). Similarly, the narrowing of the available trophic niche, and associated weakening of trophic partitioning, can increase exploitation competition among carnivore species (Karanth & Sunquist, 1995; Creel *et al.*, 2018). Under these circumstances, subordinate species can reduce competition with dominant species by switching to more abundant, usually smaller, prey (Randa *et al.*, 2009; Foster *et al.*, 2010; Drouilly *et al.*, 2018). This mechanism is, however, unlikely to be successful if the secondary prey base is also depleted, in which case the effects of dietary overlap could also be particularly detrimental to less-competitive species (Hayward & Kerley, 2008). Ultimately, increasing intraguild competition artificially among carnivores could decrease the density of subordinate species, or even exclude these species from specific habitats (Linnell & Strand, 2000; Berger & Gese, 2007).

(*b*) *Human disturbance unbalances niche partitioning*

Responses of carnivores to human modification of landscapes fluctuate among species according to their degree of ecological flexibility (Lyra-Jorge, Ciocheti & Pivello, 2008; Caruso *et al.*, 2016). Certain species can use modified landscapes as a shelter from competitors, which may not be as tolerant of human disturbance (Gosselink *et al.*, 2003). Spatial overlap between carnivores is therefore reduced, advantaging more-tolerant species that can now occupy a niche with reduced competition. The reduction of spatial overlap arising out of a different tolerance to humans was found nine times in our review, in landscapes with varied intensity of human use, ranging from heavily modified urban areas (Lesmeister *et al.*, 2015; Wang *et al.*, 2015) and agricultural systems (De Angelo *et al.*, 2011) to smaller villages (Prigioni *et al.*, 2008; Farris *et al.*, 2016). For instance, black bears, *Ursus americanus*, in North America are detected in close proximity to roads more frequently than grizzly bears, *Ursus arctos*, their dominant competitors (Apps, McLellan & Woods, 2006; Ladle *et al.*, 2018). Similarly, red foxes, *Vulpes vulpes*, in North America can use areas with higher urban development as spatial refuges to limit co-occurrence with coyotes (Moll *et al.*, 2018; Mueller, Drake & Allen, 2018). Although the reduction of spatial overlap following an asymmetrical avoidance of humans was the most reported effect in our review, it should be interpreted with caution as it indicates the spatial exclusion of species less tolerant to humans rather than an equal reduction in overall competition among species. Consequently, human disturbance could lead to the competitive exclusion or local extinction of species unable to adapt (Grimm *et al.*, 2008) and a decrease in species diversity. Indeed, switches in community composition and loss of species diversity owing to human activity have been observed in other taxa [e.g. birds in urban environments (Blair, 1996); small mammals in farming landscapes (Michel, Burel & Butet, 2006)].

Species tolerant to humans can also use modified habitats to exploit highly abundant anthropogenic food resources (McKinney, 2006; Bateman & Fleming, 2012) or prey populations benefiting from habitat transformation (López-Bao *et al.*, 2019). According to competition theory (Schoener, 1982), the diets of competing carnivores should converge when resources are abundant (e.g. Fedriani, Palomares & Delibes, 1999). Three studies observed this pattern, wherein carnivores competing in human-dominated landscapes had high trophic overlaps owing to the homogenisation of resources and abundance of anthropogenic food resources (Barrull *et al.*, 2014; Kauhala & Ihalainen, 2014; Smith *et al.*, 2018).

The ecological flexibility of generalist species allows them to increase their niche breadth by exploiting both natural and anthropogenic resources (Verdade *et al.*, 2011), thereby increasing their fitness and competitive ability (Rosalino & Santos-Reis, 2011; Concepción *et al.*, 2015). This can present a double threat to specialist species, who not only are negatively impacted by anthropogenic land alterations (Fisher, Blomberg & Owens, 2003), but must now face new dominant competitors encroaching on their niche. As human land use keeps increasing (Seto *et al.*, 2011), competitive interactions among carnivores could be destabilised, and the carnivore community reshaped into an homogenous community dominated by generalist and tolerant species (Reed & Merenlender, 2008; Ordeñana *et al.*, 2010). The paramount example of generalist predators whose competitive strength is enhanced by the use of anthropogenic resources is feral and free-ranging domestic carnivore species (e.g. dogs, *Canis familiaris*; Vanak & Gompper, 2009*b*). These species are commonly found at high densities in human-dominated and nearby natural habitats, and can have high niche overlaps with native carnivore species [e.g. trophic (Glen & Dickman, 2008); spatial (Vanak & Gompper, 2010); temporal (Farris *et al.*, 2015)]. In addition, these species can have deleterious effects on wildlife by acting as a reservoir for diseases (e.g. cross-species transmission of the canine distemper virus; Deem *et al.*, 2000). However, the effect of their presence on coexistence of native species has largely been understudied, and we only found two studies documenting an increase in spatial overlap between native species following displacement by dogs (Farris *et al.*, 2016, 2017).

(*c*) *Human disturbance facilitates niche partitioning*

When kept under extensive management, agricultural landscapes can be shaped into highly heterogeneous ecosystems (Duelli, 1997), facilitating fine-scale spatial segregation among species (Pereira *et al.*, 2012; Cruz, Sarmento & White, 2015), a key mechanism allowing sympatry (Rosenzweig, 1981). Additionally, carnivores in these communities can segregate the food resources they consume (Carvalho & Gomes, 2004), and display a wide range of activity patterns by matching those of their main prey, further promoting coexistence with competitors through temporal partitioning of activity (Monterroso, Alves & Ferreras, 2014). However, only three studies reported the facilitation of spatiotemporal niche partitioning by anthropogenic heterogeneous systems, and all were undertaken in Mediterranean landscapes (Pereira *et al.*, 2012; Monterroso *et al.*, 2014; Cruz *et al.*, 2015). Habitat heterogeneity and complexity at various spatial scales can benefit the entire carnivore guild (Williams, Marsh & Winter, 2002) by reducing intraguild competition, thus nurturing rich carnivore communities. Promoting diversity in the carnivore guild is beneficial as it increases resilience to environmental stress (Sobrino *et al.*, 2009) and overall stability of the community (e.g. Worm *et al.*, 2006). However, if current global agricultural intensification keeps expanding, the reduction in landscape heterogeneity towards more homogenous landscapes lacking different cover and refuges (Warner, 1994) could impact the beneficial effects of extensive agroecosystems on the carnivore community (Stoate *et al.*, 2001; Cruz *et al.*, 2018).

IV. IMPLICATIONS FOR CONSERVATION AND FUTURE STUDIES

Here, we provide a comprehensive framework that outlines the variety of impacts that humans, and their activities, have on competition among carnivores. This review emphasises the omnipresence of human influences on niche partitioning within carnivore communities, albeit having effects with diverse directions and magnitude. The findings we highlight could be of great benefit to the conservation of carnivores in most landscapes, and especially those impacted by anthropogenic activities. For instance, 12 species involved in this review are currently listed as globally endangered under the IUCN *Red List* of Threatened Species (Appendix S1). Eight of these species were sympatric with at least one dominant competitor species (e.g. the subordinate, endangered black-footed ferret, *Mustela nigripes*, is sympatric with the American badger, *Taxidea taxus*, a dominant competitor and intraguild predator). The competitive impact of dominant carnivores on subordinate species may be driven by the outcome of the impact of human disturbance (e.g. by aggregating these competing species in particular habitats), which would add an additional stress to the conservation of threatened species. Conversely, promoting the diversity of habitats and opportunities for segregation may help reduce the intensity of interspecific competition, and be beneficial to the conservation of threatened species.

Our findings have important implications not only for the conservation of carnivores, but for the overall preservation of ecosystems. Indeed, carnivore species have been shown to perform important ecological roles that can affect entire ecosystems (Roemer, Gompper & Valkenburgh, 2009; Estes *et al.*, 2011; Ripple *et al.*, 2014). For instance, intensive modifications of the landscape, following human activities, are typically associated with a reduction in species diversity in the carnivore community, to the benefit of highly competitive generalist species (Crooks, 2002; McKinney, 2008). This decrease in species diversity may result in the loss of ecological functions when the fulfilment of this function cannot be replaced by an alternative species (i.e. functional redundancy; Flynn *et al.*, 2009; Huijbers *et al.*, 2015), and can have detrimental effects on the resilience of ecosystems (Mori, Furukawa & Sasaki, 2013). Therefore, maintaining a diversity of habitats and trophic resources in altered landscapes may help the competitive abilities of specialist species, thus restoring species diversity and ecological functions, and be beneficial to the functioning and resilience of the ecosystem.

Our review also highlights understudied areas of research that will guide and encourage more experimental research to be undertaken on the anthropogenic influence of species coexistence in an ever-changing world. We strongly advocate an evidence-based approach that can inform policy makers and land managers about the potential impacts of human activities on carnivore communities, and how to regulate them effectively (Pullin & Knight, 2003).

Most of the selected studies mentioned potential effects of human disturbance at their study site, but only a fraction (72 out of 151) included these effects in the interpretation of the results. Additionally, only 13 studies used a design that compared values of overlap between low- and high-disturbance treatments, allowing the strength of the impact of human disturbance on niche partitioning to be measured (Fig. 2). The most plausible reason for this is the high proportion of observational studies, where the effects of human disturbance were not tested, and thus relied on the conclusions of other studies. There is a lack of experimental studies on niche partitioning within carnivore guilds, due to the ethical and logistical constraints of manipulative experiments, and the rarity of true controls in nature. The relative importance of experimental and observational studies in large carnivore science is a topic of debate (Allen *et al.*, 2017; Bruskotter *et al.*, 2017). As the human footprint on natural ecosystems keeps growing, we believe that performing more manipulative studies will be necessary to measure the effects of human disturbance on species interactions accurately. In addition, some studies pooled data from multiple locations, subject to different human pressures, to calculate niche overlap (e.g. one temporal overlap value between sympatric felids in a study area combining tropical forest and oil palm plantation; Hearn *et al.*, 2018). Although combining data from different study areas can compensate for low sample sizes (e.g. elusive species with large spatial requirements), merging the data in such a way can mask the effects of human disturbance and produce unreliable conclusions. Nevertheless, incorporating human disturbance in the study of species interactions and competition is a productive area of research, and will improve knowledge on carnivores and community composition in general.

Likewise, a small proportion of all studies (68 out of 246) took seasonal variability into account, and most of these (51 out of 68) found seasonal variations occurring naturally in the intensity of niche partitioning (e.g. Carvalho & Gomes, 2004; Vanak *et al.*, 2013; Monterroso *et al.*, 2014). Similarly, seasonal fluctuations in the intensity of human disturbance exist (e.g. high peaks in nature-based tourism in summer) and could potentially affect niche partitioning. For instance, Gosselink *et al.* (2003) observed considerable differences in the intensity of habitat partitioning between coyotes and red foxes between summer and winter, attributed to the drastic loss of cover in an intensive row-crop agricultural system in winter. Our understanding of human influences on niche partitioning cannot be complete without incorporating natural or human-induced seasonal variations in niche partitioning. Thus, we advocate future studies that enable the inclusion of seasonal variations in analyses.

Another limitation is the prevalence of studies investigating only one single niche dimension (180 studies out of 246). Niche partitioning is a multidimensional dynamic process, in which changes in one niche dimension may be balanced by opposing changes in other dimensions (Schoener, 1974). For instance, by increasing their nocturnal activities, some predators may increase their consumption of nocturnal prey species (Smith *et al.*, 2018), which could indirectly increase trophic overlap with other nocturnal predators. Unidimensional studies of the influence of humans on niche partitioning are useful, but favouring investigations of multiple niche dimensions simultaneously will greatly benefit our understanding of the processes at play.

Finally, niche overlap was used as a proxy to estimate the intensity of interspecific competition, but it is not a direct measure of competition (Schoener, 1982). As none of the studies included herein measured the intensity of competition directly, we relied on the conclusions of supplementary studies to establish how changes in niche partitioning following human disturbance could impact intraguild competition and cause community structure change. Such support was found in literature that did not measure niche partitioning, focusing purely on interspecific competition or human carnivore coexistence (e.g. Sale, 1974; Bateman & Fleming, 2012). Thus, we believe that future research juxtaposing niche overlap with intraguild competition intensity will improve our understanding of carnivore coexistence, and how it can be influenced by human disturbance.

V. CONCLUSIONS

(1) Our findings reveal that human disturbance influences all three dimensions of niche partitioning in carnivore communities, with a nearly identical number of effects reported to increase and decrease niche overlap. However, variations in niche partitioning following human disturbance are not always reflected linearly on the intensity of intraguild competition. Indeed, they can have contrasting effects depending on how the surrounding landscape and the availability of resources are affected by human disturbance.

(2) Although the trajectories of its effects can be diverse, there is no doubt that human disturbance impacts intraguild competition and community composition in carnivore guilds. By systematically including the human dimension in the analysis of interspecific competition, we will gain a better understanding of the way carnivore communities will be reshaped if human disturbance keeps increasing. Applying the systematic approach proposed herein to other animal taxa and other types of species interactions would be beneficial to research of the influence of humans on wildlife.

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Publications included in the final synthesis are indicated with an asterisk.

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VIII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Description of the studies included in the final synthesis.

Appendix S2. Description of all studies reporting an evidence-based effect of human disturbance on niche partitioning.

Appendix S3. A simplified example illustrating how to extract information from Figure 3.

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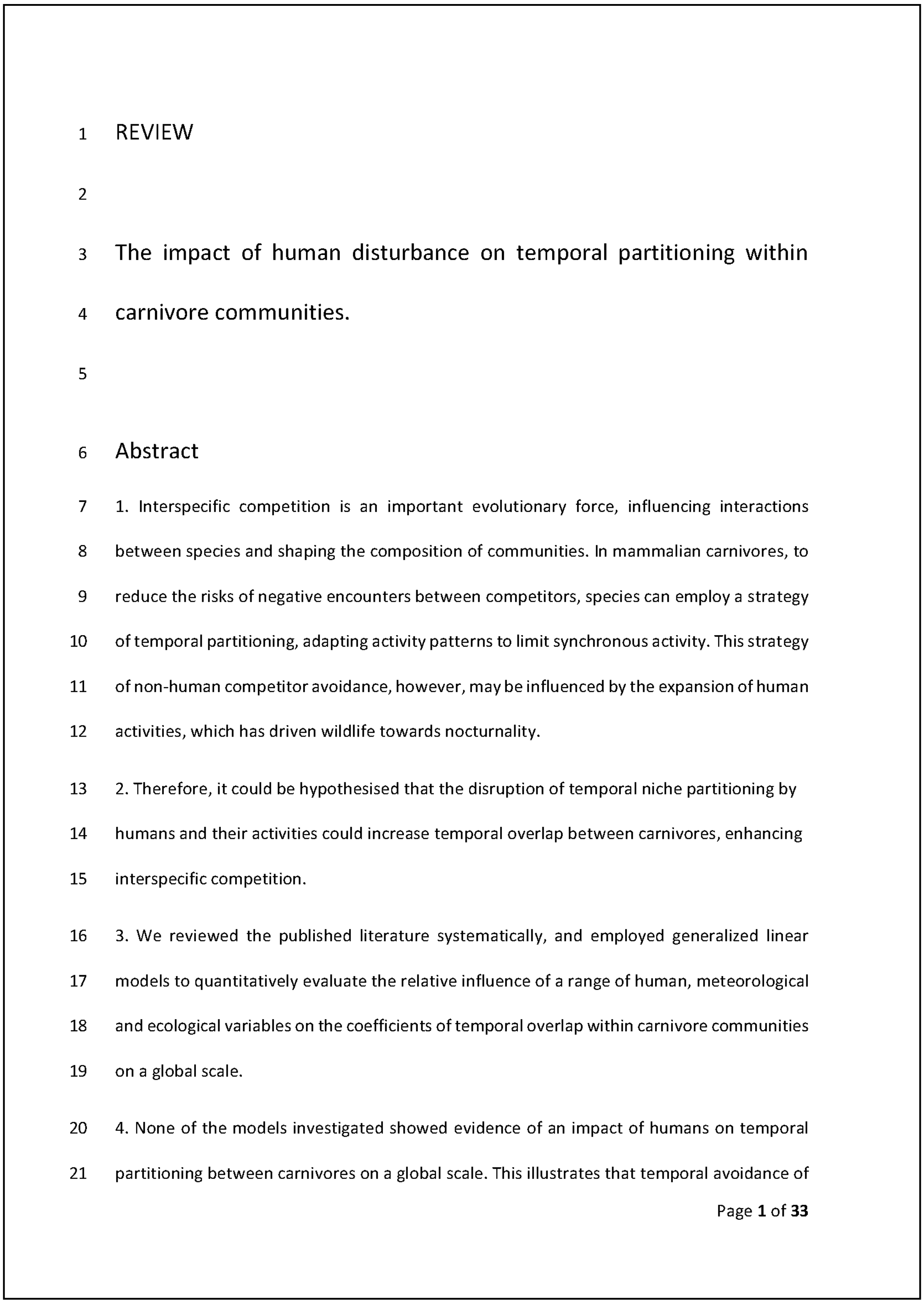
Appendix II: Sévêque A, Gentle LK, López-Bao JV, Yarnell RW, Uzal A (2021) The impact of human disturbance on temporal partitioning within carnivore communities. Mammal Review. In press.



REVIEW

The impact of human disturbance on temporal partitioning within carnivore communities.

Abstract

1. Interspecific competition is an important evolutionary force, influencing interactions between species and shaping the composition of communities. In mammalian carnivores, to reduce the risks of negative encounters between competitors, species can employ a strategy of temporal partitioning, adapting activity patterns to limit synchronous activity. This strategy of non-human competitor avoidance, however, may be influenced by the expansion of human activities, which has driven wildlife towards nocturnality.

2. Therefore, it could be hypothesised that the disruption of temporal niche partitioning by humans and their activities could increase temporal overlap between carnivores, enhancing interspecific competition.

3. We reviewed the published literature systematically, and employed generalized linear models to quantitatively evaluate the relative influence of a range of human, meteorological and ecological variables on the coefficients of temporal overlap within carnivore communities on a global scale.

4. None of the models investigated showed evidence of an impact of humans on temporal partitioning between carnivores on a global scale. This illustrates that temporal avoidance of

humans and competitors does not always follow a consistent pattern, and that its strength may be context-dependent and relative to other dimensions of niche partitioning (spatial and trophic).

5. Similarly, the regulation of activity patterns may be under strong site-specificity, and be influenced by a combination of biotic and abiotic characteristics. Temporal avoidance of both humans and competitors may be regulated by short, reactive responses that do not impact activity patterns in the longer term.

6. Although we did not detect a global disruption of temporal partitioning due to human disturbance, carnivore communities may still experience an increase in interspecific competition in other niche dimensions. Further research would benefit from using controlled experimental designs and investigating multiple dimensions of niche partitioning simultaneously. Finally, we recommend complementing the coefficient of temporal overlap with other metrics of fine-scale spatiotemporal interactions.

Key words: Carnivora, coexistence, competition, temporal overlap, temporal partitioning.

Word count: 9,994 words.

Introduction

Interspecific competition is an important component regulating community structures (Schoener 1983, Wisheu 1998), and competing species must partition the resources they utilise to allow coexistence (MacArthur & Levins 1967). Resource partitioning is mostly achieved in three, often interacting, niche dimensions, being the spatial, temporal, and trophic dimensions (Schoener 1974a). Many species can, for instance, adjust their activity patterns to reduce the risk of encountering dominant non-human competitors (Carothers & Jaksić 1984, Kronfeld-Schor & Dayan 2003). In most animal communities, temporal partitioning of activity may not be the primary strategy used to limit interspecific competition (Schoener 1974a). However, carnivores could use it more than any other taxa due to the severe risks of injuries associated with interference competition (Schoener 1974a, Palomares & Caro 1999, Hunter & Caro 2008). Indeed, temporal segregation of activity between carnivores has been observed on multiple occasions (e.g. Hayward & Slotow 2009, Bischof et al. 2014), and could be a strategy frequently used by subordinate carnivores to reduce negative encounters with dominant counterparts, fine-tuned by a reactive response to immediate risks (e.g. Broekhuis et al. 2013).

The human apex predator (Darimont et al. 2015) produces predatory cues that are comparable to that of natural competitors or predators (e.g. human voice; Frid & Dill 2002, Clinchy et al. 2016). Human persecution has driven behavioural adaptations in most species, including both predators and prey, to limit encounters with humans and reduce human-related mortality risks (Frid & Dill 2002, Ordiz et al. 2011), being also modulated by the intensity of persecution (Sazatornil et al. 2016). Such anti-predator behaviour in response to humans can be employed regardless of the underlying threat, and even non-lethal human disturbance can drive an avoidance response (Frid & Dill 2002). In this review, we use the idiom "human disturbance" as a generic term that encompasses the immediate presence of humans (lethal and nonlethal), and any anthropogenic modification of the landscape.

As humans are mostly diurnal, carnivores can switch their activity patterns towards more nocturnal hours to avoid potentially negative interactions (Gaynor et al. 2018). Indeed, local increases in wildlife nocturnality have been observed in direct response to variations in landscape-wide human-derived risks(e.g. during hunting season; Di Bitetti et al. 2008, Stillfried et al. 2015; but see Theuerkauf 2009), reinforced by a lasting response to close human encounters (e.g. Ordiz et al. 2013, Clinchy et al. 2016). The intensity with which animals adapt their circadian activity patterns to human disturbance may not be the same for all species, and depends on the behavioural plasticity and life-history characteristics (Lendrum et al. 2017). However, a recent meta-analysis by Gaynor *et al.* (2018) suggests that this pattern is observed globally and could be a common response from wildlife facing human disturbance. In undisturbed areas, carnivores need to operate a trade-off between obtaining optimal resources and avoiding dominant competitors (Hayward & Slotow 2009). In human-altered habitats, carnivores may need to incorporate a third crucial element to this trade-off by avoiding humans. Therefore, since temporal partitioning is a common strategy used by carnivore species to coexist, and humans can impact on the activity patterns of species, human disturbance could interfere with the strategy of temporal partitioning between competing carnivores.

Disruption of niche partitioning can increase interspecific competition, and carry multiple ecological and community consequences (Sévêque et al. 2020). However, niche partitioning is a multidimensional dynamic process, and an increase in overlap in one niche dimension may be compensated by a decrease in another (Schoener 1974a). Therefore, interspecific competition may not necessarily be a direct result of the niche overlap in a single dimension. Similarly, not all carnivore species may be impacted equally by human disturbance, and the intensity of the avoidance response to humans may vary among species (e.g. Caruso et al. 2016). Due to direct threat, competition with humans for food, and depredation on livestock, apex carnivores typically experience most persecution (Inskip & Zimmermann 2009) and live in a landscape of fear of human-related mortality (Oriol-Cotterill et al. 2015). As a consequence, large carnivores have indeed been observed to shift their activity towards nocturnal hours (Gaynor et al. 2018). However, mesocarnivore species that are more tolerant of human disturbance (e.g. Gosselink et al. 2003) may shift their activity pattern to a lesser degree when facing human disturbance, thus maintaining temporal partitioning with dominant apex predators (Frey et al. 2020). Unequal sensitivity to humans can induce a behavioural mesopredator release, wherein disturbance-induced alterations of activity pattern in large carnivores benefit the fitness of mesocarnivores by increasing the amount of time allocated to other activities (e.g. foraging; Brown et al. 1999). In addition, apex predators are typically found in lower densities in areas under higher human disturbance (Wolf & Ripple 2017), which may then limit the need for medium-sized carnivores to alter their activity pattern in response to the risk of encountering dominant competitors in disturbed landscapes.

Many carnivores now live in environments that are under human pressure, and are subject to a combination of bottom-up (e.g. modification of the landscape; Chapron et al. 2014, Venter et al. 2016) and top-down (e.g. hunting; Darimont et al. 2015, Ripple et al. 2016) anthropogenic forces. The impact of human disturbance on a wide range of biological interactions has been widely studied (e.g. intraspecific competition; Nevin & Gilbert 2005, predator-prey interactions; Muhly et al. 2011, animal-plant interactions; Neuschulz et al. 2016). Moreover, we know that human disturbance has already reduced the niche available to animals in other dimensions (e.g. trophic, Creel et al. 2018, spatial, Tucker et al. 2018), which can result in large-scale increases in niche overlap (Manlick & Pauli 2020). However, our knowledge of the influence of humans on coexistence and temporal niche partitioning between carnivores is still limited. Thus, there is a need to address this question, since not only can temporal displacements and reductions of activity carry costs that reduce species fitness (e.g. Beale & Monaghan 2004, Ciuti et al. 2012), it can also alter the way species interact, which can have cascading implications (Suraci et al. 2019).

To address this knowledge gap, we conducted a global systematic and quantitative review of the temporal niche partitioning between terrestrial carnivores. Based on a-priori knowledge of the factors influencing wildlife activity patterns, we investigated diverse human, meteorological and ecological factors as potential determinants of temporal partitioning within carnivore communities. Drawing on a global dataset covering a variety of ecosystems, carnivore communities and types of human disturbance, this study had two objectives: 1) investigate whether human disturbance affected temporal niche partitioning uniformly and on a global scale; 2) test the effect of additional meteorological and ecological factors, that hypothesised to influence niche partitioning, either on their own or through interactions with human disturbance.

Methods

Literature search

To investigate temporal partitioning between carnivores, we performed a literature search in December 2019, and examined all articles and grey literature citing the coefficient of temporal overlap proposed by Ridout and Linkie (2009). This method knows a growing popularity in the science of animal behaviour, illustrated by a rapidly increasing rate of citation (Figure 1). Hence, it has been widely accepted as one of the preferred methods to investigate temporal partitioning between animals, using camera trap data (i.e. time-stamped images of species in a known location). The coefficient of overlap uses a kernel density estimation method that ranges from 0 (no overlap) to 1 (complete overlap). Additionally, 95% confidence intervals can be calculated via bootstrap sampling (Ridout & Linkie 2009).

We extracted all articles citing Ridout and Linkie's (2009) method from Scopus (cited 212 times; www.scopus.com), Web of Science (cited 195 times; www.webofknowledge.com) and Google Scholar (cited 338 times; https://scholar.google.com). After removing duplicates, we assessed 356 articles for eligibility. We restricted records to studies that calculated the coefficient of temporal overlap between at least one pair of sympatric carnivore species. In addition, we removed studies in which one of the carnivores was an invasive species, because the recent sympatry of invasive species may not have allowed sufficient time for native species to develop a consistent strategy of temporal avoidance (e.g. Fancourt et al. 2019). Finally, we discarded species combinations which were present only once in the dataset. By doing so, the analysis focused on variations in temporal overlap within species combinations facing different anthropogenic and environmental conditions. Therefore, each species combination included in the analysis had at least two coefficients of temporal overlap, extracted from at least two different study areas. In the end, we included 42 studies in the quantitative analysis and final synthesis.

Data extraction

We extracted the coefficients of temporal overlap between pairs of carnivore species from the results sections of the 42 studies. For every value of temporal overlap, we recorded the following information on the interacting carnivore species: species name; taxonomic family; average adult body mass; and baseline activity pattern (Table 1).

To investigate the effect of anthropogenic and environmental conditions on coefficients of temporal overlap, we extracted the approximate geographic centre and size of every study area from the methodology section, when clearly stated, or through visual estimation of the maps provided in the articles. Based on a-priori knowledge of factors affecting circadian activity pattern of carnivores, we then averaged the following characteristics of the landscape within each study area: human density; proportion of built-up environment; proportion of pasture; Simpson's landscape diversity index; annual precipitation; annual mean temperature and carnivore community richness (see table 1 for detailed methodology, source, spatial resolution and description of each variable). To ensure maximum consistency in the landscape metrics between study areas, we solely used global databases. We therefore operated a trade-off between spatial resolution (finer when using the appropriate local databases for each study area) and homogeneity in the methods of calculation for each variable. This study did not aim to measure fine-scale temporal responses of animals to each of the variables of interest, but rather to detect a global response to human disturbance. Therefore, we did not incorporate the variability in landscape characteristics within each study area in the analysis, but instead focused on variability between sites. When studies indiscriminately grouped their camera-trap data from more than one location, we averaged the value of each study area to create a unique value that best represents the overall conditions of the surrounding landscape. Spatial analysis were performed using a Geographical Information System (ArcGIS v10.7.1; ESRI, Redlands, California).

Data analysis

Paired studies

First, we qualitatively evaluated the findings of any studies that investigated the causal effect of human disturbance on temporal partitioning between carnivores (i.e. increase, decrease, or no effect), using an experimental or quasi-experimental design (i.e. studies with a simultaneous experimental control, Hone 2007). Typically, such studies calculated and compared the coefficients of temporal overlap of similar species combinations between areas classified as under low or high human disturbance. We were interested in the type of human disturbance that was investigated, and whether the authors were able to demonstrate a clear change in the coefficients of temporal overlap between the areas under low or human disturbance (i.e. when the 95% confidence intervals of the two coefficients did not overlap).

Global models

Using knowledge from previous studies investigating factors affecting circadian activity pattern of carnivores, we explored ten models covering human, meteorological and ecological factors, that could affect the coefficient of temporal overlap between carnivore species (Table 2; see justifications below). Thus, we considered the coefficient of temporal overlap as the dependent variable, and models were fitted using Generalized Linear Mixed Models (Zuur et al. 2009), with a logit link function and beta distribution, appropriate for continuous variables restricted to an interval between 0 and 1 (Ferrari & Cribari-Neto 2004). We added species combination as a random effect in each model, with levels representing different locations where the species combinations were studied, and conducted model selection using AIC

(Akaike 1981). Having a minimum of two replicates per species combination, and adding it as a random factor, allowed us to artificially create a paired comparison design (Montgomery 2017). By doing so, we could focus on the variance in coefficients of overlap explained by the different explanatory variables within species combinations, rather than testing the variance between species combinations. The coefficient of temporal overlap is a derived measure based on modelled activity patterns, and is associated with uncertainty (commonly provided as 95% confidence intervals). However, we chose not to account for the variance associated with the dependent variable in the analysis, because numerous studies included in this review did not provide the uncertainty associated with their coefficients of temporal overlap, nor the number of detections used to model activity patterns (which is inversely proportional to the width of the confidence intervals). Discarding these studies would have significantly reduced the number of studies included in our global analysis, and we elected to favour a larger sample size over more sophisticated models. Nonetheless, coefficients of temporal overlap computed from the activity pattern of species detected less than 10 times were not included in this analysis, since their accuracy and precision cannot be guaranteed (Lashley et al. 2018). When no single model is clearly superior to the others in the set (e.g. typically $AIC_w \geq 0.90$), extracting information from single models can lead to weak inferences, and multimodel inference should be favoured (Burnham & Anderson 2002). As this was our case (see Results), we applied a model-averaging technique to the top-ranked models with similar AIC ($\Delta AIC < 2$), to build a full average model with 95% confidence. We calculated Spearman's rank correlation coefficients (ρ) to investigate multicollinearity between the continuous predictors, and prevented highly correlated variables ($\rho > 0.70$, Zar 2010) from being included in the average model. All modelling analyses were performed using the R packages `glmmADMB´ (Skaug et al. 2016) and `MuMln´ (Kamil 2019) in R version 3.6.1 (Team R Core 2018).

Models justification

Carnivores have been found to increase their nocturnal activity in habitats under higher human disturbance (e.g. urban areas; Carter et al. 2015, Lewis et al. 2015, Wang et al. 2015), which can lead to higher temporal overlap amongst carnivore species (Table 2; Hypotheses 1 and 2). Such temporal avoidance of humans may be especially predominant in pastoral landscapes, where human-related mortality risks are higher due to human – carnivore conflicts emerging from livestock depredations (Frank & Woodroffe 2001), therefore potentially increasing temporal overlap between carnivores even further in pastoral landscapes (Table 2; Hypothesis 3). Conversely, landscapes that are kept under traditional mosaic management, with a mix of natural and anthropogenic land use, can facilitate habitat selection and temporal partitioning (Monterroso et al. 2014, Curveira-Santos et al. 2017), and could reduce temporal overlap between species (Table 2; Hypothesis 4). Nevertheless, the reduction of temporal overlap attributed to higher landscape diversity may be diminished in landscapes with a higher proportion of areas associated with extensive grazing systems (Table 2; Hypothesis 5).

The daily activity patterns of animals can also be regulated by meteorological and ecological factors, which could influence the way carnivores interact with each other. For instance, in arid landscapes, where water features are a scarce and spatially-fixed resource, there is little opportunity to achieve spatial avoidance of dominant competitors (Atwood et al. 2011). Thus, subordinate species can concentrate their activity patterns at times where their dominant counterparts are less active (Atwood et al. 2011, Edwards et al. 2017), potentially reducing temporal overlap (Table 2; Hypothesis 6). In habitats with high daytime temperatures, shifting activity to night-time may help species reduce thermal stress (Fuller et al. 2016, Rabaiotti & Woodroffe 2019). However, this could reduce the temporal niche available to segregate with competitors (Astete et al. 2017), increasing temporal overlap (Table 2; Hypothesis 7). In addition, cases of extreme thermal stress may cause most or all species to shift to nocturnal activities, rendering temporal partitioning at waterpoints unachievable. Therefore, any increase in temporal overlap through increased precipitation would be negated by higher daytime temperatures (Table 2; Hypothesis 8).

The strength and outcomes of species interactions is also dependent on the community composition and the interacting species (Sentis et al. 2017). In rich, and thus more complex, carnivore communities, temporal partitioning may facilitate stable coexistence between co-occurring species (Monterroso et al. 2014). Therefore, higher carnivore species richness could decrease the average temporal overlap within the community (Table 2; Hypothesis 9). Alternatively, the temporal overlap among some pairs of species could increase in areas with higher species richness, given that there are more species to avoid, leading to trade-offs and thus higher overlap with some species in the community (Curveira-Santos et al. 2017). Additionally, carnivore species with similar body mass have higher potential for competition, especially if they have similar diets (Wilson 1975). Smaller carnivores may also be at more risk of intraguild predation from larger carnivores (Woodward & Hildrew 2002). Edwards *et al*. (2015) observed that species combinations with higher differences in body mass used spatial partitioning to a greater extent than temporal partitioning. Conversely, species combinations with lower body mass ratios may invest in temporal partitioning to facilitate stable coexistence (Di Bitetti et al. 2010, Edwards et al. 2015). Therefore, temporal overlap may increase with high values of body mass ratios (Table 2; Hypothesis 10).

Results

Description of the literature

Altogether, we extracted 217 coefficients of temporal overlap from 42 studies (Figure 2). The coefficients of overlap ranged from 0.12 to 0.95 (mean = 0.68 ± 0.16 SD), with a seemingly similar distribution between continents (Figure 3). There was a high disparity between continents, with most coefficients extracted from studies in North America (102 values from 9 studies), followed by Europe (55 values from 7 studies), Asia (42 values from 16 studies), South America (13 values from 6 studies) and, finally, Africa (5 values from 4 studies). Except for human density and built-up environment (ρ=0.78), none of the predictors extracted (Table 1) was highly correlated.

A total of 74 species combinations were investigated (the list of the data sources can be found in Appendix 1), and each species combination had on average 2.93 ± 1.93 SD (range 2 – 12) coefficients of temporal overlap. Almost half of the studies (n = 20) investigated a single species pair, whilst the other studies (n = 22) investigated 2 to 20 species pairs simultaneously (mean = 5.41 ± 4.75 SD). This review included a total of 43 species, 18 of which were strictly nocturnal, 24 were crepuscular or cathemeral, and only one species, the yellow-throated marten (*Martes flavigula*) was strictly diurnal. Felidae was the most investigated family (n = 140), followed by Mustelidae (n = 114), Mephitidae (n = 60), Canidae (n = 50), Procyonidae (n = 34), Viverridae (n = 14), Didelphidae (n = 10), Herpestidae (n = 6) and Hyaenidae (n = 6).

Paired studies

Eight studies investigated the effects of human disturbance by comparing the coefficients of temporal overlap of species pairs between areas classified as under low or high human disturbance (Appendix 2). Of these, two studies were able to clearly demonstrate that some temporal overlaps between carnivores increased in areas under high human disturbance (i.e. the confidence intervals between low and high disturbance did not overlap; Lewis et al. 2015, Wang et al. 2015), one study reported significant reductions of temporal overlap (Baker 2016), and five found no apparent (i.e. comparison of coefficients without confidence intervals; Cruz et al. 2015) or significant change attributed to human disturbance (i.e. the confidence intervals between low and high disturbance overlapped; Carter et al. 2015, Rayan & Linkie 2016, Moll et al. 2018, Sogbohossou et al. 2018). The three studies that reported either increases or decreases in temporal overlap attributed to human disturbance in some species pairs also reported no change in other species pairs.

Global models

None of the models explored had strong support (Table 3). The evidence ratios (i.e. AIC_{w1} / AIC_{w2}) for the best model (interaction between Simpson's landscape diversity index and Pasture) versus the second (Built-up environment) and third (Simpson's landscape diversity index) best models were low (2.15 and 3.07, respectively), making the model selection uncertainty high. Therefore, we applied a model-averaging technique to the two top-ranked models with similar AIC ($\Delta AIC < 2$), "Simpson's landscape diversity index * Pasture" and "Built-up environment", to build the full average model with 95% confidence.

None of the variables included in the full average model were significant predictors of coefficients of temporal overlap between carnivores (Table 4). Additionally, the standard errors of the estimate for built-up environment and the interaction between Simpson's landscape diversity index and proportion of pasture overlapped with zero, further indicating weak relationships. The Simpson's landscape diversity index and proportion of built-up environment were positively associated with temporal overlap, whilst the proportion of pasture showed a negative relationship with temporal overlap (Table 4; Figure 4). The lack of statistical significance and weak relationships found suggest that no human, environmental or meteorological variables are global predictors of carnivore temporal overlap.

Discussion

Although accumulating evidence suggests that human disturbance increases nocturnal activity in wildlife (Gaynor et al. 2018, Nix et al. 2018), we found no evidence at a global scale for an impact of the selected human, environmental or meteorological variables on temporal partitioning between carnivores.

Whilst the statistical models do not provide evidence for a global effect of human disturbance on temporal partitioning between carnivores, it cannot be said that human disturbance has no impact on temporal partitioning. Rather, the effects of human disturbance are diverse and probably context-dependent, as illustrated by findings from the eight studies that compared temporal overlap between low vs high human disturbance treatments. As hypothesised, in two of these studies, some species, but not all, increased nocturnal activity in response to higher urbanisation, which increased temporal overlap between competitors (Lewis et al. 2015, Wang et al. 2015). Conversely, Baker (2016) documented that, although human disturbance — a combination of paved roads and hiking trails — induced an increase in wildlife nocturnality, most temporal overlaps between species were lower in more disturbed areas. This is because species within disturbed landscapes might co-occur in safe areas to a greater extent, and subordinate species can fine-scale their temporal partitioning with dominant competitors by narrowing or displacing their peaks of activity. Indeed, maintaining temporal partitioning with competitors in a reduced, nocturnal, temporal window can be a strategy adopted to ensure avoidance of both humans and competitors simultaneously (e.g. Sogbohossou et al. 2018). Such fine-scale adaptations may not be detected by diel measurements of temporal overlap, and could be one of the reasons behind the lack of a significant trend in these results. Similarly, it is possible that, despite an increased nocturnality caused by human disturbance, carnivores could adjust their activity patterns on a fine temporal scale to simultaneously avoid both humans and competitors, therefore not increasing the temporal overlap among carnivores. This could explain why the remaining five studies reported relatively similar coefficients of temporal overlap in areas under low and high human disturbance (e.g. human activity; Carter et al., 2015; Sogbohossou et al., 2018; plantations and reduction in landscape diversity; Cruz et al., 2015; Rayan & Linkie, 2016; built-up environment; Moll et al., 2018). In addition, the lower density of large carnivore populations in high human density areas (Woodroffe 2000), coupled with a high anthropogenic resource availability, could relax competition among carnivores able to adapt to human disturbance (Ruscoe et al. 2011, Wolf & Ripple 2017), thus reducing the importance of temporal partitioning in promoting stable species coexistence. Another possible explanation could be that the baseline activity pattern of species included in the analysis (i.e. diurnal, nocturnal, or crepuscular/cathemeral) may influence the findings. An effect of human disturbance on overlap may be less likely between nocturnal-nocturnal pairs, but could be expected in diurnal-crepuscular pairs. However, due to a strong dearth of diurnal species in the studies included in the analysis, which created a severe unbalance between groups and low sample size for species pairs with a diurnal carnivore, we could not include the baseline activity patterns of species in our analysis. Similarly, we did not account for the uncertainty associated with the coefficient of temporal overlap, and identical weight was given to all the coefficients included in our analysis. However, the precision and accuracy of the coefficient of temporal overlap increase with the number of species detections used to model activity patterns (Lashley et al. 2018). This shortcoming may have reduced the precision of our analysis, but we do not believe that it changed the overall results and conclusions presented in this review.

None of the ecological or meteorological factors were significant predictors of coefficients of temporal overlap. Although temporal overlap increased with the Simpson's landscape diversity index, contrary to the hypothesis, the relationship was weak. Carnivore community richness, body mass ratio, temperature and precipitation were not included in the average model. Temporal overlap was hypothesised to decrease with higher landscape diversity, as complex habitats enable fine-scale habitat segregation and promotes species richness (Rosenzweig 1981, Pereira et al. 2012). However, this hypothesis was not supported by the models. Although previous studies observed that temporal segregation was indeed likely to play a role in complex communities (Monterroso et al. 2014), it is possible that, in the dataset used in this study, higher landscape diversity did not increase species richness systematically, due to other external factors (e.g. habitat fragmentation; Rybicki et al. 2020). Another possibility is that species richness did indeed increase with landscape complexity, but that temporal partitioning was not selected as a primary mechanism allowing coexistence with competitors. In the latter case, species-specific temporal preferences may reflect strategies unrelated to competitive interactions (e.g. foraging strategies; Curveira-Santos et al. 2017).

Indeed, internally, the circadian rhythm is governed by each species' biological clock, an endogenous program that dictates the timing of many behaviours (Pittendrigh 1981). Externally, this is regulated by biotic (e.g. competitor avoidance; predators matching their preys' activity; Gantchoff and Belant, 2016) and abiotic factors (e.g. daytime temperature; Rabaiotti & Woodroffe 2019). As competitor avoidance is just one the many factors regulating activity pattern, it may not be selected in systems where other factors are more limiting to the species' fitness (Schoener 1974b). For instance, this is seen in systems with harsh environmental conditions or low prey availability (Cozzi et al. 2012, Broekhuis et al. 2014, Astete et al. 2017). In other systems, where none of the governing factors exert an extreme pressure on the individuals' fitness, activity pattern can be governed by a combination of several interacting factors (e.g. moonlight and prey activity; Penteriani et al. 2013). Thus, the relative strength of each external factor regulating circadian activity pattern may be strongly related to the biotic and abiotic conditions of the surrounding landscape. This site-specificity renders the investigation of temporal partitioning on a global scale ineffective, by yielding incomplete results that cannot be applied locally.

Limitations

There are two main limitations to this study that could explain the weak relationships found between the predictors investigated and coefficients of temporal overlap. First, the data we collected may be too coarse to analyse processes happening at much smaller spatial and temporal scales. Concerns over spatial scaling and perception bias in ecology have been raised before (Wiens 1989, Levin 1992). As characteristics of the landscape change with spatial scale (Turner et al. 1989), it is possible that some environmental variables have an influence on activity pattern and temporal partitioning amongst carnivores, albeit on a different spatial grain than what was used in this analysis. For the purpose of this study, we decided to prioritise the use of standardised variables, by using the same large-scale indices for all studies. Although doing so meant using a coarser spatial grain, with reduced precision, it ensured a complete comparability between study sites. For instance, several studies measured the levels of human activity as the average number of photographs of people at camera-trap sites (e.g. Wang et al. 2015, Moll et al. 2018). Such fine-scale spatiotemporal metric cannot be determined a posteriori, and we were therefore unable to apply it to all studies in this review. To address this issue, future surveys should favour well-designed, purpose-driven data collection that record the characteristics of the surrounding landscape systematically whilst deploying cameras in the field, enabling the investigation of ecological processes on different spatial scales simultaneously (e.g. Wilmers et al. 2013). This recommendation may be particularly relevant for variables describing the immediate presence of humans. In this study, we used human density as a proxy for the probability of encountering humans, but this relationship may not always be true (e.g. some natural parks may experience peaks of human visitations on a regular basis, but have a low recorded human density due to the lack of habitations). Although measuring human activity on camera can prove ethically challenging (Brittain et al. 2020, Sharma et al. 2020), we believe it is needed to fully comprehend the fine-scale temporal responses of animals to the immediate presence of humans.

Secondly, the coefficient of temporal overlap, which is based on the daily activity patterns of species, may not be the best-fitting tool to investigate temporal partitioning. Daily activity patterns are typically calculated by indiscriminately grouping data spanning several days, months or years into a 24h window. Evaluating temporal partitioning in such a way assumes that competitor avoidance is a predictive process, with long-lasting and consistent effects. Instead, competitor avoidance may often be a reactive response, in which subordinate species adapt their use of landscape to the nearby presence of competitors in temporal scales that are too small to have lasting effects on the circadian activity pattern (Broekhuis et al.

2013, López-Bao et al. 2016). Likewise, although human's influence on wildlife behaviour may exceed that of natural predators (Ciuti et al. 2012, Clinchy et al. 2016), it is likely that the broad-scale nocturnal adaptations of carnivores to humans and human features works in combination with finer-scale immediate responses to human stimuli (e.g. Ordiz et al. 2013, Moll et al. 2018). Alone, the coefficient of temporal overlap portrays a broad picture of temporal segregation, and is best paired with an ecological interpretation of the activity curves (where the peaks are, how narrow etc), or other metrics of fine-scale temporal interactions, such as time-to-event analysis (e.g. Prat-Guitart et al. 2020). Similarly, combining metrics of temporal association with spatial displacement metrics (e.g. multispecies occupancy models; Mackenzie et al. 2004, Rota et al. 2016), or spatiotemporal models (e.g. co-detection modelling; Cusack et al. 2017, time-dependent observation modelling; Ait Kaci Azzou et al. 2021), can yield a more complete picture of fine-scale avoidance of competitors, and how human disturbance might be mediating these interactions. In this regard, the coefficient of temporal overlap is a useful tool in measuring the average temporal overlap between species and large-scale responses to human disturbance but can overlook fine-scale interactions that are essential to allow coexistence. In addition, studies that indiscriminately group data over long periods of time may overlook seasonal variations in behaviour (e.g. Monterroso et al. 2014, Caravaggi et al. 2018), especially if they do not account for the variation in daylength throughout the year in their analysis (i.e. by using solar time instead of clock time; Nouvellet et al. 2012, Vazquez et al. 2019). These studies are thus at risk of recording faulty behavioural timings, which can lead to erroneous conclusions on the way species share time. Similarly, camera-trap surveys focusing on calculating activity pattern and temporal partitioning do so by grouping the data from the different stations within their study area. However, there may be consequential variations in human disturbance or habitat features across individual camera stations which could impact on species behaviour on a fine-scale. Finally, the coefficient of temporal overlap is a pairwise approach to evaluating temporal partitioning. Interspecific competition and niche partitioning are complex systems, with many species involved. Restricting the investigation of temporal partitioning to two species, without considering the impact of the presence and activity of other species forming the community, essentially distils complex patterns of multispecies partitioning into dyads. For all the reasons detailed above, it is in the best interest of studies that employ camera traps to avoid overinterpreting the coefficients of temporal overlap to investigate the potential for competition among sympatric species.

Conclusions

Undoubtedly, humans impact on the activity patterns of wildlife, but we found no evidence that this process could impact temporal overlap between carnivores consistently on a global scale. Instead, the influence of humans on temporal partitioning could be diverse and context-specific, and thus requires further investigation due to the theoretical implications for community structure. Similarly, we found no strong evidence that the ecological and meteorological factors investigated were significant predictors of temporal partitioning globally. Therefore, temporal avoidance of competitors may be regulated by multiple factors simultaneously, with the relative strength of each factor varying with the biotic and abiotic conditions of the landscape.

Large-scale analysis, such as this one, can yield valuable and statistically powerful results. Conducting such investigations on a global scale allows the inclusion of a large range of human activities and landscape transformation, providing valuable insights into the role of humans on species coexistence in animal communities. However, they can also mask the local variability in the response of the processes investigated. Similarly, the investigation of human disturbance on temporal partitioning among carnivores suffered a lack of controlled studies, a common issue in carnivore science (Allen et al. 2017, Bruskotter et al. 2017). Complete experiments (i.e. a study comprised of replication, randomisation, manipulation, and control) with carnivores can rarely, if ever, be executed excellently in the field. We therefore strongly encourage future studies to adopt controlled experimental designs whenever possible, for instance by contrasting temporal overlap in a given species pair between ecologically-similar sites with low and high disturbance (e.g. Frey et al. 2020), or across a gradient of human disturbance (e.g. Lewis et al. 2015). Choosing the right factors to control, with the right species, would eliminate some of the biases that are introduced by pooling temporal data across days and sites, and could be pivotal in detecting the effects of human disturbance on activity overlap between co-occurring species.

Carnivore communities, where temporal partitioning is not negatively affected by humans, may still experience an increase in interspecific competition following human disturbance. Indeed, increases in nocturnality can affect other dimensions of niche partitioning (e.g. increased trophic competition for nocturnal preys; Smith et al. 2018). For this reason, future studies would benefit from investigating multiple dimensions of niche partitioning simultaneously (i.e. spatial, temporal, and trophic), in order to fully understand how human-induced changes in carnivore activity affect interspecific competition.

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Figure legends

Figure 1. Number of citations per year from 2009 to 2019 for the article by Ridout and Linkie (2009), based on the Springer citation tool (https://citations.springernature.com).

Figure 2. Geographical locations of the study areas included in this review, colour-coded by continent. In several cases, studies conducted research in more than one study areas. Photos show the carnivore pair that was the most studied in each continent. Red, North America: coyote (*Canis latrans*) and bobcat (*Lynx rufus*). Orange, South America: jaguar (*Panthera onca*) and mountain lion (*Puma concolor*). Green, Africa: African lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*). Purple, Asia: tiger (*Panthera tigris*) and leopard (*Panthera pardus*). Blue, Europe: European badger (*Meles meles*) and red fox (*Vulpes vulpes*). Authorships of photos can be found in Appendix 3; map design adapted from Prugh and Sivy (2020).

Figure 3. Distribution of the coefficients of temporal overlap extracted in this review, grouped by continent.

Figure 4. Predicted effects of the explanatory variables included in the full model average on coefficients of temporal overlap. The grey ribbon represents the 95% prediction intervals.

Tables

Table 1. Description, spatial resolution, range of variability and source of the variables extracted from each study areas and included in the *a-priori* models.

Variables	Description	Scale	Mean ± SD (range)	Source
Human density	Average inhabitants / km^2 in the study area during the year of data collection. For studies that span over more than one year, the first year was selected.	1km	84.5 ± 181.1 (0.1 - 886)	WorldPop (Lloyd et al. 2017)
Built-up environment	Fractional cover (%) of built-up environment in the study area in 2015.	100m	2.9 ± 5.8 (0 - 27.3)	Copernicus 2015 global land cover database (Buchhorn et al. 2019)
Pasture	Fractional cover (%) of pastures in the study area in 2000.	10km	20.8 ± 22 (0 - 91.1)	Global Agricultural Lands: Pastures, 2000 (Ramankutty et al. 2008)
Simpson's landscape diversity index	Simpson's landscape diversity index (SIDI) in the study area calculated from a discrete land cover classification in 2015. Land cover classes comprised shrubs, herbaceous vegetation, crops, built-up, bare, wetland, closed forest and open forest.	100m	0.3 ± 0.3 (0 - 0.7)	Copernicus 2015 global land cover database (Buchhorn et al. 2019); Fragstats v4 for calculating SIDI (McGarigal et al. 2012)
Precipitation	Annual precipitation (mm) in the study area, averaged for the 1970-2000 period.	1km	1148.1 ± 800.8 (215 - 3149.9)	WorldClim (Fick & Hijmans 2017)
Temperature	Annual mean temperature (°C) in the study area, averaged for the 1970-2000 period.	1km	18.2 ± 6.4 (0.6 - 28.4)	WorldClim (Fick & Hijmans 2017)
Carnivore community richness	Number of mesocarnivores and large carnivores inhabiting part or all of the study area using the 2019 IUCN Red List update.	n/a	LC: 1.3 ± 2.0 (0 - 8) MC: 12.9 ± 5.5 (5 - 27)	IUCN Red List of threatened species (IUCN 2020)
Body mass ratio	Average body mass of larger species / Average body mass of smaller species.	n/a	7.4 ± 11.1 (1 - 73.8)	PanTHERIA database (Jones et al. 2009)
Baseline activity pattern	Species activity pattern: (1) nocturnal, (2) cathemeral or crepuscular, (3) diurnal.	n/a	(1): 18. (2): 24. (3): 1	PanTHERIA database (Jones et al. 2009)

Table 2. *A-priori* models testing human, meteorological and ecological continuous variables as predictors of coefficients of temporal overlap between sympatric carnivores. Hypothesis justification and support can be found in the text. Hyp. = Hypothesis number.

Hyp.	Variables	Hypothesis	Impact on temporal overlap
1	Human activity	Human's diurnal activity is associated with increased nocturnality in carnivores.	Increase
2	Built-up environment	Human disturbance is higher in urban areas which leads to carnivores in urban areas being more nocturnal than in rural areas.	Increase
3	Pasture	Livestock depredation is a source of human-carnivore conflict. Frequent lethal management of carnivores in pastoral landscapes is associated with increased carnivore nocturnality.	Increase
4	Simpson's landscape diversity index	Complex habitat mosaics nurture rich communities, and temporal partitioning is selected to facilitate stable coexistence.	Increase
5	Simpson's landscape diversity index * pastures	The effects of landscape diversity are diminished in landscapes with a higher proportion of pastures.	Non-linear
6	Precipitation	Scarcity of spatially fixed waterpoints in dry areas forces temporal partitioning.	Increase
7	Temperature	Extremely high temperatures drive crepuscular or nocturnal behaviour.	Increase
8	Precipitation * temperature	The effects of precipitation are magnified in extremely hot areas.	Non-linear
9	Carnivore community richness	In richer communities, temporal partitioning is selected to facilitate stable coexistence.	Increase
10	Body mass ratio	Species combinations with higher body mass ratios invest less in temporal partitioning, and more in spatial partitioning, to improve coexistence.	Increase

Table 3. Results of the *a-priori* model selection for predictors of coefficients of temporal overlap between sympatric carnivores, with models ranked based on their AIC. Species combination was added as a random factor in each model. The "*" sign indicates an interaction. Models in bold were selected to build the full model average.

Models	AIC	ΔAIC	AIC$_w$
Simpson's landscape diversity index * Pasture	**-258.82**	**0.00**	**0.43**
Built-up environment	**-257.32**	**1.50**	**0.20**
Simpson's landscape diversity index	-256.53	2.29	0.14
Pasture	-255.68	3.14	0.09
Precipitation * Temperature	-253.96	4.86	0.04
Temperature	-253.78	5.04	0.03

Null (Intercept only)	-253.39	5.43	0.03
Precipitation	-251.97	6.85	0.01
Body mass ratio	-251.42	7.40	0.01
Human density	-251.41	7.41	0.01
Carnivore community richness	-250.96	7.86	0.01

Table 4. Full model average of the four best *a-priori* models (ΔAIC <2), with 95% confidence. Species combination was added as a random factor. All explanatory variables were standardised for comparison purposes. SE = Standard Error.

Variable	Estimate	SE	z value	p-value
(Intercept)	0.699	0.077	9.077	<0.005
Pasture	-0.056	0.053	1.054	0.292
Simpson’s landscape diversity index	0.068	0.055	1.229	0.219
Built-up environment	0.047	0.053	0.888	0.375
Simpson’s landscape diversity index * Pasture	0.025	0.043	0.588	0.557

Online appendices

Appendix 1. Data sources and species combinations included in the analysis. Species combinations that are found with only one reference still had at least two coefficients of temporal overlap included in the analysis (i.e. the coefficients were calculated from two or more study areas, within the same study).

Appendix 2. Coefficients of temporal overlap reported by the eight studies comparing temporal overlaps of similar species pairs between areas classified as under low or high human disturbance.

Appendix 3. Authorships of photos in Figure 2.