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Global patterns of carnivore spatial ecology research in agroecosystems

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Abstract

The growing needs for agricultural expansion and intensification will likely continue to reduce and fragment the terrestrial habitats fundamental to mammalian carnivores. Recent research identified benefits of agroecosystems to carnivores recognizing their multifunctionality, mostly for common species. However, the variability of carnivore ecology investigated in agroecosystems, biases in agriculture types and species targeted, and methodological approaches may affect available knowledge to reconcile conservation and production goals. To fill this gap, we conducted a systematic literature review to identify which aspects of and how is carnivore spatial ecology being investigated within agroecosystems. Of the 110 reviewed studies, most focused on agricultural crops (55%) and grasslands (47%) and half referred to monocultures. We found that 61% of the studies were conducted in Europe and North America. Eighty-four species were studied, 73% classified as Least Concern, with 67% of the studies targeting a single species and 30% focused on only seven common species. Almost all studies included some form of habitat use analysis and species' home-range and its attributes (e.g. size, resource selection) were the most common spatial ecology aspects studied. Most studies suggested that agriculture act as food provisioning areas (69%) but few used direct food availability measures. Our results highlight that studies tend to be descriptive and geographically biased towards northern hemisphere and to non-forested agricultural types. We suggest that future carnivore spatial ecology research in agroecosystem should be hypotheses-driven, with greater focus on the mechanisms and processes through which agroecosystems might affect carnivore spatial ecology in high priority regions for carnivore conservation.

Key words

Agriculture, *Carnivora*, biodiversity conservation, land use, landscape functionality, research synthesis, space use

Introduction

Unprecedented rates of agricultural expansion and intensification (Foley et al., 2011; Tilman et al., 2011) are leading to biodiversity loss, habitat loss and fragmentation, and the deterioration of ecosystem services (Cardinale et al. 2012; Visconti et al. 2016; IUCN 2016; Joppa et al. 2016). Currently, about 40% of the terrestrial earth surface is agricultural land (FAO 2015), and further expansion and intensification is expected to meet growing demands for food (Tilman et al. 2011). Land use conversion to agriculture (crops, production forests, pastures) is responsible for increasing local extinction and species turnover, decreasing local and regional diversity (Newbold et al. 2015), altering the distribution and abundance of species (Dobrovolski et al. 2013), and ultimately influencing species demographic and evolutionary processes (Verdade et al. 2014). Agriculture may have additional deleterious effects on species, through environmental contamination (Novotny 1999) or favoring the spread of invasive species (Turbelin et al. 2017). Some biodiversity might, however, be able to cope and thrive in agricultural systems with certain conditions (Cox and Underwood 2011; Mendenhall et al. 2014). For example, agroecosystems (ecosystems in which indigenous plants and animals are partially or completely replaced with crops and livestock; Altieri and Koohafkan 2004) can support moderate to high biodiversity levels depending on agricultural intensity and presence of residual native vegetation (Daily et al. 2003). However, more evidence is needed about the role of agroecosystems in conservation (Chazdon et al. 2009), as their associated biodiversity and functions are not yet clear (Henle et al. 2008). We thus need to better understand under which conditions goals for biodiversity conservation and agricultural production can be aligned (Adams et al. 2004; Scherr and McNeely 2008; Kueffer and Kaiser-Bunbury 2014).

Research about biodiversity in agroecosystems has grown exponentially over the last two decades, and it has also increased for terrestrial mammalian carnivores (hereafter ‘carnivores’) (Ferreira et al. 2018). Agriculture is considered the leading driver of carnivore extinctions and population declines (Visconti et al. 2011; Di Marco et al. 2014). Losses of carnivore species can have major cascading effects on ecosystems, as they play an important role in ecosystem regulation, via resource facilitation or top-down control of lower trophic levels (Sergio et al. 2008; Roemer et al. 2009; Prugh et al. 2009; Ripple et al. 2014). Agricultural impacts on carnivore populations may also disrupt the benefits these species provide to human wellbeing (O'Bryan et al. 2018), such as disease mitigation, carrion removal, or even as pest control agents indirectly increasing agricultural production (e.g. Williams et al. 2018).Future agricultural expansion is predicted to greatly overlap important areas for carnivore conservation (Dobrovolski et al. 2013). In recent decades, however, there is growing evidence that agroecosystems might also provide carnivore habitat (e.g. avocado orchards: Nogeire et al. 2013; cork oak agroforestry: Rosalino et al. 2005, Santos et al. 2016; agroforestry: Verdade et al. 2014, etc) and allow connectivity (Matos et al. 2009), being potentially multifunctional for many species, especially those requiring large areas for their territory and movements (Norris 2008). Agroecosystems may thus support biodiversity depending on the type of agriculture, its intensity, and whether residual native vegetation is maintained (Daily et al. 2003). Therefore, if agroecosystems provide habitat and support biodiversity, they can also act complementary to networks of protected areas to increase regional ecological integrity, by supporting population persistence and promoting connectivity (Ekroos et al. 2016).

A detailed understanding of how wildlife, specifically carnivore species, use agroecosystems is needed to answer the challenge of including agroecosystems in conservation portfolios (Sutherland 2003). Such information can be affected by literature biases and knowledge shortfalls (e.g. Wallacean, Prestonian and Darwinian; Hortal et al. 2015). Here, we conducted a systematic literature review to identify trends and inform gaps in conceptual and methodological approaches to carnivore spatial ecology research in agroecosystems. We specifically focused on spatial ecology since spatial patterns are often the starting point for more detailed ecological investigations (Cottenie 2005). Moreover, we opted to review studies conducted at the landscape scale, because this is the most suitable scale for land management. We review the literature to describe: 1) which geographical locations, agriculture systems and carnivore species, are being studied? 2) which spatial ecology patterns are being investigated and which methodological approaches are current practice? and 3) which ecological functions and properties of agroecosystems are considered to explain the observed spatial patterns? Finally, we build on the information gathered through the literature review to provide a road-map for future research needs.

Materials and Methods

Data collection

In July 2016 we performed a literature search of peer-reviewed scientific articles using the ISI Web of Science (https://apps.webofknowledge.com) and Scopus (https://www.elsevier.com/solutions/scopus) databases, and the Google Scholar search engine. We searched for terms within article title, abstract and keywords. The search terms included: 'carnivore', '*Carnivora*', 'agriculture', 'agricultural systems/landscapes', 'farm', 'crops', 'forestry', 'pasture', 'orchards', 'grove' and 'predator', as isolated and as combined terms. We extended the search by including bibliographic references cited in the initial set of articles identified in the search. We selected articles that met five criteria: 1) published between 1996-2016, to cover the most recent findings about carnivores in agricultural areas, 2) targeted at least one carnivore species, 3) focused on spatial ecology, 4) conducted at local or regional levels using landscape approaches and 5) carried in landscapes where agricultural land covered more than 15% of the study area, to assure that the proportion of this land use would be non-negligible.

For each study, we recorded information on: 1) geographical location; 2) agricultural system(s); 3) carnivore species; 4) spatial ecology aspects; 5) methodological – sampling and analytical - approach(es); 6) functions attributed to agriculture; and 7) properties of the agroecosystem considered (e.g. disturbance, production cycle). This information was coded as categorical binary variables (Table 1), except for species lists. The resulting data was used to calculate the frequency of each category in all reviewed studies.

Results

Our search generated a total of 146 articles, from which 110 fit our criteria and were used for more detailed review (a list of reviewed studies is provided in S1 Data sources). The number of publications per year increased significantly until 2016 (Spearman's Rank Correlation, r_s=0.816, $p<0.001$; Fig. 1) with a 25% average annual growth rate.

Characteristics of the studies

More than half of the studies were conducted in Europe and North America. Europe was the continent with the higher number of studies (38%), followed by North America (23%), while remaining studies were evenly distributed between South America (15%), Asia (13%) and Africa (12%) (Fig. 1-2). Our selection did not include studies conducted in Oceania given that the Order *Carnivora* is not native of this continent.

The four agricultural types were not evenly represented in the sample of studies we analyzed (Table 1). Studies on crops (55%) and grasslands (47%) dominated the literature, followed by those targeting forestry (31%) and groves (17%) (Fig. 2). Nearly half of the reviewed studies targeted a single agroecosystem type, i.e. monocultures (48%), while the remaining were conducted in mixed agroecosystems. The types of agricultural systems most studied varied per continent, with grasslands most studied in Europe and Africa, crops in North America and groves in Asia (Fig. S1). These mixed agriculture systems were mainly combinations of croplands and grasslands, and of forestry and grasslands. Groves were most often monocultures. There is a geographical bias to common agricultural systems, namely: croplands in Europe (e.g. central European farmlands;

Červinka et al. 2013; Šálek et al. 2013) and North America (e.g. row-crop plantations in Indiana; Beasley et al. 2007; Gehring and Swihart, 2003); forestry and grasslands in Europe (e.g. Mediterranean silvo-pastoral systems; Galantinho and Mira, 2009; Hipólito et al. 2016); combination of forestry, grasslands and croplands of South America (e.g. multi-use agriculture system in Southeast Brazil; Dotta and Verdade, 2011a; Lyra-Jorge et al. 2008); groves in Asia (e.g. oil palm plantations; Jennings et al. 2015; Rajaratnam et al. 2007); and grasslands in Africa (e.g. rangeland; Marker et al. 2008).

Most studies targeted a single carnivore species (67%). Studies spanned a total of 84 carnivore species, about one third of the world's carnivore species (n=284) (Fig. 2, Table S1). The highest number of species in one study was 18, in oil-palm agriculture in Peninsular Malaysia (Azhar et al. 2014) and two other studies each reported 13 carnivore species in multi-use agriculture in South America (Daily et al. 2003; Dotta and Verdade 2011b); on average studies reported on 2.7±3 species. Despite the considerable diversity in species richness across studies, seven species accounted for ~30% of all records, namely the red fox (*Vulpes vulpes*), coyote (*Canis latrans*), European badger (*Meles meles*), stone marten (*Martes foina*), mountain lion (*Puma concolor*), and raccoon (*Procyon lotor*) (see Table S1). Regarding species' IUCN conservation status, 73% were classified as 'Low Concern' IUCN status, 11% as 'Near threatened' and the remaining 17% had a higher threat status. Despite the predominance of low concern conservation status, 54% of the target species were reported to have decreasing population trends, 28% stable and only 4% increasing.

Spatial ecology and methodological approaches

Home-range studies (36%, e.g. Dellinger et al. 2013; Nakashima et al. 2013) were the most common, followed by the assessments of species distributions (22%, e.g. Nogeire et al. 2013; Ramesh and Downs 2015), and density or relative abundance (18%, e.g. Dotta and Verdade 2011a; Kent and Hill 2013; Fig. 2). Few studies focused on inventories of carnivore species (11%, e.g.

Azhar et al., 2014; Daily et al., 2003), and even fewer analyzed animal movements (6%, e.g. Elliott et al. 2015; Nogeire et al. 2015). Independently of the studied spatial ecology aspect, the vast majority of the studies (92%) focused on determining habitat use. Radio-tracking was the most common method used (45% of the studies), while sign surveys and camera-trapping were conducted in 29% and 23% of the studies, respectively.

Underlying processes

Three-quarters of the reviewed studies attributed at least one function to agriculture (Fig. 2), food provisioning being the most common function (69%, e.g. Caruso et al. 2016; Jennings et al. 2015). Fewer studies suggest agricultural land functions as shelter provider (22%, e.g. Carvalho et al. 2014; Moreira-Arce et al. 2016) or movement path (6%, e.g. Nogeire et al. 2015). About one-third of the reviewed studies associated temporal heterogeneity of the studied agroecosystem with carnivore spatial ecology patterns (36%, e.g. Marker et al. 2008; Santos et al. 2016), but only 16% related this with the agriculture's production cycle (e.g. Borchert et al. 2008; Timo et al. 2015). Similarly, 35% of the studies considered direct disturbance linked to carnivore spatial ecology (e.g. Lara-Romero et al. 2012; Vanthomme et al. 2013). Even fewer studies, 25%, integrated direct resource availability measurements (e.g. Šálek et al. 2010; Silva-Rodríguez et al. 2010).

Discussion

The growing needs for agricultural expansion and intensification will likely continue to reduce and fragment the terrestrial habitats fundamental to mammalian carnivore species, forcing carnivore conservation portfolios to extend beyond the boundaries of wilderness and consider land-sharing options (López-Bao et al. 2017). Wildlife-friendly farming, specifically, has been proposed as a solution to meet both needs for food and provide benefits for biodiversity (Scherr and McNeely 2008; Verdade et al. 2014). Mounting evidence on carnivore species' ability to exploit the heterogeneity of agroecosystems at large spatial scales (Ferreira et al. 2018) suggests the potential for agroecosystems' multifunctionality at multiple scales (see Ekroos et al. 2016). Yet, the ability to harness potential biodiversity benefits of agroecosystems hinges on our understanding of species' ecology in these altered environments. Here we reviewed conceptual and methodological approaches to carnivore spatial ecology research in agroecosystems. Our results show an exponential growth in publications and in the variety of systems studied, as well as in spatial ecology aspects assessed, and methodologies employed. However, we found a geographical bias towards research in the northern hemisphere and that most carnivore species researched in agroecosystems were of low conservation concern. Of the studies we reviewed, most described spatial ecology patterns based on species use of space, but only few have linked these patterns to population's demography, that ultimately determines the conservation potential of agroecosystems. Perhaps most fundamental was the lack of hypothesis-driven studies aimed to understand agroecosystem functionality.

Target systems

Most studies concentrated in Europe and North America, continents with historical and large-scale land conversion to agriculture (Diamond 1997). Conversely, regions like Africa and South America which are experiencing more recent and ongoing agriculture expansion (Gibbs et al. 2010; FAO 2015) were less often targeted, although these regions are projected as future hotspots of terrestrial mammal loss (Visconti et al. 2011). Most studies occurred in areas of low priority for carnivore conservation (Di Minin et al. 2016), except for several studies conducted in South East Asia, a carnivore diversity hotspot facing intense agricultural expansion (Koh et al. 2011). A recent review by Ferreira et al. (2018) assessed the global determinants in the use of agricultural lands by carnivores. They found distinct geographical research patterns and highlighted a higher interest for the topic in South America that was not captured by us. However, the reviewed studies included numerous ‘grey literature’ (e.g. Ph.D. and M.Sc. theses) for the region, which were not captured by our review criteria, and Ferreira et al. (2018) did not consider pastoral systems associated with livestock husbandry (here ‘grasslands’) which are prevalent in Europe and Africa.

Our review highlighted that the majority of studies were conducted on crops and grasslands, and fewer in forestry or groves. Production forests create low-contrast matrices with native forests and the afforestation of agricultural land has been suggested to provide complementary habitat, buffer edge effects and promote connectivity to a greater extent than the sharper ecotones associated with agricultural types that lack a tree layer (Brockerhoff et al. 2008). Such knowledge biases towards non-forested agriculture may impair our ability to verify and harness benefits of agroecosystems with proposed greater potential for carnivore conservation. Indeed, Ferreira et al (2018) reported eucalyptus, pine and oil palm plantations as the agricultural habitats most frequently used by carnivores. There is, however, some uncertainty in labelling the studied agroecosystems, because many of the studies only provide vague descriptions of the agricultural types and often only state “agriculture”.

We found studies targeted a wide variety of carnivore species that occur in agroecosystems but had a greater focus on species with low conservation status, presumably more common in these systems (Ferreira et al. 2018). It remains unclear, however, how agroecosystems contribute to these species conservation since most studies were based on occurrence data, which conveys little information on population persistence (Grouios and Manne 2009), nor on individual condition (e.g. body condition, parasite burden, etc.).

Further, many of the carnivore presence records were obtained in remaining native vegetation fragments surrounding or interspersed with agricultural areas (e.g. Azhar et al. 2014). These results corroborate the need to further evaluate the challenges and opportunities for carnivore conservation in agroecosystems (Visconti et al. 2011; Dobrovolski et al. 2013; Di Minin et al. 2016), specifically a detailed understanding of its ecological functionality (Ferreira et al. 2018) (discussed further below). Moreover, the predominance of studies targeting single focal species suggests many carnivore species present in agroecosystems remain overlooked. Studies should be expanded to a large fraction of the carnivore species globally, for example by targeting carnivore diversity hotspots in southern hemisphere areas, where agroecosystems expansion is more challenging, as also highlighted by Ferreira et al. (2018).

Spatial ecology and methodological approaches

We found a strong predominance of 'habitat use' descriptive studies, likely because understanding species-habitat relationships is fundamental to understanding the response of species to land-use change, and species-habitat relationships also form the basis of many management plans (Scherr and McNeely 2008). Home-ranges were the most studied aspect of spatial ecology, providing detailed inferences on individuals' behaviour and resource use (e.g. home-range establishment and associated environmental determinants; Magrini et al., 2009). Most of the studies were based on high-resolution spatio-temporal information mainly from radio-tracking (Boitani and Powell 2012). Home-range shapes, size and composition, which underlie many of the local ecological adaptations of carnivores (e.g. Gittleman and Harvey 1982), are driven by carnivore body-mass, physiology and interactions such as competition and co-existence, and are fundamental to scale individual behavior to understand population structure (e.g. Johnson et al. 2001), meta-populations, dispersal, and the dynamics of geographical range contraction and expansion.

Assessing distribution patterns was the second most common goal of the reviewed studies, providing spatially explicit and population level estimates of species occurrence, often for several species simultaneously. Such information of geographical distributions is important to identify areas and/or landscape features of conservation value for species-level dynamics and to determine threats (Boitani and Powell 2012). However, the robustness of species occurrence estimates is highly influenced by the sampling method and inherent caveats of presence and absence data. Only

30% of reviewed distribution studies attempted to correct survey data for imperfect detection (for example, by using hierarchical occupancy modelling, Mackenzie et al. 2006; e.g. Cruz et al. 2015), thus potentially generating biased inferences of distribution (Guillera-Arroita et al. 2014).

The detailed description and high-resolution data used to elucidate carnivore space use in agroecosystems with the above approaches, contrasts with the lack of knowledge on the demography of individual species in these environments. Fewer studies estimated carnivore relative abundance or density, and of those about two thirds related the estimates with environmental conditions by, for example, comparing estimates across landscapes with different proportions of agriculture cover (Swanepoel et al. 2015). Only a small fraction of studies provided explicit density estimates. This could be because accurate inferences on density are hard to obtain for low-abundant, wide-ranging and often cryptic carnivore species, particularly for species lacking morphological traits that allow individual identification and use of common capture-recapture approaches (Boitani and Powell 2012). Alternatively, researchers often resort to the use of relative abundance indices, in the format of capture rates, to describe disproportionate distributions of unmarked individuals across heterogeneous agroecosystems. However, such measures can rarely be used for inference about absolute population size as they need to be calibrated to do so, and are particularly susceptible to imperfect and variable detection (Sollmann et al. 2013). This lack of information on population abundance, and more importantly population size and density, hinders the evaluation of carnivore population demographics and landscape features associated with population persistence (discussed below) and limits meaningful comparisons across systems.

Underlying processes

The large majority of reviewed studies associated agriculture lands with its capacity to directly (e.g. cereals, fruits) or indirectly (e.g. rodents) provide food for carnivores (e.g. Athreya et al. 2013; Caruso et al. 2016; Jennings et al. 2015; Kaneko et al. 2006; Prange et al. 2004). This longitudinal function of food provisioning is common to several agriculture types, and is in line with previous reviews that suggest that agriculture provides a surplus of food, driving carnivore's space use, and increases carrying capacity (Verdade et al. 2011). Compared to natural vegetation areas, many agroecosystems support a higher abundance of rodents (Gheler-Costa et al. 2012) and ground beetles (da Silva et al. 2008), two taxa often consumed by carnivores (e.g. Verdade et al. 2011). Furthermore, fruit production increases the amount of available food used by carnivores, particularly in Mediterranean areas (Rosalino and Santos-Reis 2009). However, only a third of the studies hypothesized *a priori* this function of agriculture and less than 20% explicitly coupled this hypothesis with resource availability data (e.g. Rajaratnam et al. 2007; Šálek et al. 2010; Silva-Rodríguez et al. 2010). Most often, food provisioning is a *post-hoc* explanation for observed spatial patterns, suggesting functionality (e.g. Chamberlain et al. 2009).

The role of agricultural lands as shelter for carnivores (e.g. Carvalho et al. 2014; Moreira-Arce et al. 2016) and as movement paths, facilitating connectivity between habitats (e.g. Nogeire et al. 2015), is much less often mentioned. However, this could be due to the way we extracted information from the studies on the ecological functions attributed to agriculture . When such information was not explicitly mentioned by authors, we made our own interpretation of their discussion, which can be subjective. Despite the caveats associated with this approach, we considered this information valuable as it summarizes the most common functions associated with agricultural lands.

Fundamental characteristics of agroecosystems were seldom considered. Most studies did not consider the influence of phenology on carnivore spatial patterns and only a small fraction investigated the effect of temporal heterogeneity in ecosystem structure linked to agriculture production cycles (e.g. Borchert et al. 2008). This is an important aspect to consider, as temporal heterogeneity is an inherent characteristic of agroecosystems (Verdade et al. 2014). Previous studies have shown that this higher temporal heterogeneity of agroecosystems often compensates for the temporal discontinuity in resource availability in natural ecosystems (see Driscoll et al. 2013) and, consequently, drives space use patterns by carnivores (e.g. Timo et al. 2015). For example, biomass in sugarcane plantations can range annually from virtually zero to 100 ton ha^{-1} $year^{-1}$ (Goldemberg et al. 2008), and its availability may induce strong temporal dynamics in the populations of mammalian prey species (Beatriz Villa et al. 1998). Another issue often disregarded was the effect of human-induced disturbance, expected to be particularly relevant in agroecosystems with a modest to high level of human intervention, mainly around harvesting seasons (Timo et al. 2015). Direct human disturbance factors were only considered in 35% of the studies (e.g. roads, Vanthomme et al. 2013; settlements, Lara-Romero et al. 2012; carnivore interaction with domestic species, Galantinho and Mira 2009; Silva-Rodríguez et al. 2010). Not accounting for such effects will likely lead to misleading results, as disturbance may disrupt species-habitat relationships (Muhly et al. 2011; Vanthomme et al. 2013). Similarly, the demographic impacts and behavioral responses (human-induced fear) of carnivore persecution following human-wildlife conflicts (e.g. crop-raiding, livestock depredation) requires further research (Ferreira et al. 2018).

Implications for future research

While impacts of agriculture and its expansion on carnivore populations are widely acknowledged, empirical evidence on the functional role of agroecosystems is lacking. By synthesizing previous research approaches we were able to pinpoint two main areas of research that should be prioritized, namely studying the ecological function of agroecosystem components for carnivore species and understanding carnivore population dynamics in these landscapes.

Currently, we have considerable information on species richness, diversity and distribution, space use at the home-range and population level, and how these correlate to agroecosystem attributes (e.g. composition, configuration and connectivity). As we show here, there are many potential roles of agroecosystems and more information is needed to understand the suitability and the potential ecological functions agricultural matrices may provide for carnivores (Driscoll et al. 2013). Our first and main suggestion is to move towards a greater understanding of processes underlying carnivore spatial patterns by establishing mechanistic links between species' space use and resources available. Information on available resources in native and agriculture components of the agroecosystem, and how these vary in relation to their surroundings and across production cycles, can be used to test hypothesis on agroecosystems' functionality (Kupfer et al. 2006). For example, croplands and sugar-cane plantations in Brazil both support high rodent density that serve as prey for a suite of local carnivore species, while open pastures do not (Gheler-Costa et al. 2012). Further, the same agricultural type may vary its function with production management or types of harvestable species; e.g. different forestry schemes may provide distinct shelter opportunities dependent on control of understory vegetation (Moreira-Arce et al. 2016). Resulting insights should be further integrated with carnivores' morpho-ecological traits, as suggested by Ferreira et al. (2018). These mechanistic insights can then guide management options that build on the complementary role between agricultural lands and remnant native vegetation fragments (Fahrig et al. 2011).

The second suggestion is to gain more understanding on the links between agroecosystem attributes and carnivore population dynamics. Estimates of population abundance/density are the basis for designing conservation actions resilient to dynamic environments, the assessment of conservation progress, and the evaluation of system responses to management options (Nichols 2014). The state of populations can then be matched with the agroecosystem's structural and functional characteristics and across sets of management options. Manipulative experiments of land conversion to agriculture, e.g. Before-After-Control-Impact study designs, are hard to implement at carnivores' spatial scale and require long-term studies. Pair-wise comparisons or space-by-time substitution approaches may be more efficient in and sufficient to retrieve this information in the short-medium term (Pickett 1989).

Conclusions

Our ability to reconcile biodiversity and production in agroecosystems depends on detailed understanding of species ecology in these altered environments. This is particularly crucial for species such as carnivores, whose primary threats are tightly related to agriculture expansion and intensification. In the present review, we synthesized the current research on carnivore spatial ecology in agroecosystems and identified knowledge gaps fundamental to inform conservation practice (e.g. determine the amount, configuration and fragmentation of protected habitat, establish vegetation corridors, increase matrix quality; Arroyo-Rodríguez et al. 2020). We encourage researchers to expand or revisit available data to complement such gaps. Ultimately, we hope our findings can act as a catalyst towards a greater research variety and understanding of the role of agroecosystems for carnivores and other biodiversity globally, to ultimately assess and promote the conditions under which multi-functionality is possible.

Declarations

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Consent to participate

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Consent for publication

Not applicable

Availability of data and material

Not applicable

Code availability

Not applicable

Authors' Contributions

GCS and LMR conceived the ideas; LMR led the literature search; GCS conducted the review process, collected and analysed the data; All authors contributed critically during the discussion of results; GCS and MJS led the writing with the contribution of all co-authors.

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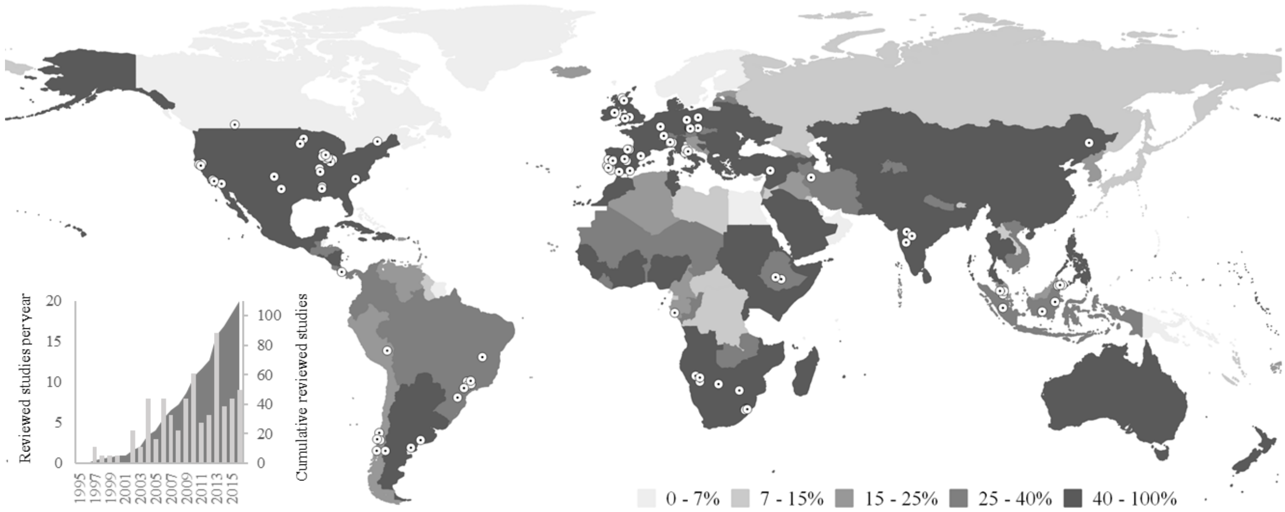

Figure 1. Geographical distribution of the reviewed studies on carnivore spatial ecology in agroecosystems. White dots represent the approximate location of each paper included in this review. The grey shading on the map represents the percentage of country area dedicated to agriculture in 2015 (FAO 2015). The bar chart shows the distribution of reviewed studies per year and the cumulative number of studies reviewed (dark grey area).

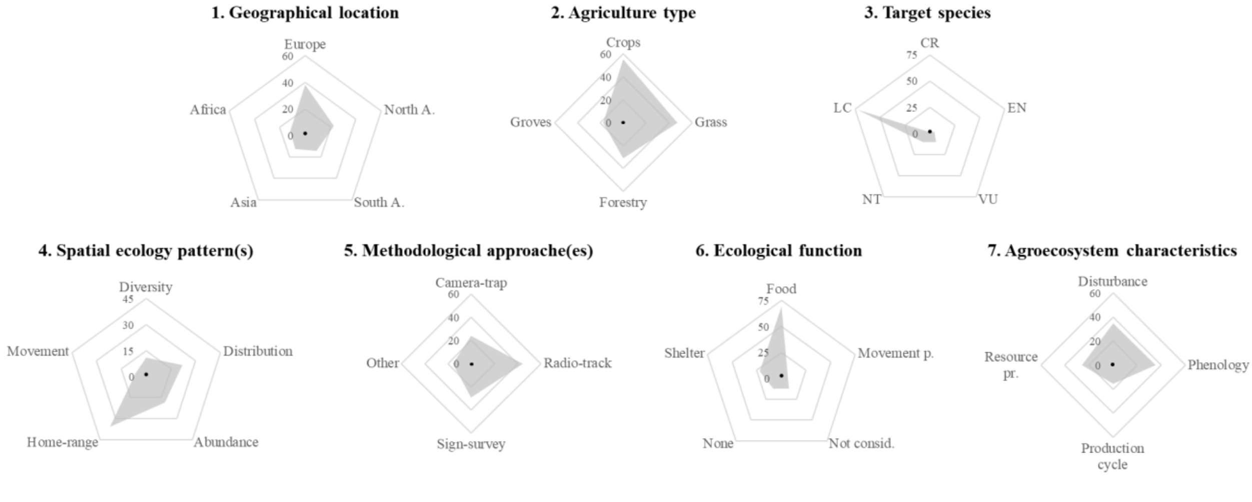

Figure 2. Radar-plots showing the characteristics of reviewed studies according to the defined characterization framework (Table 1). Results are shown as percentages of all reviewed studies (n=110). For 'Target species' variables, percentages refer to the total number of species registered (n=84).

Table 1. Variables recorded from the literature selected with the systematic search approach.

Category	**Variable**	**Description**
Target systems		
1. Geographical location	Continent	Africa, Asia, Europe, North America, South America
2. Agricultural system	Crops	Arable land planted with annual or perennial crops, mainly row crops; includes all plantations without pronounced vertical/arboreal strata (e.g. soybean, corn, sugarcane, coffee)
	Forestry	Production forest established through planting or seeding one or more tree species in the process of afforestation or reforestation, often exotic species, usually to produce timber or fuel wood (e.g. eucalyptus, pine stands)
	Grasslands	Herbaceous forage crops, either cultivated or growing wild; usually grazed (e.g. meadows, pastures)
	Groves	Tree plantations for food production or similar commodities, with pronounced vertical strata (e.g. oil palm, olive trees, orchards)
3. Carnivore species	Species list	List of species, native or non-native, mentioned in the study with exception of domestic carnivores (cats *Felis silvestris catus* and dogs *Canis lupus familiaris*)
	Red list category	Reported IUCN red list category* for each species
	Population trend	Reported IUCN population trend (decreasing, stable, increasing) for each species
	Single/multi-species	Whether studies targeted one or more species
Spatial ecology and methods		
4. Spatial ecology aspects	Diversity	Metrics of carnivore species richness, diversity, etc.
	Distribution	Information on spatial distribution (e.g. occupancy, occurrence, geographic range)

	Abundance	Metrics of relative abundance or density
	Home-range	Estimates of home-range sizes (and/or complementary metrics, e.g. core area)
	Movement	Movement metrics and behaviour (e.g. travel speed, travel distance)
	Habitat use	Information on habitat use (i.e. relationships between carnivore presence and habitat covariates)
5. Methodological approach(es)	Sampling	Camera-trapping, radio-tracking, sign surveys, other
	Detectability	Explicitly accounts for imperfect detection in data analysis. Not applicable to studies based on radio-tracking
Underlying processes		
6. Ecological function	Food	Agroecosystem is foraging habitat
	Shelter	Agroecosystem is refuge
	Movement path	Agroecosystem connects habitat
	None/Avoidance	Agroecosystem is considered 'non-habitat'
	Not considered	No ecological function is attributed, but not explicitly classified as 'non-habitat'
	Function proposed *a priori*	Agroecosystem ecological function is hypothesized and tested
7. Agroecosystem characteristics	Phenology	Includes phenology (e.g. daily, seasonal, annual) of the agroecosystem related to spatial ecology patterns
	Production cycle	Includes agroecosystem’s production cycle (e.g. harvest and non-harvest) in the assessment of spatial patterns
	Disturbance sources	Assesses effects of anthropogenic disturbance (e.g. roads, settlements, hunting or livestock presence) explicitly
	Resource provision	Explicitly includes measurements of resource availability (e.g. prey abundance) in the assessment of spatial patterns

* IUCN categories: NT – Not Threatened, LC – Least Concern, VU – Vulnerable, EN – Endangered, CR – Critically Endangered