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Wildlife ecotoxicology of plant protection products: knowns and unknowns about the impacts of currently used pesticides on terrestrial vertebrate biodiversity

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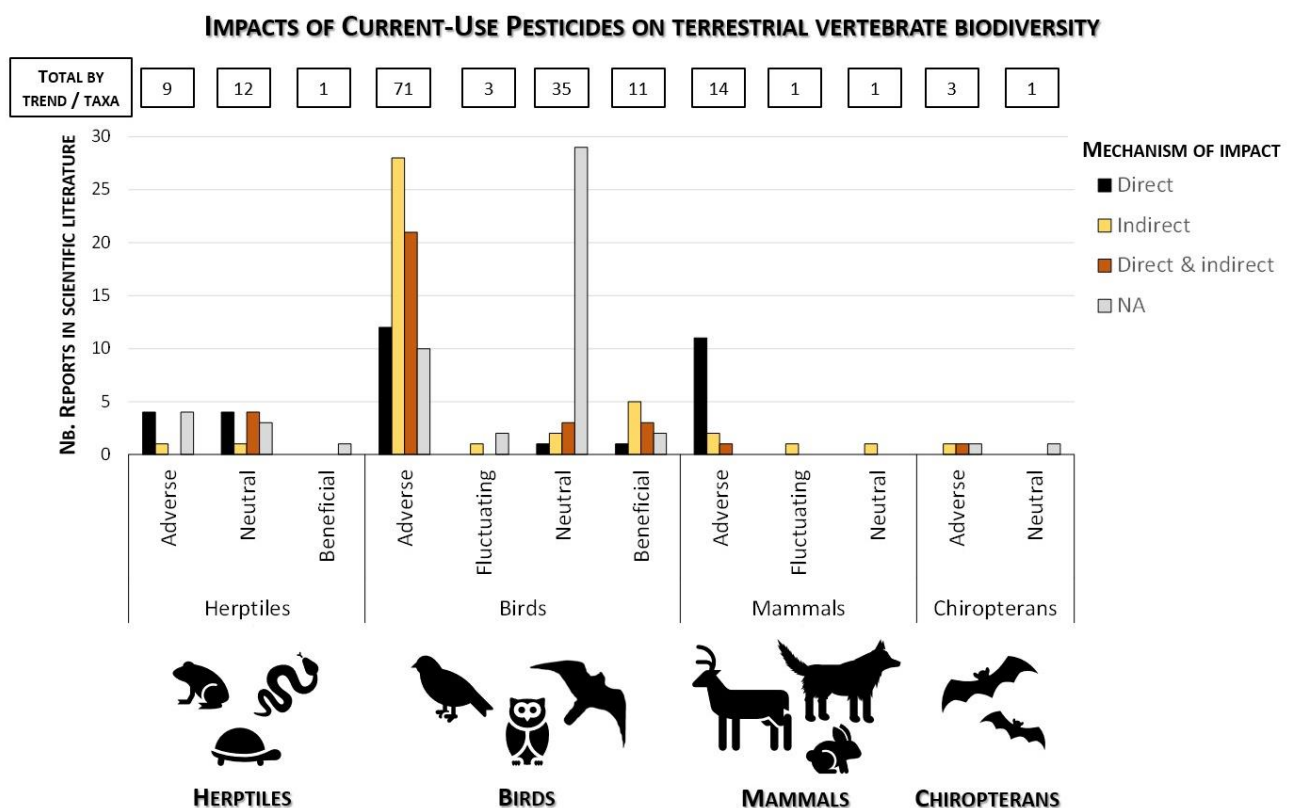
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Abstract - Agricultural practices are a major cause of the current loss of biodiversity. Among postwar agricultural intensification practices, the use of plant protection products (PPPs) might be one of the prominent drivers of the loss of wildlife diversity in agroecosystems. A collective scientific assessment was performed upon the request of the French Ministries responsible for the Environment, for Agriculture and for Research to review the impacts of PPPs on biodiversity and ecosystem services based on the scientific literature. While the effects of legacy banned PPPs on ecosystems and the underlying mechanisms are well documented, the impacts of current use pesticides (CUPs) on biodiversity have rarely been reviewed. Here, we provide an overview of the available knowledge related to the impacts of PPPs, including biopesticides, on terrestrial vertebrates (i.e., herptiles, birds including raptors, bats, and small and large mammals). We focused essentially on CUPs and on endpoints at the subindividual, individual, population and community levels, which ultimately linked with effects on biodiversity. We address both direct toxic effects and indirect effects related to ecological processes and review the existing knowledge about wildlife exposure to PPPs. The effects of PPPs on ecological functions and ecosystem services are discussed, as are the aggravating or mitigating factors. Finally, a synthesis of knowns and unknowns is provided, and we identify priorities to fill gaps in knowledge and perspectives for research and wildlife conservation.



Abbreviations used

AI(s): active ingredient(s)

ANSES: French Agency for Food, Environmental and Occupational Health & Safety

Bt: bacterium *Bacillus thuringiensis* (genetically-modified crops producing insecticides originating from *Bt* or direct use of the toxin)

CF: conventional farming

CII(s): cholinesterase-inhibiting insecticide(s)

CUP(s): currently used pesticide(s), current use pesticide(s)

DDE: dichlorodiphenyldichloroethylene

DDT: dichlorodiphenyltrichloroethane

EFSA: European Food Safety Authority

ERA: environmental risk assessment

GBH(s): glyphosate-based herbicide(s)

GLY: glyphosate

GMO(s): genetically modified organism(s)

IPBES: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IUCN: International Union for the Conservation of Nature

LD50: median lethal dose

NN(s): neonicotinoid(s)

NOAEL: no observed adverse effect level

OC(s): organochlorine(s)

OF: organic farming

OP(s): organophosphorus pesticide(s)

POP(s): persistent organic pollutant(s)

PPP(s): plant protection product(s)

SDHI: Succinate deshydrogenase inhibitor

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I. INTRODUCTION

The "history" of the unintended effects of pesticides (i.e., Plant Protection Products, PPPs hereafter) on terrestrial vertebrates began as early as the 1940s, immediately following the advent of synthetic PPPs and their growing use in the field (Rattner 2009). The adverse side effects of PPPs on wildlife were brought to light in the 1960s with Rachel Carson's book "Silent Spring" (Carson 1962). This seminal book was one of the first to report the dramatic decline in bird populations due to organochlorine insecticides (OCs hereafter) and alerted the public to the unintentional critical impacts of toxic chemicals on wildlife. Extensive studies carried out to understand this phenomenon have provided knowledge and conceptual models of PPP (and of other contaminants) transfer, exposure and effects that have paved the way for decades of research in the field of wildlife ecotoxicology and major regulatory developments. Examples include the phenomenon of biomagnification in food webs and some of its causes related to the physico-chemical properties of active ingredients (AIs hereafter), i.e., persistence and lipophilicity, or the consideration of changes in biological scales in the understanding of effects, from the inhibition of a calcium ATPase to the decline of populations (Rattner 2009). Subsequently, numerous studies have monitored the accumulation and effects of PPPs on wildlife and have shown that other families of AIs can induce mass mortalities in birds and mammals, mostly without assessing population consequences. All of these findings have led to the ban of the most persistent and/or acutely toxic substances that had the greatest impact on the environment and biota. One of the consequences of these bans is the reduction in mass mortality of nontarget vertebrates in some countries, even if certain insecticides (such as cholinesterase inhibiting insecticides, CIIIs hereafter) and diverted and illegal uses remain among the main threats, particularly for species with high conservation status (e.g., Plaza et al. 2019). Despite this evolution in regulation, several PPPs, such as neonicotinoids (NNs hereafter) and anticoagulant rodenticides, continue to cause massive poisoning of birds and nontarget mammals (Coourdassier et al. 2014; Millot et al. 2017). These PPPs were recently banned in some countries but remain widely authorised worldwide. Therefore, the paradigm has partly changed due to the less visible unintended adverse impacts of the currently used pesticides (CUPs as defined in Fritsch et al. 2022) in many countries. The scientific community has recommended better assessing their sublethal effects on wildlife as well as their indirect effects and consequences on populations, communities and ecosystem functioning (Albers et al. 2000; Köhler and Triebkorn 2013). The recent *Global Assessment Report on Biodiversity and Ecosystem Services* issued by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2019) lists pollution as one of the five direct drivers that has the greatest impact on biodiversity at the global scale (biodiversity can be defined as "*the variety of life on Earth at all its levels, from genes to ecosystems, and can encompass the evolutionary, ecological, and cultural processes that sustain life*"). Pollution is now recognised as a major threat to biodiversity conservation (Bonebrake et al. 2019). Anthropogenic chemicals have been identified as characteristics of changes in geochemical signatures that distinguish the Anthropocene from the Holocene (Waters et al. 2016) and as agents

of global change (Bernhardt et al. 2017). A growing body of research highlights the role of chemical pollution as one of the pressures affecting ecosystem health and altering the functioning of ecological processes and as a driver of biodiversity loss (Bernhardt et al. 2017; Groh et al. 2022; Persson et al. 2022). Synthetic PPPs are included in such categories of anthropogenic chemicals together with other chemicals (e.g., pharmaceuticals, biocides, surfactants), which are highlighted as threats to ecosystem health and biodiversity.

Agriculture has also been shown to be one of the prominent drivers of current biodiversity loss (Brussaard et al. 2010; Godfray et al. 2010; Maxwell et al. 2016). Postwar agricultural intensification practices decrease landscape diversity and connectivity, cause the loss of seminatural areas (e.g., woodlands, hedgerows, grasslands) and change crop management, resulting in a loss of biological diversity and leading to a decline in ecological functions and ecosystem services (Benton et al. 2003; Firbank et al. 2008; Power 2010; Robinson and Sutherland 2002; Tschardt et al. 2012). Much has been written about the impacts of land use and landscape changes in modern agriculture on biodiversity and about the different pressures caused by “intensive” agriculture affecting ecological processes (Krebs et al. 1999). Accumulating evidence now emphasises the prominent role of PPPs in the impacts of agricultural intensification on biodiversity. Recently, Dudley et al. (2017) stated that *“Continued biodiversity loss has been linked more generally to resource-intensive models of development and consumption, invasive species, nitrogen pollution, and climate change (Butchart et al. 2010); where agriculture is highlighted the focus tends to be on land use change and general intensification (Maxwell et al. 2016). While recognizing the critical importance of all these factors, we argue that the role of pesticides in driving biodiversity loss also deserves renewed emphasis, quantification and amelioration.”* In their pan-European study, Geiger and coworkers (2010) disentangled the impacts of 13 components of intensification on the diversity of wild plants, beetles and birds, showing that insecticides and fungicides were responsible for negative effects on biodiversity and biological control potential. Sánchez-Bayo and Wyckhuys (2019) highlighted that environmental pollution, especially by PPPs, was the second most important factor threatening worldwide insect biodiversity. In North America, Stanton et al. (2018) reported that PPPs were the predominant agricultural factor inducing farmland bird decline and had the most consistent negative effects. Recently, PPPs and fertilisers have been shown to be prominent factors responsible for the decline of bird populations in Europe (Rigal et al. 2023). Brühl and Zaller (2019) justified why they considered *“Biodiversity decline [in agrosystems] as a consequence of an inappropriate environmental risk assessment of pesticides”* based on the most recent literature about widespread environmental contamination by PPPs, their toxic effects, and lowered diversity and abundance of wild plants, ground beetles, pollinators and wildlife. Topping et al. (2020) also proposed recommendations to reshape environmental risk assessment (ERA) for PPPs to limit their negative impacts on biodiversity. Based on a modelling approach applied to global PPP application data and considering no-effect concentrations, Tang et al. (2021) reported that 64% of arable land worldwide is at risk of pollution by at least one PPP, which represents 24.5 million km² (Tang et al. 2021). A

high risk of PPP pollution was found in more than 31% of the global agricultural areas, among which 34% were located in high-biodiversity regions. These alarming trends are unlikely to rapidly reverse: the predictions to meet the demand in agricultural production to feed 11 billion people by 2100 in the context of climate change estimated the need to replace 7% of the global land area of natural ecosystems by cropland, resulting in an anticipated 10-fold increase in PPP use (Rohr et al. 2019).

When the use of PPPs is reviewed as a driver of biodiversity loss among the other components of agricultural intensification, PPPs are considered globally, being merged as a global category of pest-targeted compounds that thus comprise hundreds banned compounds and CUPs. Only limited distinctions between their type of use, chemical properties, modes of action, or regulatory status are provided; the focus is limited to a few compounds, such as NNs (Dudley et al. 2017; van der Sluijs et al. 2015). Currently, agrochemical practices are based on more than 500 AIs belonging to more than 100 classes with different modes of action (Bernhardt et al. 2017; Zhang et al. 2011). Hundreds of compounds spread in the environment, resulting in the exposure of wildlife to complex mixtures that could interact to induce ecotoxicological effects (Scholz et al. 2022). For terrestrial vertebrates, when the impacts of PPPs are mentioned in the literature, most illustrative examples address “historic”, legacy AIs that are no longer authorised as PPPs in many countries worldwide (e.g., OCs, some organophosphates OPs, atrazine, etc.) or NNs (which are currently withdrawn in Europe and under strengthening regulation in many other countries) (e.g., Gibbons et al. 2015; Köhler and Triebkorn 2013; Rattner 2009). Research in wildlife conservation has focused on global crucial issues other than PPPs in the last decades, likely because the ban of the most persistent, bioaccumulative and toxic substances and enforced regulation of PPPs strengthening risk assessment procedures have made severe unintentional effects of PPPs thought to be resolved or unlikely (Brühl and Zaller 2019; Dudley et al. 2017).

In France, a collective scientific assessment commissioned by the three Ministries responsible for the Environment, for Agriculture and for Research (i.e., Ministry of Ecological Transition, Ministry of Agriculture and Food, Ministry of Higher Education, Research and Innovation) was carried out in 2020-2022 to analyse the scientific knowledge relating to the impacts of PPPs on biodiversity and ecosystem services (Pesce et al. 2021). Biodiversity was considered both structurally (including taxonomic diversity and intraspecific genetic diversity) and functionally (Pesce et al. 2021). Among the main questions, the role of PPPs in the loss of biodiversity (i.e., loss of richness and/or abundance at the population and community levels and in biological and ecological functions) and the actual state of knowledge about environmental contamination and the exposure to and effects of PPPs in biota were addressed. The present article is a deliverable of the abovementioned collective scientific assessment. This review aimed to overcome the lack of synthesis about the impacts of PPPs on terrestrial wildlife and the ecosystem services they provide, highlighting both lines of evidence and major gaps in knowledge with special attention given to CUPs.

Based on the state of the science since 2000, the main objectives of the present review are as follows:

(i) To identify the AIs, types or families of PPPs for which effects on wildlife are proven, suspected or null. We mainly focus on impacts reported on populations or communities because they are directly indicative of ecological responses (i.e., the level of interest of ERA and are often more relevant from a management perspective) (Barnthouse et al. 2019). Moreover, they are generally studied *in natura* (i.e., under realistic conditions of PPP use). The responses of individuals are also reviewed even if numerous results are obtained under controlled conditions. We considered those responses measured on life-history traits, such as survival or breeding performance, because they are related to population dynamics (Albers et al. 2000). To a lesser extent, other individual (e.g., behaviour) or subindividual responses (e.g., endocrine disruption) were summarised because they are evidence of effects;

(ii) To describe the exposure of the different groups of terrestrial wildlife, focusing on compounds for which exposure is evidenced but knowledge on effects is lacking;

(iii) To identify the main mechanisms, both direct (i.e., toxicity) and indirect (i.e., ecological interactions), that induce the effects (Albers et al. 2000) and their main drivers (e.g., agronomic, ecological); and

(iv) To assess the impact of PPPs on ecological functions and the ecosystem services provided by terrestrial vertebrates.

Depending on the robustness of the knowledge or the gaps highlighted, this assessment will make it possible to propose action levers (e.g., ranking of the authorised PPPs with the greatest impact on wildlife, changes in ERA) and lines of research for the coming years.

II. MATERIALS AND METHODS

II.1. Review scope and approach

The general process corresponds to the conduct of a systematic review (*sensus* Grant and Booth 2009). The bibliographic queries were initially made on the basis of keywords common to all the working groups of the collective scientific assessment (i.e., PPP categories, ecotoxicology) and keywords specific to each working group, i.e., terrestrial vertebrates, in the present review. To obtain a more targeted corpus, exclusion terms were defined to exclude studies carried out on aquatic species (e.g., fish or marine mammals) or toxicological studies carried out on animals used mainly as experimental laboratory models (rat, mouse, hen, quail, rabbit) and often working with unrealistic doses with regards to environmental exposure or *in vitro* studies carried out on cell or tissue lines and, ultimately, contaminants other than PPPs. Other keywords, such as "human", "antibacterial", "antimicrobial", and "xenobiotic", were also excluded because they generated significant background

noise unrelated to this review. The final list of used and excluded keywords and the final queries are presented in the supplementary material. These keywords were searched in the title, abstract and keywords of the articles. The queries were performed via the Web of Science on 18/12/2020, including only articles published from 01/01/2000 onwards. An initial corpus of 4,027 references was obtained. A description of this initial corpus, such as the scientific area of publication or the number of articles per year, is presented in Text S11 in the supplementary information.

II.2. Selection and description of the final corpus

First, this initial corpus of 4,027 references was shared between the members of the working group so that each one handled a temporally homogeneous sample of 1,006 or 1,007 articles. A selection was then made by expert opinion to include only those articles deemed relevant on the basis of their title and abstract (and full text when needed). This screening step resulted in the selection of a consolidated corpus of 1,154 articles in total.

In the second phase, each article of this corpus was described using the following information: taxonomic group/species, type of PPP/chemical family/substance, type of methodological approach (i.e., field, lab, modelling), study dose (environmental/agronomic/high), type of response (exposure/effect, individual/population), type and mechanism of effect (mortality/sublethal, direct/indirect), and type of reference (i.e., article/review). The results of the descriptive analysis of this consolidated corpus are presented in section III. 1. "Global analysis of available literature". Finally, each article was ranked according to a reading priority ordered from 1 to 7 and defined as follows:

- Priority 1: Field experimental or correlative studies, studies based on experimental designs in the field or in the laboratory measuring effects at environmentally realistic doses, and literature reviews (excluding OCs);
- Priority 2: Field or design-based studies measuring exposure/accumulation at environmentally realistic doses (excluding OCs);
- Priority 3: Experimental laboratory studies measuring individual effects on life history traits, microbiota, behaviour or transgenerational effects;
- Priority 4: Experimental laboratory studies measuring subindividual effects;
- Priority 5: OCs and other PPPs banned from use in Europe before 2000;
- Priority 6: Studies on alternatives to PPPs;
- Priority 7: Control of alien or invasive species.

The present review is based mainly on articles classified as priority 1 to 4, with few other articles being retained if necessary for a specific point. We focused on studies working with environmentally relevant doses (e.g., recommended application rate as an exposure dose in laboratory studies or studies *in natura* in agrosystems) when available and focused on the parts of the results that correspond to environmentally relevant doses in studies that included high doses. The final corpus used was also completed by articles that were not included in the initial corpus of 4,027 articles but

that the experts identified as relevant (nonreferenced scientific reports, theses, etc.). We have added some relevant references published between 2021 and 2023 and identified them on the basis of the same queries as above.

II.3. Overall analysis of the effects of PPPs on terrestrial vertebrate biodiversity

To conduct this systematic review, a final selection was carried out in the corpus of 1,154 references. First, reviews were excluded to avoid redundancy with original publications in this particular quantitative analysis (i.e., contrary to the other sections of the review where they were included). Articles based solely on modelling approaches were not used in this specific analysis. For the articles with priorities of 1 to 3, only the studies focusing on responses related to ecological levels of organisation (i.e., on reproduction, demography, population dynamics, communities or ecological functions; see below), which are more directly linked to impacts on biodiversity than subindividual effects measured alone, were considered. Studies dealing with exposure/accumulation only or subindividual effects were excluded. The following responses were included in this corpus sorting:

- Abundance (i.e., number of individuals) and equivalent measurements (other units or proxies, e.g., density, activity for chiropterans, etc.),
- Species richness (i.e., number of species), and diversity (i.e., diversity indices),
- Temporal or spatial trends (e.g., range, population decline) and dynamics (e.g., population dynamics parameters such as population growth rate),
- Population structure (e.g., *sex ratio*, age structure),
- Survival rates (i.e., mortality events not explicitly related to population size or impact on population dynamics have not been considered here),
- Reproductive success (e.g., number of young, reproductive parameters that can be linked to population dynamics).

For each of the articles meeting these criteria, the following additional information was collected:

- Type of use of the studied PPPs (e.g., fungicide, herbicide, insecticide);
- Chemical families of the studied PPPs (e.g., NNs, OPs, triazoles);
- Taxonomic group studied (e.g., amphibians/reptiles, birds, mammals);
- Trend categories of the measured effect (i.e., adverse effect of PPPs, beneficial effect, fluctuating effect, neutral corresponding to no significant effect);
- Mechanism of effect: direct or indirect (e.g., direct toxic effect or indirect effect on trophic resources or habitat).

In studies where several species and/or several response endpoints were studied, the article was subjected to several entries to account for the different categories of effect. Overall, this analysis was conducted on a total of 79 bibliographic references, corresponding to a total of 162 effect reports. This approach is presented in section III. 1. "Global analysis of the available literature".

III. RESULTS

III.1. Global analyses of the available literature

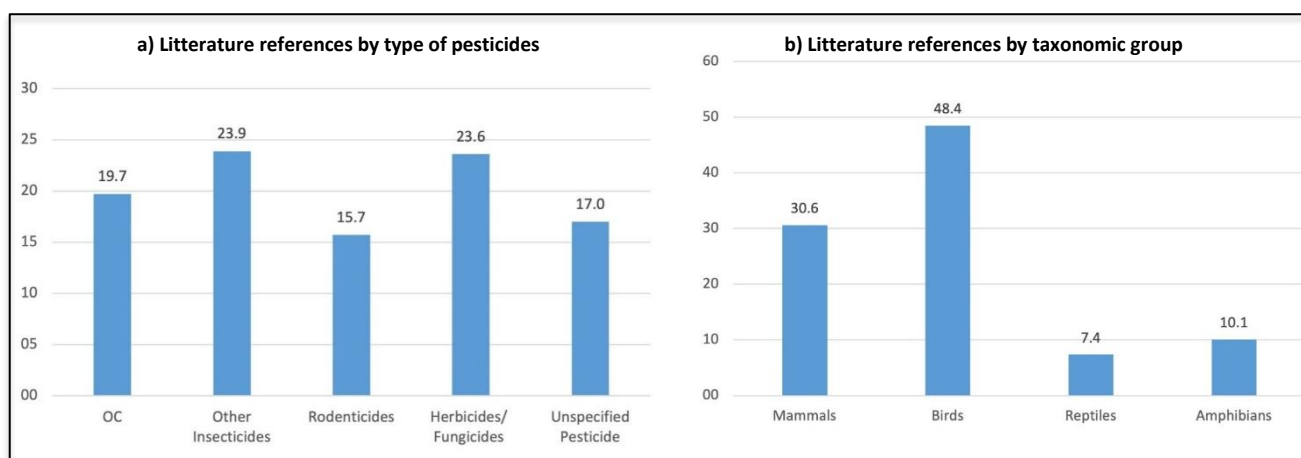
Based on the expertise of the working group and an analysis of the final corpus, it was found that the ecological and biological features (diet, physiology, habitats, etc.) of the various taxa and/or guilds resulted in situations that may differ from an ecotoxicological point of view (e.g., pathways of exposure, metabolism rate). Thus, below, we decided to distinguish six taxonomic and/or ecological groups: birds other than raptors, raptors, mammals other than chiropterans, bats and/or nonflying insectivorous small mammals, which are sometimes covered in dedicated parts of the text, reptiles and amphibians (terrestrial stages only).

III.1.1. Available data

The 1,154 articles selected included laboratory studies, field studies and correlative analyses between PPP use and wildlife (exposure, effects). The figures below give an overview of the respective share of studies for each taxonomic group as well as on the PPPs studied.

The available literature on “terrestrial vertebrates”, “pesticides” and “biodiversity” has obvious pitfalls and, consequently, questions that could not be answered in this scientific review. More than 40% of the papers dealt with insecticides, while herbicides and fungicides (which represent the vast majority of PPPs used, both in terms of total amount and frequency of use), are rarely studied (< 25% of the papers) (Fig. 1a). Finally, a large body of references still focuses on OCs and anticoagulant rodenticides, many of which have been banned for agricultural use in many countries.

Figure 1 Distribution of literature references (a) by pesticide type and (b) by taxonomic group (% of 1154 articles from 2000 to 2021) (OC organochlorine insecticide)



Among terrestrial vertebrates, birds have been most extensively studied and represent almost 50% of the literature. Mammals follow next. The terrestrial stages of amphibians or reptiles account for only 17% of the literature (Fig. 1b).

The bibliography also does not reflect the varying biological diversity or sensitivity of species.

Obviously, the species studied are largely influenced by the large number of studies focused on OCs (these studies were still largely present during the initial years of our study period from 2000 to 2005), their effects on birds (including continental and marine top predators), and recent rodenticide studies in raptors and mammals. The structural and functional components of biodiversity are rarely considered in studies conducted on terrestrial vertebrates.

Few available resources focus on effects at the population, community or ecosystem levels. However, these effects are sometimes analysed using mathematical models. In terms of the type of effects, direct effects have long represented the vast majority of studies (> 90% in the corpus analysed). The articles also mention potential indirect effects (mainly trophic effects via the reduction of food resources for predators), which are recognised as important issues in terms of the ecological impacts of toxicants (Rattner et al. 2023) but often without factual demonstration. Generally, the demonstration of a causal relationship is rarely made apart from experimental studies on laboratory species, whereas numerous data describing exposure (measurements characterising environmental contamination or accumulation via measurements of residues in tissues) are available, at least for insecticides and rodenticides. A few *in situ* studies, nevertheless, linked exposure to individual or infra-individual effects to reproductive parameters.

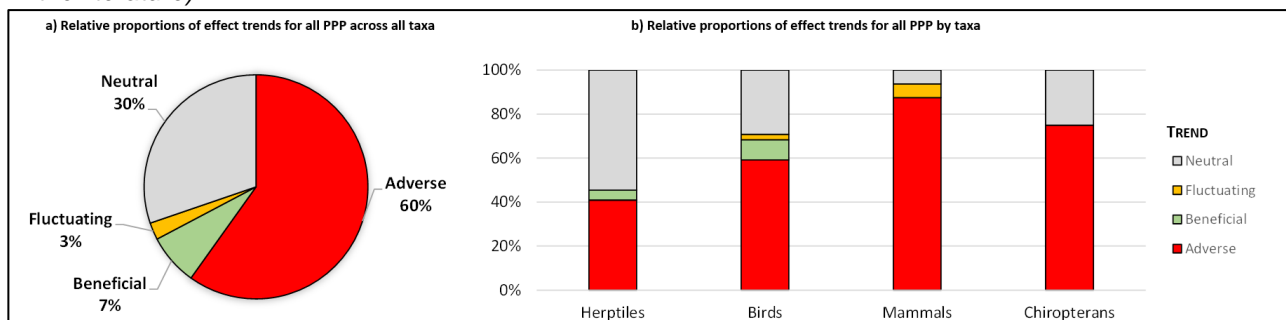
A critical analysis of the references indicates a lack of experimental data on wildlife (except for toxicological data on laboratory rodents) compared with other terrestrial or aquatic taxonomic groups and as noted by others (Kattwinkel et al. 2015). This is likely due to:

- limited regulatory requirements (less than for aquatic ecosystems)
- studies involving terrestrial vertebrates require more space, time and equipment than studies on invertebrates, plants or microorganisms. This is related to longer life cycles and more complex spatial requirements, which increase the complexity of field testing.
- compliance with animal welfare regulations, which means that animal use is reduced, refined or replaced and that experiments on vertebrates require specific authorisations.

III.1.2. General overview of the effects of PPPs on biodiversity

The overall analysis across taxa and PPP uses showed predominantly adverse effects on biodiversity in 60% of cases (Fig. 2a).

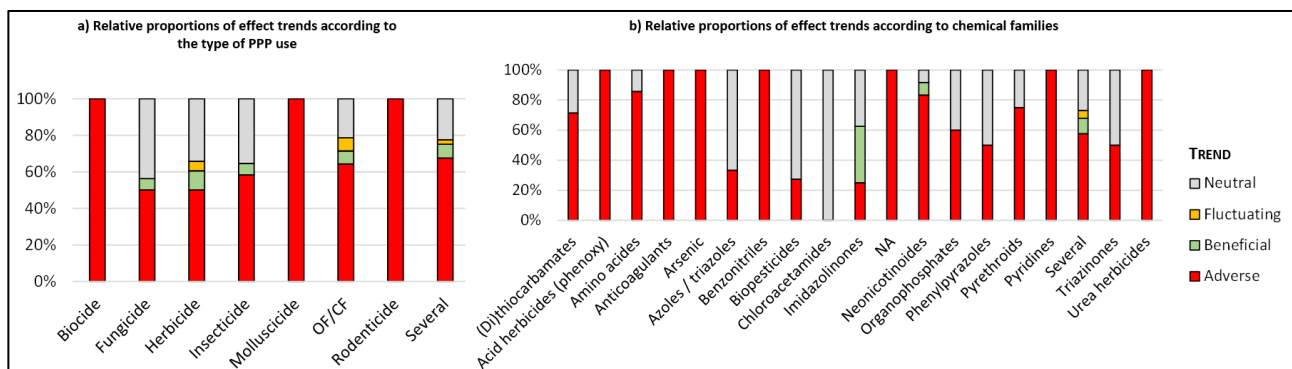
Figure 2 Relative proportions of effect trends for all pesticides (a) across all taxa, and (b) by taxa (% reports in the literature)



No significant effects were reported in 30% of cases, while positive and fluctuating effects accounted for 7% and 3%, respectively. Considering the different taxa separately, the effects mostly remain adverse, and a minority are favourable. Beneficial or neutral effects are reported mainly for amphibians/reptiles and birds (Fig. 2b).

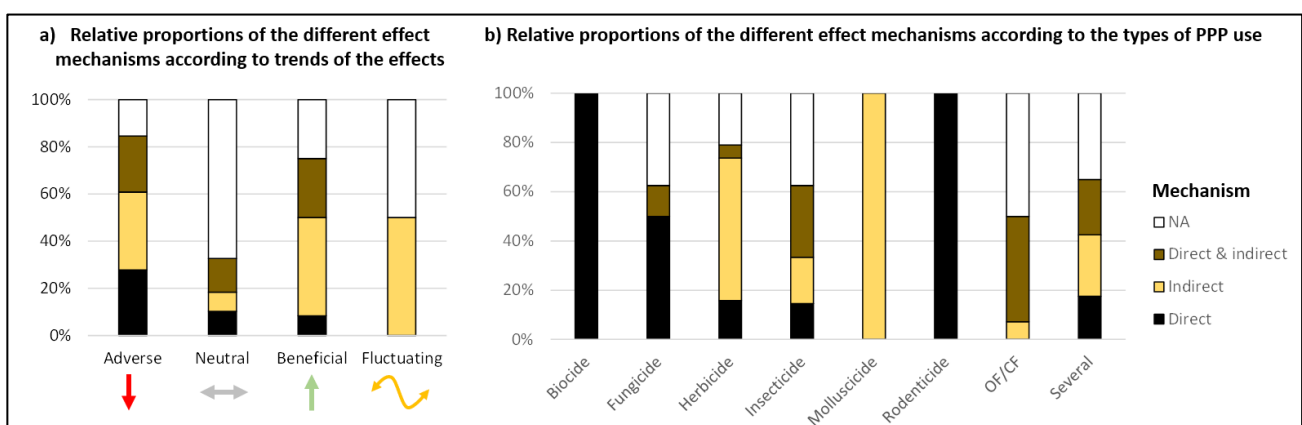
Adverse effects on biodiversity represented the majority of occurrences, regardless of the type of PPP use (Fig. 3a). Neutral and favourable effects are reported for fungicides, herbicides, insecticides, several concomitant uses and in studies comparing organic farming (OF) and conventional farming (CF) production systems. Only adverse effects are reported in works on molluscicide and rodenticide use. Adverse effects are more common for most chemical families except for azoles/triazoles, biopesticides, chloroacetamides, and imidazolines, for which neutral effects are mostly reported (Fig. 3b). This overview shows that negative effects are reported for the different uses and chemical families (with the exception of chloroacetamides) and that adverse effects are predominant.

Figure 3 Relative proportions of effect trends according to (a) the type of pesticide use (OF organic farming, CF conventional farming) and (b) chemical families (% reports in the literature)



The type of mechanism involved in the responses, direct or indirect, was not specified in many of the studies (Fig. 4). Excluding these studies where the mechanism was not addressed, indirect and joint direct and indirect effects accounted for the majority of the processes involved in biodiversity responses (Fig. 4a).

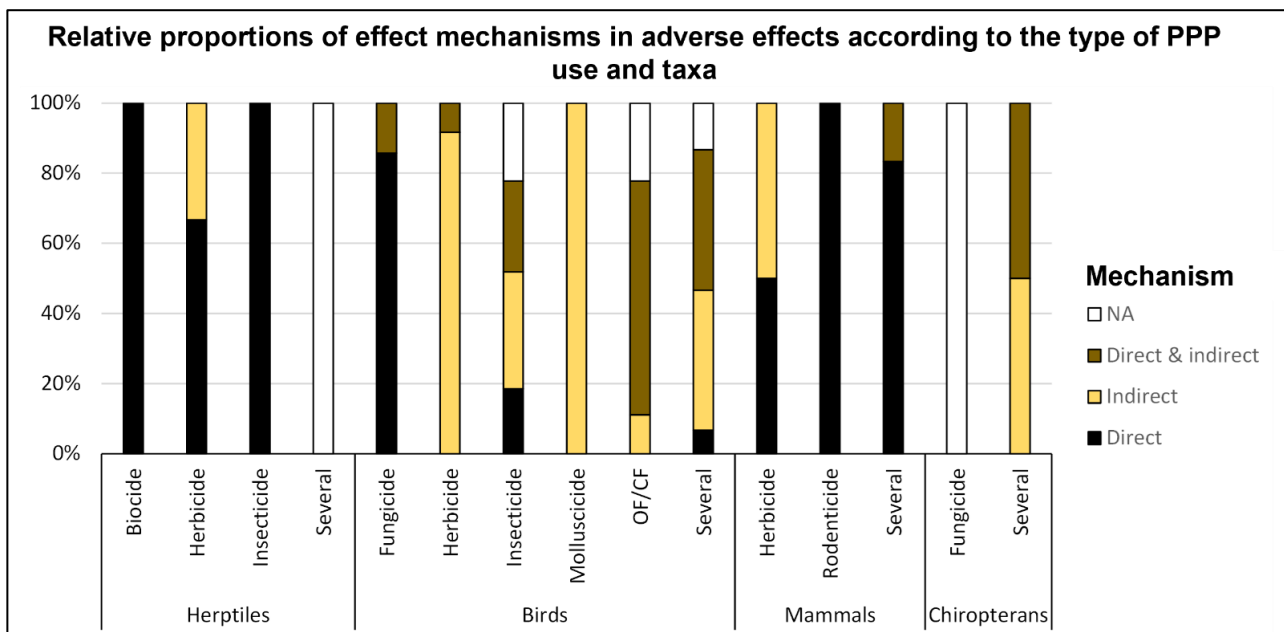
Figure 4 Relative proportions of effect mechanisms according to (a) the trends of the effects, and (b) the types of pesticide use (OF organic farming, CF conventional farming) (% reports in the literature)



Direct, indirect and both processes are involved in adverse, beneficial and neutral effects, while in the 'fluctuating' category, direct effects are not involved (Fig. 4a). Both direct and indirect effects are reported for the majority of the types of uses (Fig. 4b). Rodenticides and biocides are associated with direct effects only. Fungicides are related to direct or joint direct and indirect effects but not to indirect effects alone. Conversely, molluscicides are associated only with indirect effects. In general, both direct and indirect mechanisms are involved in the adverse effects of the different types of PPP use. Similarly, considering the various chemical families, both types of mechanisms are reported alone or together (data not shown).

Considering the negative impacts only, direct and indirect effects are reported for the different taxa and for the different types of use (Fig. 5). The proportion of direct effects seems to be predominant in herptiles (i.e., amphibians and reptiles) compared to other taxa and for mammals because of the effects of rodenticides. In birds, the most studied taxa group, both direct and indirect processes are involved for fungicides, herbicides, insecticides, and several use patterns. The part of indirect effects is generally as large or larger than the proportion of direct mechanisms. The situations where direct and indirect effects are combined represent the majority of cases and reach high relative proportions (almost 70%) of the mechanisms mentioned. This is the case, for instance, in system comparisons between responses in CF with PPP use and those in OF without synthetic PPP use.

Figure 5 Relative proportions of effect mechanisms, for adverse effects, according to the type of pesticide use and taxa (% reports in the literature)



III.2. Effects of PPPs on terrestrial wildlife

III.2.1. Effects on populations and communities

Numerous studies have reported population declines in insectivorous, granivorous and/or carnivorous vertebrates. Agriculture and pollution are often mentioned among the main causes, but PPPs are clearly identified in only a few cases (e.g., vultures). Most of the studies conducted to assess the effects on populations or communities compare agricultural management practices globally (e.g., CF *versus* OF) or use correlative approaches relating population densities or trends and treatment intensity, often over a large spatial scale and/or even temporal scale. In some cases, PPP quantities are estimated (sale trends or national tonnage used), which limits the possibility of inferring observed responses. These works do not always consider confounding factors (climate, landscape, agricultural practices) that can influence trends and abundances. Overall, these methodologies rarely make it possible to disentangle the contributions of all other agri-environmental factors and of PPP pressure, making it difficult to identify the mechanisms responsible for the measured responses.

Birds other than raptors

The literature indicates a general decline in farmland birds, especially passerines, in Europe and North America (Stanton et al. 2018; Bowler et al. 2019; Rosenberg et al. 2019; Fontaine et al. 2020; Reif and Hanzelka 2020; Rigal et al. 2023). Some species, especially generalists, showed stable or increasing trends. A common characteristic shared by almost all declining species is a diet that includes insects, not only strict insectivores but also numerous other species preying on insects in spring for nestling rearing. Strict insectivores and some ground-nesting species (both granivorous and insectivorous) show the greatest declines in field crops and grasslands (Stanton et al. 2018; Li et al. 2020; Bowler et al. 2019; Rigal et al. 2023). Among farmland birds, seedeaters are also reported to be exhibiting strong declines (Bowler et al. 2019; Rigal et al. 2023; Bright et al. 2008).

From a general perspective, bird population declines need to be considered in a broader context, including land use changes (e.g., urbanisation and agricultural intensification), landscape homogenisation, direct causes of mortality induced by anthropogenic activities (e.g., collision, predation by domestic cats), and climate change (Stanton et al. 2018; Spiller and Dettmers 2019; Brain and Anderson 2019; Rigal et al. 2023). The role of postwar changes in agricultural practices in such biodiversity loss is well recognised. Some works have focused on distinguishing the contribution of PPPs from the role of other concomitant developments in CF (e.g., landscape homogenisation, low crop diversity, mechanisation) (Robinson and Sutherland 2002; Donald et al. 2006; Guerrero et al. 2012; Mineau and Whiteside 2013; Hill et al. 2014; Hallmann et al. 2014; Belden et al. 2018). Considering the convergence of findings, PPP use is one of the predominant factors influencing the decline in biodiversity of birds in agrosystems via direct and/or indirect effects (Fox 2004; Mineau et al. 2005; Bright et al. 2008; Gibbs et al. 2009; Mineau and Whiteside 2013;

Chiron et al. 2014; Jeliaskov et al. 2016; Stanton et al. 2018; Møller 2019). The most recent articles or reviews highlight the prominent role of CUPs in bird population decline in North America and Europe (Stanton et al. 2018; Rigal et al. 2023).

Where insecticides have been used for 30 years or are still used, particularly carbamates and NNs, large-scale correlative analyses strongly suggest the involvement of PPPs in bird population declines. In a study about the population consequences of carbofuran-induced mortality in the USA, Mineau and coworkers (2005) estimated several tens of millions of passerines likely victims of acute poisoning. Since, the potential mortality of birds by poisoning seems to have decreased, with some exceptions such as berry crops. These results are largely the consequence of regulatory changes leading to the replacement of the most toxic compounds by other insecticides with lower acute toxicity in birds (Mineau and Whiteside 2006; Bright et al. 2008). For example, in North America, bird declines in grasslands were more strongly correlated with the use of insecticides of high acute toxicity to nontarget species than with the loss of grassland habitat over the period 1990-2000 (Mineau and Whiteside 2013). Reanalyzing the data used by Mineau and Whiteside (2013), Hill and coworkers (2014) reached the opposite conclusion; i.e., habitat-related changes could more plausibly explain the decline in grassland bird populations than the acute toxicity of PPPs. Nevertheless, in this new analysis, PPP use still had a significant negative effect on grassland bird dynamics. Recent studies based on large-scale correlations between long-term monitoring of songbird abundances and estimated PPP use (all or some chemical families) (e.g., Stanton et al. 2018; Li et al. 2020; Rigal et al. 2023) have reinforced the conclusions reached by Mineau and Whiteside (2013) by revealing the influence of CUPs (especially insecticides), even if they are not the only cause shaping population dynamics (see III.6). Significant relationships have been demonstrated between the decline of breeding bird populations in the USA (2008 and 2014) and the increase in NN use, particularly for grassland and insectivorous species (Li et al. 2020). Tennekes and Zillweger (2010) hypothesised that NN contamination of surface waters could be a factor responsible for the decline in insect biomass that would drive widespread bird declines at the continental scale via a reduction in food supplies. In Europe, negative spatial and temporal correlations between the abundance of several breeding bird species and the use of NNs have been found (Hallmann et al. 2014, Lennon et al. 2019). Population declines were correlated with imidacloprid concentrations in surface waters for six (the Eurasian skylark *Alauda arvensis*, the barn swallow *Hirundo rustica*, the yellow wagtail *Motacilla flava*, the European starling *Sturnus vulgaris*, the common whitethroat *Sylvia communis*, and the mistle thrush *Turdus viscivorus*) of the 15 passerine species studied in the Netherlands (Hallmann et al. 2014). Neonicotinoid-related negative population changes were found in England for four species (the house sparrow *Passer domesticus*, the Eurasian skylark, the red-legged partridge *Alectoris rufa*, and the turtle dove *Streptopelia turtur*) out of 13 showing significant correlations over 22 species studied (Lennon et al. 2019).

In North America, the populations of 57 out of 77 (74%) farmland bird species declined between 1966 and 2013, with the most severe decline affecting aerial insectivores, followed by grassland and shrubland species (Stanton et al. 2018). A strongly concordant decrease was observed for numerous species from 1960 to 1980. The literature review of 122 studies showed that PPPs (42% of studies) followed by habitat loss and land use changes (27% of studies) were the dominant factors influencing the negative effects on agricultural birds. PPPs and mowing/harvesting consistently had the most negative effects, with 93% of the observed responses being negative for PPPs and 81% for mowing/harvesting (Stanton et al. 2018). Rigal et al. (2023) investigated whether four widespread anthropogenic pressures could be responsible for the declines in European bird populations that have been reported over the last decades. Their study was based on relationships between indicators of the four pressures and population time-series of 170 common bird species monitored over 37 years in 28 European countries at more than 20,000 sites. They reported that agricultural intensification, estimated by the mean of the uses of PPPs and fertilisers, is the main pressure negatively related to species trends; for most bird population declines and, in particular, invertebrate feeders, while the effects of the other pressures (i.e., forest cover, urbanisation, and temperature change) were more species specific. In Denmark, from 1983 to 2001, the halt in decline (10 out of 27 species) or even increase (12 out of 27 species) in the abundance of farmland birds coincided with a decrease in the use of PPPs and fertilisers and a significant increase in OF areas (Fox 2004). A negative impact of PPP use on bird abundance and diversity has been shown through controlled or semiexperimental field studies. Comparing OF and CF paired sites, Kirk et al. (2011) showed that overall bird abundance, but not richness, was greater at OF sites than at CF sites, and more species were observed for five guilds (including grassland birds) on OF sites. No guild had higher richness or abundance on CF. Compared to other factors (e.g., habitat or predation alone and all types of factors), farming practices alone best explained the total bird abundance, grassland bird richness, aerial insectivore bird richness and abundance, and ground nesting species abundance. Five of the 10 agricultural practice factors, including herbicide use, were significant and explained the total or guild abundance and/or richness. Through a risk analysis, the authors indicated that herbicide use could decrease grassland bird richness by an average of one species (35% decrease, variation from 3.4 to 2.3 species) and that OF is of conservation concern (49% increase, variation from 7.6 to 11.4 grassland species) (Kirk et al. 2011). In a related study, Kirk and Lindsay (2017) showed the importance of landscape features and diversity in land use on bird diversity. When controlling for this landscape effect in statistical analyses, PPP use (seed treatments, herbicides and number of applications) emerged as a negative driver of avian biodiversity. Kragten et al. (2008) showed that, in cereal cropland, the breeding performance of skylarks improved in OF plots but that mechanical interventions also induced a high rate of nest destruction. Other studies based on farm networks have shown that the reduction in the use of PPPs associated with crop diversification favoured several farmland bird species (Henderson et al. 2009).

In agricultural environments in England, the phenology and reproductive success of several

passerine bird populations have been monitored for several years, with regard to agricultural practices, seminatural landscape elements and the dynamics of availability of their food items (Brickle et al. 2000; Boatman et al. 2004; Morris et al. 2005; Hart et al. 2006). In general, PPPs (insecticides, fungicides, herbicides) have been associated with decreases in reproductive success (i.e., number of fledged chicks, survival of chicks) in the gray partridge *Perdix perdix*, the yellowhammer *Emberiza citrinella*, the corn bunting *Emberiza calandra*, and, to a lesser extent, in the Eurasian skylark and the barn swallow (Bright et al. 2008). Sabin and Mora (2022) highlighted that the use of NNs in the South Texas Plains Ecoregion (USA) is likely to harm the region's northern bobwhite quail (*Colinus virginianus*) populations. These authors conducted an ecological risk assessment using crop surfaces and use of NNs, computing daily intake, and using dose–response relationships and toxic endpoints from the literature. In both juvenile and adult northern bobwhites, the levels of exposure assessed were high enough to induce adverse effects on growth, reproductive success, and long-term survival, revealing that the current trend in NN application endangers the region's northern bobwhite.

In orchards surveyed during 1988–1994, adverse effects of former OCs (DDT and its metabolites) were reported on the hatching rates of two passerine birds, the Eastern bluebird (*Sialia sialis*) and the tree swallow (*Tachycineta bicolor*), in addition to a negative influence of the 35 commercial PPP formulations used in the 1990s on reproductive success (i.e., egg fertility, chick survival, breeding success) (Bishop et al. 2000). Overall, these effects induced a decrease of up to 14% in the reproductive rate (Bishop et al., 2000). Over the period from 1988 to 2018, the clutch size of eastern bluebirds was smaller in orchards, and the hatching success was 4%–5% lower than that of nonorchards, despite the ban of many insecticides in the 1990s and 2000s (Read et al. 2021). Read and coworkers (2021) suggested that this reduction in hatching success was most likely due to long-term exposure to DDT and its metabolites and its bioaccumulation in eggs rather than to other PPPs used after DDT prohibition. Bouvier et al. (2016) showed that, compared with those in OF or sustainable agricultural orchards, the *sex ratio* in young great tits *Parus major* deviated in favour of females in populations from CF orchards. In the context of PPP use in forests, herbicides (mainly glyphosate GLY) or insecticides have been studied following a single treatment on a small plot. Falcone and DeWald (2010) found no evidence of an effect of soil treatment with imidacloprid on the composition of avifauna. Several studies have been published on American sites using the before-after/control-impact (BACI) approach (Betts et al. 2013; Kroll et al. 2017; Rivers et al. 2019; Stokely et al. 2021). Overall, these studies demonstrated negative effects of PPP treatments on the abundances of some species and a reduction in the species richness of forest bird communities. In addition, a few years after the cessation of herbicide treatments, recovery was observed. These effects are mainly indirect via the loss of habitat (lower regeneration stratum) as long as herbicide pressure persists. In these studies, large areas of nonimpacted forest surrounded the local treated forest patches, which likely influenced the results, especially for species with a large home range.

Most of these studies are based on correlation analyses between population trends or bird diversity and PPP use, without demonstrating the causality at these large scales. However, recent works using epidemiological approaches (e.g., spatial and temporal correlations, meta-analyses, and biological plausibility) have allowed to gather lines of evidence on the significant role of PPPs. Moreover, their combination with *in situ* studies and experimental studies under controlled conditions identifying causal links between exposure and effects reinforces the hypothesis that CUPs are a major factor in the decline of birds in agricultural environments via direct toxic effects and/or indirect effects through the limitation of their resources.

Raptors

During the 20th century, the impact of OCs on raptor populations (Espin et al. 2016) was widely studied and was one of the first examples of the effects of PPPs on wildlife and biodiversity. Exposure of raptors occurs commonly through trophic transfer, and their vulnerability is associated with their position at the top of food webs, their scavenging habits and their long-life span (Rowe 2008; Espin et al. 2016). Currently, 52% of raptor species show declining populations worldwide, and 18% are classified as threatened (McClure et al. 2018). Agriculture is one of the main threats identified for raptors, especially through the destruction and degradation of their habitats. Pollution from all sources and types is reported to affect 25% of threatened species, including 100% of Eurasian and African vultures, but the contribution of PPPs to recent trends has not been accurately assessed (McClure et al. 2018).

Overall, since 2000 research mostly focused on three groups of PPPs: CIIIs, anticoagulant rodenticides and OCs, each of which involve specific contexts of use that have led to effects on raptors. For CIIIs, all the available publications refer to the illegal use of AIs which are most often banned as PPPs in many countries (e.g., carbofuran, aldicarb or mevinphos) and are introduced into meat baits distributed in the wild to kill vertebrate carnivores. These illegal uses occur on all continents. Two main families of rodenticides can be used to control rodents in agrosystems: compounds with anticoagulant properties, i.e., derivatives of 4-hydroxy-coumarin and 1,3-dione; and inorganic compounds such as zinc phosphide. Anticoagulants are prohibited as PPPs but still authorized as biocides in many countries around the world. The large-scale application of anticoagulants has been responsible for numerous events involving secondary poisoning of raptors, which are well documented in the scientific literature. Finally, all OCs have been progressively banned for agricultural use in many countries worldwide. Thus, the majority of studies carried out since 2000 relate to the accumulation and effects due to past uses of these persistent compounds and their derivatives. Finally, no study has measured the effects of CUPs on raptor populations, either under authorised or unauthorised conditions of use.

Through their illegal use, CIIIs affect 18 species of vultures among the 23 existing in the world, but their contribution to population decline has not yet been quantified (Plaza et al. 2019). Only three studies, all on the red kite *Milvus milvus*, have estimated the effects of these intended poisoning on populations. Based on correlative or modelling approaches, CII illegal use is estimated to be

responsible for population declines of 31-43% over 20 years in Spain (Mateo-Tomas et al. 2020) and 20% on the Spanish island of Majorca (Tenan et al. 2012). In populations in Scotland, the total illegal destruction of kites, mostly due to deliberate poisoning by CIIIs, causes decreases in survival rates ranging from 0.03 to 0.17 depending on the age class considered. A projection carried out with a population dynamics model suggested that this additional mortality resulted in a 0.14 decrease in the population growth coefficient, which jeopardised conservation efforts for red kites in some regions (Smart et al. 2010). These banned PPPs continue to pose a threat to raptors worldwide (Berny et al. 2015; Plaza et al. 2019; Kitowski et al. 2021).

In the case of anticoagulant rodenticides, no specific study has examined their impact on populations despite the numerous episodes of mortality reported (see section III.2.2.). In Spain, the rodenticide campaigns carried out in open fields between 2004 and 2008 in Castilla y León would have led to declines varying between 27 and 42% in the number of breeding pairs of red kites depending on the intensity of the treatments (Mougeot et al. 2011). On a more local scale in Central France, the intensive use of bromadiolone is suspected to have caused a decline of nearly 50% in the breeding population (Coourdassier et al. 2014a). In both cases, these estimates are based on field observations without considering other possible causes of variation, which makes it difficult to draw robust conclusions. A study conducted on the Réunion harrier *Circus maillardi*, a raptor endemic to Réunion Island, showed that anticoagulant rodenticides were one of the main threats to the viability of the population (Coourdassier et al. 2019). In island contexts, the application of rodenticides (anticoagulants and others) to control introduced rodents has also been responsible for declines, mostly temporary, in populations of some native birds and mammals (Howald et al. 2015; Hindmarch and Elliott 2018).

While the population responses of raptors exposed to OCs (e.g., DDT and cyclodienes), including decline and resilience, are among the most documented responses of wildlife during the period 1950–2000, the effects of these PPPs on their populations or communities have not been subsequently assessed. Since 2000, the majority of studies on OCs have monitored residues in raptor populations, particularly in the Northern Hemisphere. Potential effects on populations or individual life traits (survival, reproductive success) have rarely been assessed but most often discussed on the basis of comparisons between measured concentrations and toxicological reference concentrations. While lethal poisoning by chlordane, cyclodienes and derivatives was reported in the USA in the early 2000s (Okoniewski et al. 2006), overall levels of OC accumulation have tended to decrease for several decades in many parts of the world, including Europe (Helander et al. 2008; Newton 2013; Gomez-Ramirez et al. 2014; Gomez-Ramirez et al. 2019; Sun et al. 2020). However, in some countries, such as Argentina, where these PPPs are still used, recent studies have shown that the plumage concentrations of OCs are much greater than those measured in European or Asian raptors (Martinez-Lopez et al. 2015). Overall, DDE is detected most frequently (often in 50-100% of individuals analysed) and at the highest concentrations compared to DDT and other OCs and their derivatives (van Drooge et al. 2008; Berny et al. 2015; Sun et al. 2020). While

accumulation levels measured in most regions of the world are below toxic thresholds (e.g., Scharenberg and Struwe-Juhl 2006; Berny et al. 2015), DDE concentrations compatible with reproductive disturbance have been measured in several raptor species in Spain (Martinez-Lopez et al. 2007; Garcia-Fernandez et al. 2008; Gomez-Ramirez et al. 2012).

Mammals other than chiropterans

The population effects of CUPs have rarely been studied on mammals; therefore, little evidence has been found overall. In France, the relative densities of red foxes *Vulpes vulpes* were negatively correlated with the intensity of treatment with bromadiolone, an anticoagulant rodenticide applied in agricultural use (Jacquot et al. 2013). The most heavily treated area had densities close to 0 foxes per km² over 120 km² and < 0.5 foxes per km² over 1000 km² in the year following the treatments; direct poisoning most likely explained the effects observed. Impacted fox populations require at least 2 years to recover densities close to those of other areas of the department. In the same context, Fernandez-de-Simon et al. (2018) suggest that bromadiolone treatments may lead to seasonal small mustelid declines.

Chiropterans and non-flying insectivorous small mammals

Populations of chiropterans dramatically declined during the second half of the 21st century, and despite somewhat reassuring trends regarding the status of European populations, many species are still endangered (Zhang et al. 2009; Bayat et al. 2014; Park 2015; Hernandez-Jerez et al. 2019). The physiological, behavioural and ecological characteristics of chiropterans make them a unique and high-risk group among terrestrial vertebrates with respect to the nontarget effects of PPPs, as they are directly exposed to PPPs during application via the ingestion of contaminated prey or due to indirect consequences via the reduction of their food sources (Mineau and Callaghan 2018; Hernandez-Jerez et al. 2019; Oliveira et al. 2021). This observation is true for both frugivorous and insectivorous bats (Oliveira et al. 2021). Exposure of bats may occur directly when feeding in treated fields on fruits, flowers and insects exposed to PPPs and bats may further be exposed through biomagnification in food webs even while foraging outside of agricultural areas (Williams-Guillén et al. 2016).

Exposure to contaminants, including PPPs, has been identified as a possible cause of the decline in bat populations and susceptibility to "white-nose syndrome", a disease caused by a fungal infection in the USA and Europe (O'Shea and Johnston 2009; Bayat et al. 2014; Oliveira et al. 2021; Torquetti et al. 2021). The negative impact on chiropteran population dynamics and diversity of "historical" PPPs, OCs (DDT and lindane) and CIIIs (e.g., chlorpyrifos), and pyrethroids used both in agriculture and for wood treatment (to which chiropterans may be exposed in their roosting and maternity sites such as roof timbers) are suspected (O'Shea and Johnston 2009; Bayat et al. 2014). Exposure to and impacts of OCs have been documented in both agricultural and other types of landscapes since essentially the 1970s to the last decades of the 20th century. However, recent reports on the migratory species *Tadarida brasiliensis* in India and Benin may be due to continued

illegal or uncontrolled usage or biocidal use (e.g., malaria control) (Williams-Guillén et al. 2016). PPPs have been identified as potential causes of declines in chiropteran populations, but significant gaps in knowledge make it difficult to identify quantified trends in the population impacts of CUPs, although negative impacts of NNs and pyrethroids are suspected (Bayat et al. 2014; Afonso et al. 2016; Mineau and Callaghan 2018; Oliveira et al. 2021; Williams-Guillén et al. 2016).

As with many other groups, the decline in chiropteran populations seems to be particularly marked in "intensive" agrosystems and associated with agricultural practices, including the use of PPPs, as well as landscape changes (Jones et al. 2009). Pocock and Jennings (2008) showed an association between agricultural intensification and a decrease in the relative abundance of shrews (*Sorex araneus* and *Neomys fodiens*) and the common pipistrelle (*Pipistrellus pipistrellus*) between OF and CF farms in England. They stated that this trend was linked to the reduction in seminatural habitats at the edges of plots, which was greater in CF than in OF. Based on a literature review including studies in Europe and in the Neotropics, Park (2015) highlighted the benefits of low-intensity farming systems, particularly OF and agroforestry, which are associated with higher abundance, specific richness and diversity of chiropterans and more highly used by feeding bats. Recent studies showed higher specific richness, abundance and/or activity of chiropterans in OF than in CF (Barré et al. 2018; Put et al. 2018).

However, the available data are limited and have focused mainly on the contamination of bats by insecticides. Overall, the studies show either contamination or an association between contamination and effect without demonstrating a causal link, as is the case for most studies on mammals (Hernandez-Jerez et al. 2019).

Reptiles

For several decades, reptiles have experienced marked population declines worldwide. Twenty-one percent of the species are classified as threatened by the International Union for the Conservation of Nature (IUCN) (Cox et al. 2022). There are multiple causes which can act alone or in combination, including habitat degradation and fragmentation, invasive species and toxic substances (McConnell and Sparling 2010; Todd et al. 2010). PPPs are among the main assumed threats, especially due to the use of cultivated agricultural areas by reptiles and their presence at treatment times (Ockleford et al. 2018). According to the EFSA (Ockleford et al. 2018), 42% of European reptile species (50 out of a total of 120) are present in agrosystems, and 33-50% of them have high PPP exposure risk factors (Mingo et al. 2016). Although no overall difference was observed between taxonomic groups, 16 of the 20 species with the highest exposure risk factors were lizards, making them the most vulnerable group of reptiles to PPPs (Mingo et al. 2016). The European ERA procedure does not sufficiently take reptiles into account (Brühl et al. 2013) and a recent EFSA expertise (Ockleford et al. 2018) highlighted the lack of data and studies about the toxicity of PPPs on this taxon (Köhler and Triebkorn 2013), despite their vulnerability (De Lange et al. 2009). Recently, the EFSA has proposed specific objectives for the protection of reptile populations and communities in relation to the use of PPPs. At the individual level, the proposed objective takes as a "tipping point" the initiation

of effects considered negligible¹ on adult and juvenile survival, whereas at the population level, it is about weak¹ and temporary (a few months) effects on abundance and/or spatial distribution and/or population growth coefficient. Thus, studies on the effects of PPPs on populations and life history traits (survival, reproduction, growth) are more specifically developed here.

Few studies have investigated the effects of PPPs on reptile communities and/or populations, and those available are mainly on lizards. Six out of the eight studies reviewed showed decreases in abundance, survival rates and/or changes in the structure of the exposed populations, particularly in terms of *sex ratio*, demonstrating the potential of PPPs to negatively affect reptile populations. In Australia, the application of chemicals (fipronil, Adonis®) or biologics (*Metarhizium anisopliae* var. *acridum* Green Guard®) to control locust densities had no effect on the lizard community or population abundance (Maute et al. 2015). In Madagascar, decreases in population abundance of 53% and 45% were measured for two lizard species, *Chalarodon madagascariensis* and *Mabuya elegans*, respectively, five months after aerial application of fipronil (Adonis®) (Peveling et al. 2003). Treatment with the pyrethroid insecticide deltamethrin (Decis®) resulted in population declines of 7.6% and 0.1% for the same two species (Peveling et al. 2003). The difference in the effects of fipronil between these two studies could be explained by the sixfold lower concentration applied in the Australian study and by differences in the sensitivities of the studied populations. In Greece, the use of the herbicides 2,4-D and 2,4,5-T between 1975 and 1984 resulted in a decrease of 0.34 in the survival rate of the Hermann's turtle *Testudo hermanni*, particularly in juveniles, causing the almost total disappearance of the population (Willemsen and Hailey 2001). In the absence of a decline in body condition, these additional mortalities were attributed to acute herbicide toxicity rather than to a lack of food caused by the destruction of the vegetation cover. In the same study, the lack of effects of other herbicides (paraquat or atrazine) on Hermann's turtles in surrounding areas was mentioned without further information (Willemsen and Hailey 2001). In cultivated areas in Portugal, no overall difference in density or *sex ratio* was found between populations of the lizard *Podarcis bocagei* living at the edge of plots in which a combination of herbicides was detected (mesotrione, GLY, bentazone, dicamba, dimethenamid-p, alachlor, and terbuthylazine) or managed under OF, but in the most intensively treated plot the measured *sex ratio* was biased toward males (Amaral et al. 2012a). In a vineyard, Mingo et al. (2017) sampled individuals from four populations of *Podarcis muralis* lizards along an exposure gradient defined according to the proportion of vines. A total of 23 formulations containing fungicidal AIs (including 2 succinate dehydrogenase inhibitors SDHI, boscalid and fluopyram), and herbicidal GLY were applied. The *sex ratio* of the populations in treated sites was biased toward males, but a direct cause-and-effect relationship could not be established (Mingo et al. 2017). Alexander et al. (2002) investigated the effects of deltamethrin at the recommended application rate and 1.4 times this rate on 2 species of South African lizards in experimental enclosures. Survival rates measured within two months of treatment ranged from 0 to

¹ Cf Ockleford et al. (2018) for more information on the meaning of "negligible" and "weak" in this context

40%, while in control pens, survival rates were >75%. In the wild, where only the recommended dose was tested, the abundance was reduced by 52-72% four weeks after insecticide treatment. These populations returned to similar numbers to those in the control sites after 18 months (Alexander et al. 2002).

Amphibians (terrestrial stages)

Amphibians are among the taxonomic groups most affected by the massive loss of biodiversity at the current global scale. Among vertebrates, they are the most endangered group and are experiencing a faster rate of decline than mammals and birds are (Ockleford et al. 2018). Habitat loss and environmental pollution are considered the main reasons according to the IUCN. Various causal factors, including habitat destruction, climate change, UV radiation, pathogens and invasive species, have indeed been identified, as well as PPPs (Blaustein et al. 2003; Hayes et al. 2010; Kiesecker 2011; Köhler and Triebkorn 2013). These factors can act in combination and by interaction, resulting in drastic declines or even extinctions of populations (Blaustein et al. 2003; Hayes et al. 2010; Kiesecker 2011; Köhler and Triebkorn 2013). Declines in amphibian populations have been linked to disease occurrence, and several authors have indicated that PPPs may be the cause of the increased prevalence of infections and deleterious effects related to pathogens and parasites. These effects are manifested through direct immunotoxicity and endocrine disruption and through indirect impacts via changes in the dynamics of pathogens or parasites and their different vectors and hosts (Christin et al. 2003; Gendron et al. 2003; Kiesecker 2011; Köhler and Triebkorn 2013; Rohr et al. 2008). Episodes of mortality, developmental anomalies and reproductive failure following exposure to PPPs, including low doses and CUPs, have also been reported (Rohr et al. 2008; Brühl et al. 2013; Köhler and Triebkorn 2013). The physiological traits and biological features of amphibians make them a particularly vulnerable group of fauna with regard to the impacts of PPPs (Ockleford et al. 2018). Moreover, the occurrence of amphibians in arable lands including during periods of PPP treatment, and the spatial ecology features of these taxa (see section III.6) are recognised as factors likely to enhance the risk of PPP exposure in amphibians (Ockleford et al. 2018). The deleterious impacts of PPPs have been demonstrated for various AIs (Hayes et al. 2010), with only a limited number of studies concerning CUPs. Moreover, most research has been conducted on larval stages and in aquatic environments and will not be detailed in the present article. Over the last decade, a few studies have linked population declines to PPP use. The analyses involve data on terrestrial stages or terrestrial species, but it is not possible to quantify the proportion of PPP effects linked to strictly aquatic or strictly terrestrial exposure or both.

A study in the USA strongly suggested that airborne PPPs may be a significant factor in the decline of the California red-legged frog *Rana draytonii* in the studied area (Davidson et al. 2001). Davidson et al. (2002) subsequently studied the potential drivers of population dynamics in 8 amphibian species (e.g., habitat destruction, UV-B, climate, and PPP drift) and showed a strong association between the decline of four species and the risk of exposure to airborne PPPs. Local extinctions and

range reduction in the arboreal endemic species *Scinax caldarum* in Brazil are thought to be due to massive agrochemical inputs (Ferrante et al., 2019). In Argentina, Sanchez et al. (2013) observed differences between amphibian populations at various sites located along an agricultural land use gradient: the richness was lower while the diversity and regularity were higher in agricultural sites compared to transitional and forest sites. Differences in the reproductive parameters of amphibians in agricultural areas, with changes in the number of breeding species, variations in the use of microhabitats and differences in the timing of breeding were also observed. While these authors suggested that habitation in agricultural settings has adverse effects on amphibian reproduction, they did not quantitatively relate these effects to PPP use (Sanchez et al. 2013).

Finally, the effects of PPPs on sexual abnormalities and demasculinisation/feminisation, parameters essential for recruitment and population viability, have been shown in laboratory and field studies. Extremely skewed *sex ratios*, up to 100%, in favor of males or females depending on the PPPs of concern, have been observed in amphibians exposed during adult or terrestrial stages to fungicides such as carbamates or dithiocarbamates, or herbicides such as atrazine (Harris et al. 2000; Hayes et al. 2010).

III.2.2. Direct effects at the individual level on terrestrial wildlife

Most of the studies targeting individual or subindividual effects in vertebrates have attempted to identify causal links between exposure to one or more PPPs and their effect(s) on life history traits or other fitness parameters (survival, reproduction, behaviour, health status) and, where possible, to characterise the mechanisms involved. Thus, to limit or control possible confounding factors (age, sex, nutrition, other environmental stress factors), the vast majority of the dedicated studies are conducted under controlled experimental conditions on a limited number of laboratory model species. Moreover, most works have assessed subindividual responses (e.g., biochemical markers) without analysing actual physiological outcomes or fitness impacts. Our review will focus on the most relevant findings related to wildlife and biodiversity conservation.

Within the last decade, the literature has increasingly emphasised that some sublethal effects are likely to cause long-term population impacts, especially endocrine disruption, effects on immunity and on the microbiota (the microbial community living in a particular environment such as the gut microbiota or skin microbiota) or the microbiome (the genomes from all the living microorganisms in a defined environment that can be an entire organism or a specific location in the organism, such as the gut or oral microbiome) (e.g., Acevedo-Whitehouse and Duffus 2009; Köhler and Triebkorn 2013, Meng et al. 2020). The population relevance of endocrine-disrupting effects on nontarget vertebrates is acknowledged in regulation and has been subjected to the guidance and development of assessment methods (e.g., Crane et al. 2019). A focus on such effects is provided in the section III.2.2.

Lethal and sublethal toxic effects

A topic common to all vertebrate taxa is the case of GLY, for which a growing body of evidence raises concerns about its environmental impacts based on the risk of lethal and sublethal toxic effects in biota following chronic exposure to low doses in the environment (Gandhi et al. 2021; Kissane and Shephard 2017; Ojelade et al. 2022; Peillex and Pelletier 2020; Székács and Darvas 2018; Van Bruggen et al. 2018). GLY could be more harmful to wildlife and ecosystems than expected and may be more bioaccumulative than predicted from its physico-chemical properties (Kissane and Shephard 2017; Richmond 2018; Ojelade et al. 2022). Impairments in numerous components of animal health, such as increased oxidative stress, cytotoxic and genotoxic effects, endocrine disruption, neurotoxicity, reproductive and growth issues, hepatotoxicity, cardiovascular system troubles, effects on the immune system, potential for carcinogenicity, lethality in placental cells, decreased fertility, influence on the intestinal microbial community, and even mortality in amphibians, have been mentioned in relation to subchronic and chronic toxicity (Bai and Ogbourne, 2016; Gandhi et al., 2021; Ojelade et al., 2022; Peillex and Pelletier, 2020; Van Bruggen et al., 2018). Further information on GLY is provided hereafter, with specific studies detailed for each taxonomic group.

Birds other than raptors

In studies focusing on PPP lethal and sublethal effects on birds, the compounds most studied for a long time were OCs and OPs. For the last 15 years, NNs (imidacloprid, thiamethoxam, clothianidin) and carbamates (thiram, mancozeb) have been studied, and more recently, triazole fungicides and a few herbicides were considered as well as.

CIIIs have long been implicated in primary and secondary poisoning events in granivorous, insectivorous, and other guilds of birds (Wobeser et al. 2004; Mineau et al. 2005; Köhler and Triebkorn 2013; Millot et al. 2015). These PPPs have the highest acute toxicity among insecticides and the greatest number of documented poisoning events, especially in North America (Mineau and Callaghan 2018).

The European Phytopharmacovigilance networks (e.g., France, UK, Spain) have revealed a large number of cases of accidental direct poisoning of birds by CUPs. The vast majority of cases since the beginning of the 2000s concern poisoning following the ingestion of seeds coated with NNs (especially imidacloprid) and, more occasionally, other AIs, such as fungicides (thiram). Recently, primary poisoning from zinc phosphide, a rodenticide used in open fields, has been reported in Eurasian cranes (*Grus grus*) (Fanke et al. 2011) and Canada geese (*Branta canadensis*) (Bildfell et al. 2013). Measurements of PPP residues in carcasses have linked the mortality of granivorous species (e.g., gray partridge, various pigeons, and passerines) to imidacloprid intoxication following the consumption of coated seeds (Berny et al. 1999; Bro et al. 2010; Mineau and Palmer 2013; Millot et al. 2017; Buchweitz et al. 2019). Cases involving passerines were less frequently reported, despite a higher potential risk due to lower body mass and greater energy requirements (Mineau and Palmer 2013; Buchweitz et al. 2019). However, they were well represented in network mortality figures (~5%

of the 15,000 dead birds recorded by the French SAGIR network; Decors et al. 2011). A biological feature of their feeding behaviour may limit their exposure: the peeling of seed husks, which many passerine species practice before ingesting seeds (Avery et al. 1997; Prosser and Hart 2005). Nevertheless, they are probably undersampled by this type of monitoring because of detection biases related to their small size and the rapid disappearance or decay of corpses (Ponce et al. 2010). Despite these biases in field detection (Vyas 1999; de Snoo et al. 1999) and diagnostic biases (proven causal link), a significant number of individuals and species have been categorically identified as victims of acute and lethal intoxication induced by NNs used in seed coating. Millot et al. (2017) estimated the degree of certainty of poisoning by imidacloprid as “probable” in more than 70% of the 103 incidents of wildlife mortality recorded between 1995 and 2014 for which toxicological analyses revealed the detection of imidacloprid residues. Fall sowing was identified as the most impactful practice in terms of NN-induced mortality (Millot et al. 2017). Nevertheless, by using long-term data on NN use and bird surveys, Lennon et al. (2019) reported that dietary exposure to NNs via ingestion of treated seeds and seedlings could not be confirmed as a causal factor of farmland bird declines. Overall, accidental mortality events are not considered a primary cause of most farmland bird species decline, but they are undeniably a contributory factor (Millot et al. 2017). Other cases of passerine poisoning by NNs have been reported, for example, following drench tree treatments in California (Rogers et al. 2019). Several syntheses about the individual and subindividual effects of NNs have recently been released (Gibbons et al. 2015; Pisa et al. (2015); Wood and Goulson 2017). Even though the compounds in these studies (e.g., chlorpyrifos, fipronil, and imidacloprid) are now banned in some areas, they continue to be widely used as seed coatings or spray AIs in many countries around the world. Migratory birds have no known regulatory boundaries. Since sublethal (physiological, behavioural) and indirect effects of NNs have been demonstrated (see the sections below for more details), impacts at the population level may occur beyond accidental lethal poisoning (Mineau and Palmer 2013; Gibbons et al. 2015; Wood and Goulson 2017).

Other PPPs that are commonly used nowadays, are less commonly identified in poisoning event reports because of the absence, or at least rarity, of fatal intoxication detection in the field. During environmentally realistic exposure or contamination, currently used fungicides, herbicides and insecticides have been shown to induce sublethal effects in birds that may affect population dynamics. This is the case for instance for triazole fungicides and strobilurins, some pyrethroid insecticides, and some herbicides (GLY, sulfonyleureas and phenyl-ureas) which can induce sublethal and even lethal effects. For example, exclusive consumption of cereal seeds treated at the recommended application rate for seed coating (imidacloprid, thiram, difenoconazole) can result in mortalities of up to 50% of females within 5 days (Lopez-Antia et al. 2013; Lopez-Antia et al. 2015). Both laboratory and field studies have shown various deleterious effects of several chemical families of PPPs, mainly OCs, OPs, carbamates and more recently NNs and to a lesser extent azoles, on parameters related to reproductive success in birds (e.g., decrease in sperm quality and fertility,

reduction in clutch size, reduction in hatching success, variation in the time lag of egg laying, decrease in survival or developmental disruption in juveniles, decreased number of fledglings) (Bishop et al. 2000; Brickle et al. 2000; Hart et al. 2006; Lopez-Antia et al. 2013, Lopez-Antia et al. 2015; Lopez-Antia et al. 2021; Pandey and Mohanty 2015; Ertl et al. 2018; Eng et al. 2019; Humann-Guilleminot et al. 2019a; Kitulagodage et al. 2011).

Red-legged partridges fed flutriafol-treated seeds below (20%) or at the recommended application dose showed a 50% decrease in reproductive success (Lopez-Antia et al. 2018). Chick mortality was 26% and 24% greater following environmentally realistic exposure of the eggs of red-legged partridges by overspray with the fungicide tebuconazole and the herbicide 2,4-D, respectively, than in the control group (Ortiz-Santaliestra et al. 2020). Moreover, exposure of the eggs to tebuconazole or 2,4-D via contaminated soil or overspray induced alterations in several biochemical parameters of the chicks post-hatching (Ortiz-Santaliestra et al. 2020).

A reduction in feeding and activity, often resulting in weight loss and impaired survival due to debilitation and/or increased vulnerability to predation, is known to occur in wildlife exposed to carbamates or OPs (Köhler and Triebkorn 2013). Exposure to OPs (e.g., chlorpyrifos), NNs (e.g., imidacloprid), and phenylpyrazoles (e.g., chlorfenapyr) has been shown to induce weight loss or reduce energy reserves in various birds (Albers et al. 2006; Eng et al. 2017; Eng et al. 2019). In the ruby-throated hummingbird *Archilochus colubris*, the consumption of imidacloprid in flower nectar induced a decrease in energy expenditure (English et al. 2021).

Liebing et al. (2020) investigated the factors contributing to the decline of the pheasant *Phasianus colchicus* population in an agricultural landscape in Germany through pathomorphological, parasitological, virological, bacteriological and toxicological investigations of chicks. A large number of chicks exhibited poor nutritional status and poor health conditions, which were associated with inflammation in several tissues and organs and with bacterial and parasitic pathogens. Among the nine individuals with liver or kidney inflammation analysed for PPP residues, GLY was detected (Liebing et al. 2020).

Exposure to PPPs can induce behavioural alterations, for instance, in the case of NNs (Eng et al. 2019). Disruption of flight and/or orientation efficiency has emerged as a sensitive and relevant endpoint of exposure and sublethal effects of PPPs in birds (OPs, Vyas et al. 1995; OPs and carbamates, Brasel et al. 2007; Moye and Pritsos 2010; OPs and NNs, Eng et al. 2017). These effects have been associated with a loss of energy reserves. Thus, although transient under the conditions tested (doses < 25% of the median lethal dose, LD50), these sublethal effects could lead to altered migration success in passerines when agricultural environments are used as staging areas (Eng et al. 2017; Eng et al. 2019). Moreau et al. (2022) reported that the vitality of several passerines was greater in OF fields than in CF fields, but no measurements of PPP exposure or contamination were undertaken to identify causal links.

Raptors

Mortality related to deliberate poisoning by CIIIs or to the large-scale application of anticoagulant

rodenticides is the most documented individual effect in the literature for the period 2000-2021. Reported worldwide, cases of deliberate poisoning with baits containing CIIIs involve the death of a few individuals to several hundreds, with the species concerned most often being scavengers (e.g., Plaza et al. 2019). These practices are therefore considered major threats to the conservation of many species on all continents (Smart et al. 2010; Margalida 2012; Berny et al. 2015; Katzenberger et al. 2019; Plaza et al. 2019). It is difficult to define a trend in the evolution of these practices between 2000 and 2021, but several articles reporting recent cases have been published, revealing that they remain a problem on a global scale (Alarcon and Lambertucci 2018; Plaza et al. 2019). Despite the different contexts, the agricultural use of anticoagulant rodenticides has also led to secondary and lethal poisoning of raptors in different parts of the world (Olea et al. 2009, Winters et al. 2010; Coeurdassier et al. 2014b; Moriceau et al. 2022). The fact that rodents are prey for many raptors partly explains the vulnerability of raptors to anticoagulants (Coeurdassier et al. 2012). In addition, raptors are likely more sensitive to these compounds, with the LD50 of diphacinone for the American kestrel *Falco sparverius* being 20 to 30 times lower than that measured for model bird species used in ERA such as the bobwhite quail or the mallard *Anas platyrhynchos* (Rattner et al. 2011). In addition to mortality episodes, the frequent exposure of raptors to mixtures of anticoagulants has been highlighted by several national monitoring networks (López-Perea and Mateo 2018; Badry et al., 2021). Most of these cases were due to purely biocidal uses since agricultural use is not authorised in the countries of concern (Denmark, UK, Germany) or because the exposure contexts are mainly urban (USA). Considering 40 studies involving 3048 individuals belonging to 34 species, López-Perea and Mateo (2018) determined that residues of one or more anticoagulants were detected in 58% of the birds analysed, with reported liver concentrations above $0.1 \mu\text{g g}^{-1}$, a threshold compatible with the occurrence of coagulopathy (Rattner et al. 2014), which was recently discussed by Rattner and Harvey (2021). Specific ecological traits generally associated with high levels of accumulation include specialisation of the diet on rodents and/or even opportunistic scavenging habits (López-Perea and Mateo 2018). However, high frequencies of anticoagulant residue detection (> 80% of individuals analysed) have also been reported for a species with different ecological traits, the Northern goshawk *Accipiter gentilis* (Badry et al. 2021). Apart from coagulopathy, the sublethal effects potentially induced by low levels of exposure and their consequences for populations have been assessed in only a few studies. In Malaysian oil palm plantations or Spanish cultivated plains, the use of anticoagulants has been correlated with decreased reproductive success and/or chick growth in the barn owls *Tyto alba* and kestrels *Falco tinnunculus*, respectively (Naim et al. 2010; Naim et al. 2011; Martinez-Padilla et al. 2017). Potentially direct and/or indirect causes (see section III.4.1.) are mentioned by the authors but have not been precisely studied. Individual effects induced by "legacy" OCs or CUPs on raptors have not been the subject of any scientific publication since 2000.

Mammals other than chiropterans

The most common data and information for mammals come from regular monitoring networks. At

the European or national level, these networks (e.g., SAGIR in France, Wildlife Incident Investigation Scheme WIIS in the UK) have published reports or data, which made it possible to identify PPPs associated with mortality *in natura*. The substances most often identified are CIIIs, such as aldicarb, carbofuran, parathion and chlorpyrifos-ethyl, and anticoagulant rodenticides (Naim et al. 2011). Various taxa are represented in poisoning events, herbivores such as leporids and ungulates, insectivores such as European hedgehogs (*Erinaceus europaeus*), and carnivores such as red foxes (Guitart et al. 2010; Luzardo et al. 2014). In Europe, carnivores were the most common group in records (39%), followed by leporids (35.4%). Red foxes accounted for 23.6% of all mortalities, hares (*Lepus* spp.) accounted for 26.2%, and rabbits (*Oryctolagus cuniculus*) accounted for 9.2% (Guitart et al. 2010).

In a recent study in Northern Italy, a high risk of poisoning of wild mammals was identified for metaldehyde or insecticides in relation to agricultural or breeding areas. In all these instances, the illicit use of banned or authorised PPPs to poison mammals considered as pests is the main cause (Di Blasio et al. 2020). All these data were obtained by opportunistic sampling. It is not possible to estimate the potential impact of these mortality events on the populations and diversity of species but a conclusion from these networks is the adverse impact of acutely toxic PPPs and the limited effect of restriction or prohibition regulations on the illicit use of a product when still in use in other parts of the world. It was suggested that the control of stocks, sales, and imports be strengthened to decrease the likelihood of illicit use of these PPPs (Martinez-Haro et al. 2008).

Although studies on the effects of PPPs *in vivo* in wild mammals are rare, many studies are available demonstrating the effects of PPPs on rodents and rabbits. In a few instances, acute toxicity experiments have been conducted in captive wildlife species. McComb et al. (2008) investigated the toxicity of GLY administered orally or intraperitoneally and compared their results with those from a field survey on different wild small mammal species in Oregon (including the deer mouse *Peromyscus maniculatus*, the Trowbridge's shrew *Sorex trowbridgii*, the Townsend's tamia *Tamias townsendii* and the Oregon vole *Microtus oregoni*). The toxicity of GLY was low (LD50 > 1000 mg kg⁻¹), necropsies did not reveal any lesions, and field data were consistent with these findings. When applying a dose close to the agricultural application rate or close to the upper recommended dose, no adverse effects, including movements recorded by telemetry, was detected in the animals (McComb et al. 2008). Several literature reviews have identified metabolic disturbances such as dyslipidemia or hyperglycemia in mammals exposed to the OP diazinon (Aramjoo et al. 2021; Farkhondeh et al. 2021). In bank voles (*Myodes glareolus*), chlorpyrifos is responsible for thermoregulation disorders (Dheyongera et al. 2016).

Chimpanzees (*Pan troglodytes schweinfurthii*) and baboons (*Papio anubis*) living in a mid-altitude rainforest in western Uganda sometimes feed in gardens and crops. Abnormalities such as facial dysplasia, reproductive impairment and hypopigmentation were observed in 25% of the 66 chimpanzees monitored, and 17% of the baboons from a 35-individual troop showed nasal deformities (Krief et al. 2017). Investigating the potential role of PPPs in these situations, Krief et al.

(2017) reported that farmers use GLY, cypermethrin, profenofos, mancozeb, metalaxyl, dimethoate, chlorpyrifos and 2,4-D amine. According to chemical analyses, recommended thresholds were exceeded in maize stems and seeds, soils, or river sediments for several PPPs, such as DDT and its metabolite pp'-DDE. In coated maize seeds and in fish from the area, imidacloprid was detected. Krief et al. (2017) hypothesised that exposure to PPPs may induce thyroid hormone disruption in these monkey populations, which can lead to facial dysplasia.

Chiropterans

In their review of global mortality events in bats, O'Shea et al. (2016) identified exposure to environmental contaminants as one of the causes of death. They recorded 43 reports in 16 species of bats since 1952 in Australia, Europe, New Zealand and North America caused by chemicals and stressed that such an estimate is likely underestimated. The most prevalent chemicals involved in multiple mortality events were OCs such as DDT, dieldrin, heptachlor, endrin, and lindane (O'Shea et al. 2016). The following other PPPs were also mentioned: carbamate insecticides, the rodenticide diphacinone, and pentachlorophenol. It is reported that poisoning can also be due to biocidal treatments of timber at roosts in buildings.

Some physiological characteristics, such as hibernation, thermoregulation and echolocation, are unique among mammals and can cause bats to be potentially more at risk, particularly for neurotoxic compounds involving these functions, as has now been demonstrated in birds. It has been shown that repeated exposure to imidacloprid in an Asian bat (*Hipposideros terasensis*) at an oral dose of 20 mg kg⁻¹ causes impaired movement, despite echolocation learning. Memory loss was associated with apoptotic lesions in the hippocampus. The effect of imidacloprid has thus been demonstrated, but no published data confirm its existence in the field or the level of *in natura* exposure of chiropterans to NNs (Hsiao et al. 2016). However, a recent study reinforced these behavioural effects and suggested that the alteration of bats' echolocation movements probably affects their movements and hunting activities (Wu et al. 2020). Testing the effects of the fungicide tebuconazole at the commercially recommended concentration in the frugivorous bat *Artibeus lituratus* after 7 and 30 days of oral exposure (bats fed tebuconazole-treated fruits), Machado-Neves and coworkers (2018) observed alterations in the epididymis after 7 days and both testicular and epididymal alterations after 30 days. These histomorphometric changes suggest that tebuconazole may be harmful to the reproductive system (Machado-Neves et al. 2018).

Reptiles

The effects of insecticides on reptiles have been studied through a dozen studies, mainly on lizards and under controlled conditions. The responses measured were life history traits (survival, reproduction, embryo development), morphology (size, mass or body condition), clinical signs of intoxication (tremors, convulsions) and/or feeding or locomotor behaviour. The disparity of the experimental conditions used (AIs alone, in mixtures or commercial formulations, duration and mode of exposure, species studied) makes it difficult to draw conclusions on the relative toxicity of these

insecticides for reptiles. Moreover, the realism of the exposure doses used is rarely mentioned. Thus, while it is possible to conclude that the tested AIs induce effects in exposed species under experimental conditions, the potential of most of them to affect individuals and populations has not been demonstrated *in natura*. In the wild, screening of PPP residues in liver following wildlife poisoning events reported the detection of carbamates in Western Canaries lizards *Gallotia galloti* (Luzardo et al. 2014). In the laboratory, mortality due to exposure to insecticides has been observed, at doses close to (i) the chronic NOAEL in birds for chlorpyrifos-ethyl (in a mixture with lead and DDT), (ii) three times the LD50 in birds for fipronil (Adonis®), and (iii) four times lower than the LD50 in birds for lambda-cyhalothrin (Peveling and Demba 2003; Ciliberti et al. 2013; Weir et al. 2015). No acute toxicity was found for endosulfan or lambda-cyhalothrin following dermal exposure (Weir et al. 2015). Regarding sublethal effects, decreases in body mass or condition, relative organ weights, feeding or locomotor activity, reproductive effects and/or clinical signs of intoxication were demonstrated in lizards exposed to fipronil (Peveling et al. 2003), alpha-cypermethrin (Chen et al. 2019b), malathion (Holem et al. 2006) (Holem et al. 2008), carbaryl (DuRant et al. 2007) or chlorpyrifos (Amaral et al. 2012b). Combining field observations and controlled experiments, Rauschenberger et al. (2007) showed that parental exposure to a mixture of OCs may contribute to the low hatching rates observed in wild alligator (*Alligator mississippiensis*) populations. This study provides further evidence of the effects of parental transfer of PPPs on oviparous reptiles. No effect was observed on the body temperature, standard metabolic rate or food consumption of bearded agamas (*Pogona vitticeps*) exposed to a high dose of fenitrothion regarding residues in prey sampled in the field following spraying, 20 mg kg⁻¹ bw (Bain et al. 2004). Peveling et al. (2003) concluded that the myco-insecticide *Metarhizium anisopliae* var. *acridum* is unlikely to pose a risk to the lizard *A. dumerili* at the recommended field application rate. The available studies on the individual effects of anticoagulant rodenticides on reptiles are broadly consistent. Experiments under controlled conditions have revealed the low sensitivity of reptiles to these PPPs (Fischer et al. 2011; Weir et al. 2015; Mauldin et al. 2020). Field reports (Herrera-Giraldo et al. 2019; Mauldin et al. 2020) mention no or limited mortality in a few individuals (with the exception of Merton 1987) following anticoagulant treatments in New Zealand, Australia, Africa or the Mediterranean and Caribbean islands. However, some studies suggest differences in sensitivity between taxonomic groups and/or species (Merton 1987; Mauldin et al. 2020), which limits generalisation.

The individual effects of herbicides and fungicides were evaluated in seven studies, all conducted under controlled conditions. For herbicides, the AIs studied were GLY, glufosinate ammonium or its active enantiomer L-glufosinate ammonium or atrazine. Exposure of *Oligosoma polychroma* skinks to commercial formulations of GLY had no impact on the mass of individuals over the following four weeks, but those exposed to Roundup Weedkiller® exhibited heat-seeking behaviour interpreted as a response to physiological stress (Carpenter et al. 2016). Zhang et al. (2019) showed a decrease in mass and changes in locomotor behaviour in male *Eremias argus* lizards exposed to soils contaminated with 20 mg kg⁻¹ ammonium glufosinate or L-glufosinate ammonium, corresponding to

1% of the LD50 in birds. Finally, increased mortality and impaired reproduction were observed in pregnant females of the aquatic snake *Nerodia sipedon* exposed to increasing doses of atrazine (Neuman-Lee et al. 2014). For fungicides, Weir et al. (2015) observed no mortality in lizards exposed to chlorothalonil doses up to 1750 mg kg⁻¹ (close to the LD50 in birds). The increase in liver and testicular masses found in male *E. argus* exposed to 20 mg kg⁻¹ myclobutanil (LD50 in birds = 510 mg kg⁻¹) suggested that this triazole may be hepatotoxic and reprotoxic (Chen et al. 2017). de Solla and Martin (2011) exposed turtle eggs to soils containing a mixture of herbicides (GLY 'Roundup Rain Proof'® + atrazine '480'® + dimethenamid 'Frontier'®) or an insecticide (tefluthrin 'Force 3G'®) at one, 5.5 and 10 times the field application rate. No effect on hatching rate was found, while hatchlings exposed to the highest dose of tefluthrin had greater deformity rates than those in the other treatments according to de Solla and Martin (2011). In a methodologically similar study, the deformity rates and masses of turtle hatchlings were not affected by a mixture of chlorothalonil, S-metolachlor, metribuzin or chlorpyrifos applied at a rate 10 times the field rate (de Solla et al. 2014). Several field and mesocosm studies have evaluated the individual effects of mixtures of commercial PPP formulations. A comparison of lizard populations (*P. bocagei* and *P. muralis*) undergoing different intensities of PPP treatments *in situ* revealed a decrease in body condition at the treated sites (Amaral et al. 2012d; Mingo et al. 2017), while no differences were detected in other traits, such as adult size, fluctuating femoral pore asymmetry or prevalence of ectoparasites (Amaral et al. 2012c; Amaral et al. 2012d), indicating that the measured responses provide a consistent picture of animals undergoing metabolic stress at the treated sites. In mesocosms, *P. bocagei* lizards exposed to a mixture of commercial herbicide formulations only (alachlor + terbuthylazine + mesotrione + GLY) or including chlorpyrifos showed no difference in survival, locomotor behaviours or metabolic rate, but their growth rates were greater than those measured in the absence of treatment (Amaral et al. 2012b). *In ovo* exposure of *Salvator merianae* lizards to commercial formulations of GLY, chlorpyrifos and cypermethrin alone or in combination did not affect hatching rates, embryonic development or hatchling size (Mestre et al. 2019). Higher rates of malformations or lesions are reported in snake or turtle populations colonising PPP-contaminated sites without identifying the causes of these teratogenic effects, PPPs and/or others (Garces et al. 2020). Finally, in a recent review on the impacts of pollutants on both terrestrial and aquatic reptiles, Barraza et al. (2021) reported that a high diversity of individual and subindividual reproductive responses were associated with PPP exposure, including sex reversal, altered sexual development, developmental abnormalities, reduced hatching success and reproductive output.

Amphibians (terrestrial stages)

Only a few studies have examined the effects of PPPs, and particularly CUPs, on strictly terrestrial stages or species. However, the EFSA (Ockleford et al. 2018) highlights significant risks for amphibians of being exposed to and/or affected by PPPs during their terrestrial life stages.

Studying infections caused by the fungal pathogen *Batrachochytrium dendrobatidis* in 49 amphibian

species over a large spatial scale, Rumschlag and Rohr (2018) showed that fungal infections increased with PPP use. Multiple herbicide use was associated with low infection risks in the aquatic larval stage but with high infection risks in the terrestrial stage (Rumschlag and Rohr 2018). Rumschlag and Rohr (2018) indicated that since the use of herbicides, fungicides and insecticides are correlated, it is not relevant to consider that fungicides and insecticides do not definitely influence the distribution of the pathogen. In India, in coffee plantations where PPPs and other chemicals such as fertilisers are widely used, altered individual health status (higher hepato-somatic and gonado-somatic indices), lower tissue acetylcholinesterase activity in the brain and liver and high incidences of morphological abnormalities have been observed in amphibian populations (Hegde et al. 2019). Christin et al. (2013) reported that, juvenile *Rana pipiens* frogs in agricultural regions in Canada were smaller and showed a reduction in both the number of splenocytes and the phagocytic activity compared to frogs sampled in areas with lower levels of PPPs. The AIs detected in water in agricultural areas at higher levels than in water from reference sites were 2,4-D, 2,4-DB, atrazine and deisopropyl-atrazine, bentazone, bromoxynil, clopyralid, dicamba, dimethenamide, S-ethyl-dipropylthiocarbamate (EPTC), 2-methyl-4-chlorophenoxyacetic acid (MCPA), and mecoprop. Such a poorer body condition and alteration of the immune system might make them more vulnerable to infections and diseases (Christin et al. 2013).

Contact with contaminated soil is a likely and important route of exposure in terms of toxicity to amphibians, although it is less hazardous than direct spraying (Van Meter et al. 2015; Cusaac et al. 2017; Ockleford et al. 2018). Scenarios developed to mimic the exposure of terrestrial juvenile amphibians via direct spraying or exposure to treated soil showed strong lethal effects of different PPP commercial products when used at recommended doses or even at lower doses. Relyea (2005) reported high mortality (68-86% of individuals) in postmetamorphic juveniles of three species (*Rana sylvatica*, *Bufo woodhousii fowleri*, *Hyla versicolor*) exposed via direct spray to the commercial formulation Roundup®, a GBH, at the recommended dose. In several mesocosm and laboratory experiments on three amphibian species, *Acris blanchardi*, *Anaxyrus woodhousii* and/or *Anaxyrus (Bufo) cognatus*, Cusaac and coworkers measured the toxicity of different commercial fungicide formulations, including *Headline*® (pyraclostrobin) and *Headline AMP*® (pyraclostrobin + metconazole). Mortality rates were low and independent of fungicide treatments in an *in situ* experiment where residue interception by vegetation was high (Cusaac et al. 2015), but mortality reached 48% and 30% for pyraclostrobin and pyraclostrobin + metconazole, respectively, when amphibians were exposed to contaminated soils at the maximum recommended dose (Cusaac et al. 2016). Direct spraying of *Headline AMP*® caused dose-dependent mortality in juveniles, reaching up to 33% at the recommended dose of *Headline AMP*®, while no mortality was recorded in adults. In juveniles exposed to soil, dose-dependent mortality was also found, with the intensity of the effects decreasing with the time between soil treatment and animal introduction. No mortality was found in toads dietary exposed to pyraclostrobin via contaminated prey (Cusaac et al. 2017). These works showed that acute toxicity of pyraclostrobin fungicides in amphibians can occur even at the

recommended usage dose and revealed greater toxicity of these fungicides (i) by dermal exposure than by trophic exposure and (ii) in juveniles than in adults. In the toad *A. cognatus*, the fungicide *Headline*® induced mortality in juveniles at the recommended dose, suggesting that young amphibians exposed to spray treatments under normal conditions had a low probability of survival (Ockleford et al. 2018). *Rana temporaria* juveniles exposed for seven days to soil treated at recommended rates with seven PPPs independently (four fungicides, two herbicides and one insecticide) exhibited mortality rates ranging from 20% to 100%, depending on the compound and formulation (Brühl et al. 2013). Mortality reached 100% for pyraclostrobin in the fungicide *Headline*® within 1 hour and 20% for pyraclostrobin in the fungicide *BAS 500 18F*®, 60% for bromoxynil-octanoate in the herbicide *Curof B*®, 100% for captan in the fungicide *Captan Omya*®, 40% for fenoxaprop-P-ethyl in the herbicide *Dicomil*®, 60% for spiroxamine in the fungicide *Prosper*®, and 40% for dimethoate in the insecticide *Roxion*®. Three of the formulations caused mortality rates greater than 40% at 1/10th of the authorised field dose (i.e., *Captan Omya*®, *Dicomil*® and *Roxion*®). For a given AI, as exemplified above for pyraclostrobin, the intensity of the effects varies according to the commercial formulation (Ockleford et al. 2018). The acute toxicity of two different commercial formulations on *R. temporaria* frogs exposed by spraying can differ by a factor as great as seven for the same AI. Ockleford et al. (2018) stressed that the available information confirms that AIs determine the toxicity of PPPs and that the formulation modulates such toxicity.

Several studies have reported deleterious effects, such as malformations, deformations, metabolic and endocrine disorders, increased infections and prevalence of parasites, and decreased immunocompetence in amphibian populations. However, it was not possible to clearly determine (i) the PPPs and other toxic compounds involved or the "cocktail effects", (ii) whether the exposure occurred at the larval and/or terrestrial stage, (iii) whether the onset of effects occurred at the aquatic and/or terrestrial stage (Blaustein et al. 2003; Hayes et al. 2010; Kiesecker 2011; Köhler and Triebkorn 2013).

Several recent studies have jointly investigated bioaccumulation in laboratory effects assessment, revealing accumulation in tissues of atrazine, bifenthrin, cypermethrin (and metabolites), fenoxaprop-ethyl (accumulation of the metabolite fenoxaprop), fipronil, imidacloprid, metconazole, metolachlor, pendimethalin, pyraclostrobin and triadimefon, when exposed orally and/or dermally (Glinski et al. 2019; Jing et al. 2017; Van Meter et al. 2016; Van Meter et al. 2015; Yao et al. 2017). With regard to the effects observed in field studies, the EFSA (Ockleford et al. 2018) highlighted the high sensitivity of amphibians to PPPs due to several specific features of these taxa (see section III.6).

PPPs can induce behavioural effects in amphibians, including impacts on feeding, abnormal swimming movements, activity levels, antipredatory behaviour, predation features, and reproductive behaviour (Sievers et al. 2019). The meta-analysis by Sievers et al. (2019) mentioned that research work frequencies are largely dominated by studies on aquatic stages: 81% of the studies concern larval stages, only 16% adults, and only 6% metamorphic stages. The available information indicates

that for terrestrial stages, reproductive behaviour is impaired when animals exposed to contaminants (-20% overall, including all types of organic and metallic contaminants). More specifically, fungicides and insecticides PPPs have significant negative effects. There are no studies in this meta-analysis on herbicides or other PPPs, such as molluscicides. The negative effects of PPPs observed in tadpoles could affect survival and fitness in adults. The authors noted that there is a lack of knowledge about the impacts of contaminants on adult amphibians, including the effects of exposure during the larval stage, which may not manifest until adulthood (delayed or carry-over effects).

Subindividual effects

Toxicological studies on laboratory animals were not systematically detailed in the present review. Although they are numerous and can potentially provide information on toxic or pathological processes, most of the laboratory data are produced for ERA. The unrealistic exposure conditions used in these experiments (i.e., doses too high relative to plausible or predicted environmental concentrations, short-term exposure, irrelevant exposure design, etc) and the interspecific differences in physiology and sensitivity to PPPs limit or even prevent the extrapolation of this information to wild species exposed in nature.

These responses are indicative of cellular or physiological disturbances, and remain difficult to interpret in terms of impacts at the population or community levels.

Birds other than raptors

Numerous studies have investigated the relationship between acetylcholinesterase inhibition and poisoning, which can result in bird mortality. These works have been developed mainly for diagnostic purposes. These studies focused mainly on AIs now banned worldwide and will not be discussed (e.g., Shimshoni et al. 2012; Bang et al. 2019).

A wide range of subindividual effects (e.g., molecular, cellular, and organ-level) have been observed in birds in relation to exposure to various chemical families of PPPs, including CUPs. For exhaustive summaries, refer to Gibbons et al. (2015), Wood and Goulson (2017) and Moreau et al. (2022). Moreover, in the context of field monitoring, interpretation is hampered by the nonspecificity of these responses and the significant influence of confounding factors that are not always considered (other pollution and environmental stresses). For example, oxidative stress markers lack specificity in field application settings (Abu Zeid et al. 2019; Lopez-Antia et al. 2015; Wang et al. 2018). Plasma biochemistry-related responses were also tested. Lopez-Antia et al. (2018) showed that exposure of red-legged partridges to flutriafol (a fungicide applied as seed coating) at recommended dose, resulted in a reduction in plasma cholesterol and triglycerides. Bellot et al. (2022a) showed alterations in metabolic functions in house sparrows exposed to the triazole fungicide tebuconazole through drinking water at an environmentally relevant dose in a 7-month experiment. In adult cockerels dosed with GLY from below to equivalent to the chronic 21 days no observed adverse effect level (NOAEL) in birds, Hussain et al. (2019) reported adverse clinico-hematological (red blood cell counts, haematocrit, and haemoglobin) and serum biochemical responses with (i) a lower

quantity of total proteins and albumin; (ii) greater concentrations of liver enzymes alanine aminotransferase, aspartate aminotransferase, and alkaline phosphatase; (iii) increases in urea and creatinine, which are related to kidney functioning; (iv) increases in CK-Mb, triglycerides, and cholesterol; and (5) increases in oxidative damages and genotoxicity in birds. The birds exposed to the highest doses showed clinical signs of intoxication (e.g., ruffled feathers, dullness, tremors) and a decrease in food consumption and body mass (Hussain et al. 2019). In Japanese quails (*Coturnix japonica*) exposed to the GBH RoundUp Flex® in food to a dose about ten times lower than the NOAEL in birds, offspring showed adverse effects, with altered embryonic development, and embryonic brain tissue expressed 20% greater lipid damage than controls (Ruuskanen et al. 2020a). In Japanese quails fed from the age of 10 days to 12 months food with added with the GBH Roundup Flex® corresponding to a dose well below the NOAEL in poultry, adverse effects on the development of body and flight feathers were found in females (Ruuskanen et al. 2020b). In Japanese quails fed from the age of 10 days to 12 months food added with the GBH RoundUp Flex® at a dose approximately ten times lower than the chronic NOAEL for poultry, the birds exhibited decreased hepatic activity of the antioxidant enzyme catalase and decreased testosterone levels in males. However, the levels of other oxidative stress biomarkers, acetylcholinesterase activity, maturation, testis size and egg production did not differ between exposed and control birds (Ruuskanen et al. 2020c).

Raptors

Few studies have examined the subindividual effects of PPPs on raptors, probably due to the constraints of conducting experiments under controlled conditions. To diagnose nonlethal exposures to CILs, Roy et al. (2005) proposed reference values for plasma β -esterase activities (including acetylcholinesterase) for 20 European raptor species. The work carried out on anticoagulant rodenticides has mainly concerned the disruption of blood coagulation, the target of these compounds, and some allowed to propose methods for measuring various coagulopathy markers and to define diagnostic values in two North American raptor species (Rattner et al. 2011; Rattner et al. 2012; Rattner et al. 2014). It has been shown that preexposure of American kestrels to brodifacoum, a second-generation anticoagulant, induces more severe coagulopathy with subsequent exposure (Rattner et al. 2020). Considering the frequency of residue detection in raptor tissues (Lopez-Perea et al. 2019), it is likely that raptors are repeatedly and chronically exposed to anticoagulants, which is also due to their biocidal use. The potentiation following repeated exposure shown by Rattner and Harvey (2020) therefore sheds new light on the mechanisms of anticoagulant toxicity and should be considered in future studies.

It has been shown that hepatic OC concentrations correlate with alterations in protein and lipid structures that are precursors of neurodegenerative diseases in the brain of the Eurasian hawk *Accipiter nisus* (Heys et al. 2017). A link between the number of nuclear abnormalities or micronuclei in haematocytes and the season, the use of PPP (unquantified) and the density of cultivated areas around the nest was found in American kestrels (Frixione and Rodriguez-Estrella 2020).

Mammals

Many studies have explored the subindividual effects of PPPs in rodents and rabbits, which are experimental models for regulatory toxicology. A few studies have more specifically targeted either exposure conditions close to the agricultural use of PPPs or relevant animal models. For example, Aramjoo et al. (2021) provided a meta-analysis on the effects of diazinon on lipid metabolism. Although transposition to wild animals remains difficult, the systematic approach makes it possible to strengthen the weight of the studies.

Shinya et al. (2022) showed that the cytochrome P450-dependent metabolism of NNs in the liver of wild racoons *Procyon lotor* was one-tenth to one-third lower than that of rats.

Reptiles

The subindividual responses induced by PPPs under experimental or *in situ* conditions are among the most studied. Regardless of the exposure context, i.e., AIs or commercial insecticide, herbicide or fungicide formulations alone or in combination, effects related to the induction of oxidative stress, organ pathologies (liver, gonads) or endocrine, haematological, enzymatic, gene expression or nervous system disturbances have been demonstrated on different life stages of lizards, caimans and more rarely snakes (Barraza et al. 2021; Basso et al. 2012; Bicho et al. 2013; Burella et al. 2017, Burella et al. 2018; Cardone 2015; Chang et al. 2018b; Chang et al. 2019; Chen et al. 2019a; Chen et al. 2019b; Freitas et al. 2020; Latorre et al. 2013; Latorre et al. 2016; Lopez-Gonzalez et al. 2013; Lopez-Gonzalez et al. 2017; Mestre et al. 2019; Mestre et al. 2020; Mingo et al. 2017; Neuman-Lee et al. 2014; Schaumburg et al. 2016; Wang et al. 2014; Wang et al. 2019a; Wang et al. 2019b; Wang et al. 2019c; Wang et al. 2020a;). Effects on individual life history traits or population structure were assessed in conjunction with subindividual effects in only five studies. Three of these studies detected both subindividual and individual responses in exposed animals (Chen et al. 2019b; Mestre et al. 2019; Mingo et al. 2017). Only Mingo et al. (2017) demonstrated cellular effects related to oxidative stress, decreases in body condition and changes in the population structure of lizards in vineyards sprayed with fungicides (17 commercial formulations including 24 AIs) and the GBH Clinic Ace®.

Amphibians (terrestrial stages)

The insecticide chlorpyrifos and the herbicides 2,4-D and GLY were found to cause neurotoxicity and oxidative stress, as assessed using measurements of biomarkers in blood samples from adult male toads (*Rhinella arenarum*) dermally exposed in a controlled experiment (Lajmanovich et al. 2015). Two studies have characterised the responses of terrestrial juvenile *Lithobates* frogs exposed for 8 h to PPPs alone or in mixtures (duo and trio) in contaminated soil based on a metabolomic approach. Glinski et al. (2019) studied the responses of *Lithobates sphenoccephala* following exposure to contaminated soil by bifenthrin (an insecticide), and/or metolachlor (an herbicide) and/or triadimefon (a fungicide) at maximum and 1/10th application rates. On average, exposure to the maximum application rates resulted in changes in 22 metabolome molecules and exposure to 1/10th

of the recommended dose in changes in 38 metabolome molecules. When applied as a single-substance, PPP showed overall fewer over- or under-regulated metabolome molecules compared to exposures to mixtures of two or three AIs. The exposure resulted in the up- or down-regulation of amino acids and other key metabolites involved in glutathione-related metabolic pathways and energy balance, suggesting increased energy requirements and potential for energy depletion in exposed animals (Glinski et al. (2019). Van Meter et al. (2018) studied five PPPs, comprising three herbicides (atrazine, metolachlor and 2,4-D), an insecticide (malathion) and a fungicide (propiconazole). The hepatic metabolomic profile of juveniles *Lithobates clamitans* exposed to soils contaminated with a single AI, a duo of AIs or mixtures of three AIs reveals both single and interactive effects on the alteration of biochemical processes. Metabolic profiles indicated different responses when AIs are present in combination. The metabolic responses of amphibians appear to be dependent on each AI and each mixture, depending on the potential for disruption of metabolic and biochemical networks (Van Meter et al. 2018). Recent reviews highlighted the chronic toxicity of GBHs in amphibians (e.g., Ojelade et al. 2022).

Focus on the effects of PPPs on key physiological functions likely to impact populations

Endocrine disruption

Endocrine disruption and its population-wide consequences in wildlife have been demonstrated for many AIs that are now banned or which use is regulated (e.g., OCs, OPs, carbamates, triazines) (Köhler and Triebkorn 2013; Matthiessen et al. 2018). However, while CUPs are globally considered to have less endocrine disrupting potential, evidence of endocrine disruption for different taxa is emerging for several families of insecticides and fungicides, such as OPs, pyrethroids, thiocarbamates, NNs and triazoles (Köhler and Triebkorn 2013; Lopez-Antia et al. 2013; Lopez-Antia et al. 2018; Matthiessen et al. 2018). Numerous studies, mostly conducted on rodents in the laboratory, have confirmed and characterised endocrine disruption-related responses (e.g., Rieke et al. 2017). Exposure to endocrine disruptors, in adulthood or during growth but also during pre- and neonatal development can affect long-term hormonal regulations and behaviours, either associated to reproduction or to survival. Various compounds, such as GLY, vinchlozolin, haloxyfop-p-methyl ester, and fipronil have been shown to have behavioural effects on birds and mammals (Engell et al. 2006; Satre et al. 2009; Magalhaes et al. 2015; Mendes et al. 2018; Dechartres et al. 2019; Krishnan et al. 2019). The direct link with endocrine disruption has not been systematically demonstrated, and behavioural alterations may be caused by other mechanisms, such as neurotoxicity or other physiological alterations. A growing body of evidence highlights endocrine disruption and reproductive issues in response to GLY exposure in vertebrates (Gandhi et al. 2021; Ojelade et al. 2022).

Birds

Jaspers et al. (2013) attempted to identify different focal species of birds according to different types

of endocrine disruption, including cases of exposure to PPPs. However, the assessment of potential adverse effects due to exposure is further complicated by the wide variation between avian species in terms of reproductive strategies, sexual differentiation and migration or longevity. Differences in reproductive strategies, particularly in chick development patterns, predispose birds to wide variations in response to steroid-type endocrine disruptors (Ottinger and Dean 2011). Hormonal disruptions in birds have been shown to target the hypothalamic-pituitary-thyroid axis, with disorders in thyroid hormone levels (Pandey and Mohanty 2015; Leemans et al. 2019), or affecting the hypothalamic-gonadal axis (Mohanty et al. 2017), with proven consequences for reproduction (Pandey et al. 2017; Pandey and Mohanty 2015). The potential for endocrine disruption due to their estrogenic activity has been shown for different AIs, such as diazinon, tolclofos-methyl, pyriproxyfen, prothiofos and thiabendazole, with synergistic effects of mixtures varying effective doses by a factor of 10 (e.g., prothiofos + pyriproxyfen or thiabendazole + orthophenylphenol mixture) (Manabe et al. 2006). In house sparrows exposed for 6 months to environmentally realistic doses of tebuconazole by drinking water, a decrease in the thyroid hormone T4 levels was found and females exhibited an alteration in feather quality, suggesting that the azole fungicide affects the thyroid endocrine axis (Bellot et al. 2023).

Mammals

Köhler and Triebkorn (2013) stated that more than 120 AIs are considered endocrine disruptors among PPPs. They cite OCs, OPs, carbamates, pyrethroids, thiocarbamate fungicides, triazine herbicides and triazole fungicides in rodents. Ruiz and coworkers (2019) showed sex-dependent effects of the fungicide tolylfluanid on energy metabolism in mice. After *in utero* exposure, females showed increased insulin sensitivity, normal glucose synthesis activity via gluconeogenesis and decreased adipose tissue production, whereas in males, insulin sensitivity and adipose tissue development were not altered. Tsetsatsi and coworkers (2019) reported decreased sperm vitality and number, reduced sex organ mass and decreased production of the sex hormone follicle stimulating hormone FSH and the luteinising hormone LH in male rats exposed to NNs such as imidacloprid. A recent review on the effects of NNs alone or in combination highlights the multiple effects observed on gonads and on thyroid, as well as the effects of these substances in combination with other insecticides (OPs) or fungicides such as propineb or mancozeb (Zhao et al. 2020). Unfortunately, field studies on endocrine disruption issues confirming or demonstrating the extent of this effect are rare, apart from those involving OCs or OPs, but often associated with other persistent organic pollutants, such as polychlorobiphenyls.

Reptiles

There is evidence of endocrine disruption by PPPs in reptiles. Most field studies have focused on OCs. Hormonal disturbances affecting sex steroid concentrations and disturbances of sexual dimorphism in alligator populations colonising lakes contaminated with DDT and its derivatives have been shown (Boggs et al. 2011). Only Bicho et al. (2013) addressed the endocrine disruption

potential of PPPs other than OCs *in situ*. Compared with individuals from untreated sites, adult male *P. bocagei* lizards captured at sites treated with several herbicides (alachlor, bentazone, dicamba, dimethenamid-P, mesotrione and/or terbuthylazine) showed histological changes in the thyroid gland and testes as well as activation of testicular thyroid hormone receptors. No difference in plasma testosterone concentration was detected. These results suggest that these herbicides may induce thyroid disruption, affecting the male reproductive system in lizards. Alachlor, which has been shown to have thyroid effects in mammals, could be the main driver of the observed effects according to Bicho et al. (2013). Following exposure to different AIs under controlled conditions, changes in thyroid, stress or sex hormone levels, endocrine gland damage or changes in the expression of genes involved in endocrine function have been detected for fungicides (triadimenol, Wang et al. 2020b; methyl thiophanate, De Falco et al. 2007; insecticides (dinotefuran, thiamethoxam and imidacloprid, Wang et al. 2019a, Wang et al. 2020a; flufenoxuron, diflubenzuron, Chang et al. 2019; alpha-cypermethrin, Chen et al. 2019b; lambda-cyhalothrin, Chang et al. 2018a; or herbicides (L-glufosinate-ammonium, Zhang et al. 2020)) in several reptile species. Of these studies, only Zhang et al. (2020) established relationships between these hormone disruptions, the physiological functions they control, and the consequences for life history traits, including reproduction. These findings demonstrate the potential of PPPs belonging to different chemical families to induce disturbances in the neuroendocrine system, but the causal mechanisms and consequences for individuals have rarely been described or evaluated. No study has attempted to evaluate the relationship between endocrine disruption and its effects on populations. A review showed that, even in OF areas, applied substances including fertilisers can be sources of steroids that can affect lizard reproduction (Silva et al. 2020).

Amphibians (terrestrial stages)

Amphibians are considered a taxonomic group particularly sensitive to endocrine disruption. Endocrine disruptors can have severe impacts on these animals through alterations in processes regulated by thyroid hormones, which are involved in development and metamorphosis, and/or oestrogenic hormones, which are involved in maturation and sex determination (Ockleford et al. 2018). The hormonal effects of PPPs in amphibians have been described in various reviews and involve both banned AIs and CUPs (Blaustein et al. 2003; Hayes et al. 2010; Köhler and Triebkorn 2013). Recently, endocrine disruption has been reported, with incidences of feminisation in male amphibians in “intensive” agricultural areas and a gradual reduction in the expression of secondary sexual characteristics in males in environments with an increasing degree of agricultural activity. This effect may indicate an anti-androgenic effect, while various widely used PPPs (e.g., imidazoles) have demonstrated anti-androgenic activity *in vitro* (Ockleford et al. 2018).

Immune system

Immunocompetence is reported to be crucial to wildlife survival through its role in wound healing, resistance to parasites and pathogens and hence survival and longevity and to play a potential role

in reproduction via hormonal changes, inflammatory responses and energy trade-offs (Acevedo-Whitehouse and Duffus 2009). Associations have been reported, particularly in amphibians and birds (taxa extensively studied in relation to these issues), between PPP exposure and reduced immune responses, as well as between viral, fungal and helminth infections and even mortality (especially for amphibians, for which interactions between PPP exposure and other stressors may be the cause of their global decline) (Acevedo-Whitehouse and Duffus 2009). Alterations of the immune system in terrestrial vertebrates have been shown for many families of banned PPPs or CUPs, namely, OPs, OCs, carbamates, acid (phenoxy) herbicides, triazines and NNs (Köhler and Triebkorn 2013; Mason et al. 2013). These alterations in the immune response at the individual level can result in increased vulnerability to pathogens and parasitic pests, even leading to population-level effects. The consequences at the population or community level remain to be demonstrated for the most recent AIs. Indeed, the apparent increase in bacterial disease in birds over the past two decades has been speculatively attributed to altered immunity due to exposure to PPPs (Mason et al. 2013). The emergence or occurrence of zoonotic and parasitic diseases affecting birds, bats and amphibians shows some congruence with trends in PPP use in the USA (Mason et al. 2013).

Birds other than raptors

Several studies have shown negative effects of imidacloprid and thiram on the immune status of adult and juvenile birds (Lopez-Antia et al. 2013; Lopez-Antia et al. 2015). However, for NNs, the effects on the immune response are variable across studies depending on dose, species and endpoints (Gibbons et al. 2015; Lopez-Antia et al. 2015; English et al. 2021). A positive correlation between the prevalence of parasites in feces and clothianidin concentrations in the liver has been shown in partridges (Lennon et al. 2020). Sigouin et al. (2021) highlighted the interaction effect of haematophagous ectoparasite abundance and trophic exposure to PPPs on the decrease in haematocrit levels in young insectivorous passerines.

Mammals

The effects of NNs and other PPPs on immune status have also been highlighted in mammals, especially in bats, whose immune function is altered during hibernation, favouring the development of the fungus responsible for white-nose syndrome (Bayat et al. 2014; Kannan et al. 2010; Mineau and Callaghan 2018; Oliveira et al. 2021). Upon awakening, bats undergo a phase of "massive inflammatory response", in which part of the immune tissue is destroyed before reconstruction (Mineau and Callaghan 2018). In mammals, exposure to CIIIs has been associated with increases in infections, parasitism and epidemics, which may be linked to the immunotoxic effects of these substances (Köhler and Triebkorn 2013).

Reptiles and amphibians (terrestrial stages)

In amphibians, the immune function has a particular component consisting of cutaneous antimicrobial peptides. They are of major importance in fighting infections, such as deadly infections

caused by fungal pathogens such as those of the genus *Batrachochytrium*, which are involved in the decline and extinction of amphibians worldwide (Ockleford et al. 2018). The effects of PPPs on the immune system and infection prevalence are among the main causes highlighted in the literature to explain the global decline in this taxonomic group. Numerous studies have shown immunotoxicity and a decrease in immunocompetence in amphibians exposed to PPPs, but most have focused on banned AIs (Blaustein et al. 2003; Kiesecker 2011; Köhler and Triebkorn 2013), and only a few cases were reported for reptiles (Siroski et al. 2016). Again, it is difficult to dissociate aquatic and terrestrial components in PPP exposure and the stage of concern in induced immune responses. In a laboratory study on adult male toads (*Rhinella arenarum*), dermal exposure to the insecticide chlorpyrifos and the herbicides 2,4-D and GLY caused immunological depression (Lajmanovich et al. 2015).

Microbiota and microbiome

Research on the microbiota, the holobiont, the microbiome and links to host health and pathogen dynamics is currently expanding. This recent field of research is gradually extending to the study of the role of PPPs in modifying microbial biodiversity and microbiota responses in hosts. However, this topic has been understudied in wildlife, despite the potential consequences on population and community of both microorganisms and hosts. Cases of dysbiosis (disturbance of the microbiota in terms of taxonomic and functional composition) have been described in birds, mammals or amphibians exposed to GLY or trichlorfon (Crisol-Martinez et al. 2016; Mendes et al. 2018; Dechartres et al. 2019; Zhao et al. 2021; Ruuskanen et al. 2020c). The cecal microbiota of sharp-tailed grouse *Tympanuchus phasianellus* and greater prairie chickens *Tympanuchus cupido* living in extensive croplands or in uncultivated grasslands was studied by Drovetski and coworkers. For both species, the microbiota differed between birds from uncultivated habitats while those of individuals from crop-areas converged. Although the microbiota richness was greater than that in birds from grasslands, dysbiosis was observed in birds from croplands since some beneficial bacteria were not found or declined and were replaced by potential pathogens (Drovetski et al. 2022). A greater load of the virulome and resistome was also detected in birds from croplands. Importantly, the diet of the birds differed between grasslands and croplands. The use of PPPs might have triggered such changes in the microbiota and potential for dysbiosis through alterations in source environmental microbial communities, disturbances in the immune system and/or changes in the gut microbiota of the chicks, as well as through indirect effects of PPPs on food resource diversity (Drovetski et al. 2022). Recent reviews, mostly focused on laboratory model animals, provide a comprehensive and detailed overview of the current knowledge (Chiu et al. 2020; Syromyatnikov et al. 2020; Meng et al. 2020). A review about the effects of GBHs revealed shifts in microbial compositions and a potential role of GLY in the proliferation of plant and animal pathogens (Van Bruggen et al. 2018). The effects of such disruptions on the gut microbiota could have implications for wildlife health that have yet to be determined.

III.3. Exposure to and accumulation of CUPs

The aim here is to characterise the PPPs (or families or mixtures) for which wildlife exposure is proven or likely *in natura* but for which the study of effects is too incomplete to allow any interpretation from a toxicological point of view. Thus, the following paragraph summarises the studies that report exposure to and/or accumulation of PPPs without any systematic link to effects on individuals, populations or communities.

Exposure is defined as contact between an organism, and one or more AIs. It can occur via various nonexclusive routes depending on the characteristics of the PPP and its use, the environment and its contamination, and the organism. It is a dynamic process in space and time. The exposure routes for terrestrial vertebrates include the oral route (trophic via food and drinking water), which is often considered the main route, and the dermal and respiratory routes, which have not been studied much overall but may be significant for several taxa. It is now common practice to distinguish between exposure, i.e., contact with PPPs, and accumulation, which results from exposure and corresponds to the presence of residues in the tissues of organisms.

Birds other than raptors

A fairly rich body of literature exists for coated seeds (mainly with NNs or anticoagulant rodenticides), notably due to PPP analyses conducted in the framework of toxicovigilance (Lennon et al. 2020; Millot et al. 2017; Nakayama et al. 2019). Different types of seeds are used (e.g., wheat, barley, maize, rape, etc), leading to potential exposure of many species (Lopez-Antia et al. 2016; Roy et al. 2019; Lennon et al. 2020). For example, based on field monitoring, it was estimated that 15 to 30 bird species were likely to consume coated seeds following sowing (Lopez-Antia et al. 2016; Millot et al. 2017; Prosser and Hart 2005). In North America, McGee et al. (2018) identified two species, the blue jay *Cyanocitta cristata* and the American crow *Corvus brachyrhynchos*, which consume maize seeds treated with a NN. Fernandez-Vizcaino et al. (2020) reported that digestive contents sampled from red-legged partridges in Spain contained eight AIs among the 21 screened, and residues were detected in 33% of the birds. The detected AIs were mostly fungicides (in 32% of the partridges), which included flutriafol, metalaxyl-M, triticonazole, tebuconazole, prothioconazole, fluoxastrobin, and difenoconazole. Triazoles were found in all the positive samples, and tebuconazole occurred the most frequently. By computing risk based on dietary intake and toxicological data, Fernandez-Vizcaino et al. (2020) highlighted concerns for granivorous bird populations. The beet seed appears to be less palatable due to the appearance of the pellet (Avery et al. 1997; Prosser and Hart 2005), which may limit exposure. Such exposure to PPPs through the consumption of coated/treated seeds or poisoned baits represents a particular case of primary direct ingestion of PPPs. In most cases, it involves AIs with a high risk for nontarget vertebrates. To assess the probability of exposure of breeding birds in agricultural areas, an approach combining PPP treatment schedules in the field and telemetric monitoring of gray partridges before and during incubation was carried out in France (Bro et al. 2015). More than 70% of partridge nests were

exposed to one or more treatments, which involved fungicides (53%), herbicides (25%) and/or insecticides (16%) and could lead to cumulative exposure to up to 22 AIs (Bro et al. 2015).

With the development of multiresidue analytical techniques, recent information on bird exposure to both banned PPPs and CUPs has been obtained through measurements of residues in body fluids, tissues or other biological matrices. The prevalence of exposure to NNs varies from one study to another and some studies have detected NNs in only a few individuals (e.g., Graves et al. 2022). Overall, the majority of publications converge toward systematic ubiquitous exposure in farmland species and other birds, with reports of high detection frequency sometimes occurring. Roy and Chen (2023) reported that at least one NN among the seven screened was detected in 93% and 80% of the faecal pellets of the sharp-tailed grouse and the greater prairie chicken, respectively, sampled along agricultural gradients in Minnesota (USA). The occurrence of at least one NN reached 90% and 76% in the livers of sharp-tailed grouse and greater prairie-chickens, respectively (Roy and Chen 2023). In North America, imidacloprid was detected in more than one-third of wild birds (36% of 55 species across 17 avian families) from diverse Texas ecoregions, with higher incidences of exposure during fall and spring than other seasons (Anderson et al. 2023). Clothianidin, dinotefuran, nitenpyram, or thiamethoxam residues were not detected in birds, possibly due to the higher limits of detection compared to those of imidacloprid. In the omnivorous house sparrow, analyses of residues in feathers collected from conventional, integrated-production and organic farms in Switzerland revealed pervasive exposure since at least one NN was quantified in all samples (Humann-Guilleminot et al. 2019b). Thiacloprid was the most frequently detected NN (99%), and clothianidin reached the highest concentrations. Higher concentrations of NNs were found in CF than in integrated-production farming and OF but NNs were quantified in feathers collected from different types of farms. In wild turkeys (*Meleagris gallopavo*) in Canada, MacDonald et al. (2018) reported NN accumulation in the liver of individuals collected during the hunting season (clothianidin, thiamethoxam, or both) and the presence of the fungicide fuberidazole in some individuals. Prouteau (2021) analysed 8 NNs and several NN metabolites, flupyradifurone and sulfoxaflor (recent systemic insecticides belonging to the butanolide and sulfoximine chemicals, respectively), as well as azole fungicides (14 triazoles and 2 imidazoles), in the plasma or feathers of birds from southwestern France (European blackbird *Turdus merula*, great tit, white stork *Ciconia ciconia*, lesser black-backed *Larus fuscus* and herring gull *Larus argentatus*). Residues of NNs (acetamiprid, clothianidin, dinotefuran, imidacloprid, thiacloprid, thiamethoxam, and metabolites acetamiprid-N-desmethyl and imidacloprid-guanidin) were quantified at very high frequencies, reaching 100% for several of them. Many azole fungicides were also detected in 100% of the analysed individuals, i.e., bromuconazole, cyproconazole, difenoconazole, epoxiconazole, fenbuconazole, flusilazole, imazalil, metconazole, myclobutanil, penconazole, prochloraz, propiconazole, tebuconazole, and tetraconazole. Overall, these findings show a generalised contamination of birds by numerous compounds. Moreover, the number of detected compounds, quantification frequencies and PPP concentrations were greater in agricultural contexts than in coastal, forest or urban sites. As some of the quantified NN residue

values approach toxicity thresholds, Prouteau (2021) suggested the possibility of physiological or behavioural consequences in the most exposed individuals. Moreover, following the 2018 restrictions on the use of NNs, there was no significant decrease in NN concentrations in feathers in the following years, while a reduction in the number of NNs detected/quantified in plasma was observed. A time frame of 2 to 3 years is probably not sufficient to detect the effects of the ban because the AIs could be used unlawfully and/or because of the persistence of the AIs in the soil (Prouteau 2021). Similarly, Fuentes et al. (2023) studied bird blood samples (passerine birds: the European blackbird, the ciril bunting *Emberiza cirilus*, the common nightingale *Luscinia megarhynchos*, the gray partridge, and the Montagu's harrier *Circus pygargus*) and detected the presence of residues of five NNs: three banned since 2018 in France (clothianidin, thiacloprid, thiamethoxam) and two used for veterinary purposes only (dinotefuran and nitenpyram). The gray partridge was the only species exposed to the five compounds. The concentrations of the three banned NNs were similar to or greater than the concentrations found in birds monitored elsewhere before the ban. Overall, residue analyses in the USA and Europe have shown ubiquitous exposure of nectarivores, granivores, insectivores, and carnivores to different NNs in use, or recently banned and occurrence of metabolites (Bro et al. 2016; Humann-Guillemint et al. 2019b; Bishop et al. 2020; Lennon et al. 2020; Humann-Guillemint et al. 2021; Prouteau 2021). Residues of NNs have even been found in the feathers of seabirds (Distefano et al. 2022).

Rial-Berriel et al. (2021) screened 351 substances (including CUPs, persistent organic pollutants POPs, and drugs) in 151 samples of wild animals that died in care centres without any suspicion of poisoning. In addition to OCs and anticoagulants, which are present in all species, PPPs were found in a small percentage of birds (< 5%). They were mainly fungicides (e.g., flutriafol, fludioxonil, boscalid) and insecticides (e.g., permethrin). The different classes of substances, i.e., CUPs, OCs/OPs or rodenticides, were detected at higher concentrations in terrestrial than in water birds. For CUPs, mainly birds other than raptors were contaminated.

Direct exposure to PPPs during or following treatments was revealed through residue analyses on skin tissues (skin, paws) or feathers, especially for OPs (e.g., azinphos-methyl, malathion, diazinon, chlorpyrifos), carbamates (e.g., carbaryl) and NNs (e.g., acetamiprid, imidacloprid) (Alharbi et al. 2016; Graves et al. 2019; Vyas et al. 2004; Vyas et al. 2007).

As many wildlife taxa are vermivorous and/or insectivorous, chronic exposure via the trophic route likely occurs due to contamination of their prey, in which mixtures of CUPs have been found (Bertrand et al. 2018; Pelosi et al. 2021; Brühl et al. 2021; Kraus et al. 2021). The pollen, nectar and/or fruits or seeds of various cultivated and wild plants are contaminated by PPPs including OPs and NNs (Botias et al. 2016; Bishop et al. 2018; Bishop et al. 2020; Humann-Guillemint et al. 2019c; Schabacker et al. 2021). Trophic exposure has been shown in insectivores and omnivores, such as swallows (Poisson et al. 2021) and swifts (Humann-Guillemint et al. 2021), and in 24 of 25 avian species sampled in orchards in the USA (Cobb et al. 2000). In tree swallows, 54 AIs or transformation products, including 9 fungicides, 18 herbicides and 24 insecticides (10 OPs, 7 carbamates + 3

derivatives and 7NNs), were monitored in food boluses (Poisson et al. 2021). The results revealed ubiquitous exposure to at least one compound detected in 46% of the food boluses and at least one compound at a quantifiable concentration in 30% of the food boluses. In total, 47 AIs were detected (i.e., 87%). Mixtures of PPPs (with a range of 2-16 compounds and an average of almost 10 PPPs per farm) were detected in 45% of the contaminated boluses. The most frequently detected PPPs were atrazine (25% of the samples), S-metolachlor (16%), imazethapyr (10%), and clothianidin (9%). The detected insecticides included four carbamates (out of six tested), eight OPs (out of nine tested), and five NNs (out of seven tested). In swifts, the concentrations of at least one NN were quantified in 75% of the food boluses, acetamiprid, thiacloprid, and thiamethoxam being the most frequently detected (Humann-Guillemint et al. 2021). Cloacal fluid analyses of the nectarivorous hummingbirds confirmed their exposure to NNs (imidacloprid, thiamethoxam, clothianidin, and acetamiprid) with a quantification rate of 26.5% to at least one NN, and to flupyradifurone which was also found in bee nectar (Bishop et al. 2018; Bishop et al. 2020).

In the gray partridge, multiresidue analyses of eggs revealed the presence of several insecticides (pyrethroids and NNs: cyhalothrin, clothianidin, and thiamethoxam), herbicides (e.g., diflufenican) and fungicides (e.g., cyproconazole, difenoconazole, tebuconazole, fenpropidin and prochloraz) (Bro et al. 2016). The underlying mechanisms of egg contamination have not been elucidated and could include parental transfer and/or deposition of PPPs during crop treatments. The transfer of tebuconazole to eggs was confirmed in the house sparrow experimentally exposed to this fungicide (Bellot et al. 2022b). While tebuconazole was quantified in all the eggs analysed from the exposed parents, the concentrations were below the limit of quantification (0.23 ng g^{-1} dry weight) in 85% of the eggs from the control birds. GLY residues were quantified in eggs following the parents of Japanese quails (*Coturnix japonica*) were exposed to RoundUp Flex®, revealing the possibility of maternal transfer of GBHs in birds (Ruuskanen et al. 2020a). In Japanese quail exposed experimentally from the age of 10 days to 12 months to doses of RoundUp Flex® approximately ten times lower than the chronic NOAEL for poultry, GLY was accumulated not only in eggs but also in muscle and liver tissue (Ruuskanen et al. 2020b). Food selection was also examined, and females preferred glyphosate-contaminated food to control food. Following environmentally realistic exposure to the fungicide tebuconazole or the herbicide 2,4-D by overspray or contact with contaminated soil, residues of tebuconazole were found both in eggshells and egg contents of the red-legged partridge, while residues of 2,4-D were detected in eggshells only (Ortiz-Santaliestra et al. 2020). Accumulation in the eggshell or content was 3 to 14 greater when eggs were exposed via overspray than via contact with soil.

In summary, most of the related work dealing with exposure and accumulation has focused on the analysis of insecticide residues, particularly OPs, and, in the last decade, NNs. There is evidence of ubiquitous and widespread exposure to OPs and NNs in the different trophic guilds. These findings are similar when pyrethroids are investigated. The few studies that have targeted the recent butenolide and sulfoximine insecticides also reported detection and quantification. Research on a

wider range of PPPs has shown the accumulation of fungicides such as azoles and herbicides. The most recent research provides insights into the exposure of birds to mixtures of PPPs, including multiple banned ones and CUPs belonging to several chemical families used as fungicides, herbicides or insecticides. The limited number of studies does not permit further generalisation of the frequency of exposure by type of use or guild or to identify "at risk" contexts.

Raptors

There is little information on the accumulation of PPPs other than OCs and anticoagulant rodenticides in raptors, and in all cases, no relationship was sought between the concentrations measured and effects at any level of biological organisation. Following the investigation of residues of the fungicide chlorothalonil and 12 AIs belonging to the chlorophenoxy herbicide family, only the herbicide chlorthal-dimethyl (DCPA) was detected in osprey *Pandion haliaetus* eggs in the USA (Chu et al. 2007). In a review of contaminant survey programs for raptors in Europe, Gomez-Ramirez et al. (2014) reported that fungicides and molluscicides are searched for in more than 50% of the countries where such monitoring was carried out, but no data (positive or negative) were published on these types of PPPs before 2017. The available studies have mainly shown the accumulation of NNs in raptors. Of the NNs quantified, imidacloprid was detected in European eagle owls *Bubo bubo* (among the seven AIs analysed; Taliensky-Chamudis et al. 2017), imidacloprid and thiacloprid were detected in the honey buzzard *Pernis apivorus* (among three AIs analysed, Byholm et al. 2018) and thiacloprid, acetamiprid, clothianidin and thiamethoxam in the barn owl (among five analysed AIs, Humann-Guillemot et al. 2021). Contrasting detection frequencies were found, with 3% of the samples analysed being positive in the European eagle owl, whereas in the honey buzzard, imidacloprid and thiacloprid were detected in 40 and 70% of the samples, respectively. In the barn owl, more than 80% of individuals were positive, especially for thiacloprid, with residues frequently found in chicks, strongly suggesting trophic transfer. Thus, the dietary specialisation of the honey buzzard on insects would not be sufficient to explain the high detection frequency of NNs. The findings of Badry et al. (2021) provide a more complete picture on the accumulation of CUPs belonging to different families and of different types of use in raptors. Residues of 28 AIs including 12 fungicides, eight herbicides and eight insecticides were investigated in the livers of 186 individuals belonging to five species and coming mainly from the northern half of Germany. Only thiacloprid was detected in two red kites (i.e., 1% of the individuals analysed). An OP insecticide, dimethoate and its active oxon omethoate, were also measured at high concentrations in two individuals but these cases were linked to deliberate poisonings of wildlife by CIIIs. Although the scope of this single publication is limited in terms of large-scale predictions, it is based on a large sample covering a near-national spatial scale and combining species with different ecological traits. It indicated relatively low accumulation levels of CUPs in birds of prey, but the detection limits of the analytical methods used ($\geq 10 \text{ ng g}^{-1}$ for 59% of the AIs analysed) must be considered, as well as the organ selected, liver), in which certain AIs are rapidly metabolised. The authors recommended the use of other biological matrices, such as blood, for future assessments of the accumulation of CUPs in

wildlife. In Brazil, chlorpyrifos-ethyl was detected in the livers of two *Megascops ssp.* specimens (Dal Pizzol et al. 2021).

Mammals (other than chiropterans)

Predatory mammals have been the subject of studies on exposure via contaminated prey. This route of exposure has been described for many years for anticoagulant rodenticides via the consumption of rodents contaminated by rodenticides (Baudrot et al. 2020; Hindmarch and Elliott 2018; Nakayama et al. 2019). According to the available studies, the carnivorous mammal populations studied are often contaminated by up to 50-60% of the individuals. Several scenarios have been described for contamination via the food web, sometimes with several successive levels of transfer involving contaminated invertebrates, which generally show no symptoms of rodenticide consumption. The other substances for which such exposure routes are classically described are mainly older insecticides (banned OCs, mostly banned OPs or pyrethroids).

Available data show that exposure to anticoagulant rodenticides is frequent, generally at low concentrations, but little is known about the impact of this exposure on animals (apart from hemostasis disorders). The authors reported detection frequencies of more than 50% for predators. In Finland, for example, Koivisto et al. (2018) described the distribution and quantification of various second-generation anticoagulant rodenticides in a wide range of carnivorous predators.

A few publications mention the impacts of OCs on mammals, particularly mustelids, which are considered highly sensitive to the reproductive effects of these compounds. Unfortunately, distinguishing the role of each compound in effects is difficult since these substances are systematically analysed together and their tissue contents found to be correlated. These compounds are still present, although the general trend is toward a decrease. Limited data are available on carnivorous mammals for the other CUPs.

A spatially explicit assessment of exposure suggested that the European hare *Lepus europaeus* frequents both recently treated and untreated plots indiscriminately and therefore does not behave in such a way as to limit its direct exposure (Mayer et al. 2020). Because of their behaviour and frequent movements between plots, hares could be preferentially exposed to sprays, both directly (during spraying) and indirectly (through coat contact with treated crops and grooming activities) (Mayer et al. 2020). In the end, PPP uptake by hares could be 7 times greater by spraying than by feeding (Mayer et al. 2020). In one of the largest multiresidue accumulation studies to date, 480 substances were simultaneously analysed in the muscle of 42 wild boars, *Sus scrofa*, 79 roe deer, *Capreolus capreolus* and 15 red deer *Cervus elaphus*, in Poland (Kaczynski et al. 2021). A total of 28 substances were detected, mainly OCs (6 in all: DDT and its metabolites in particular), NNs (5 including acetamiprid, imidacloprid and clothianidin) and other insecticides (chlorpyrifos), as well as herbicides (4 including diflufenican and methoxychlor) and fungicides (9 with tebuconazole, difenoconazole, carbendazim and benalaxyl). Among the 136 animals tested, more than 80% exhibited trace residues of at least one PPP, with DDT alone detected in more than 100 individuals. The levels measured were low, within the $\mu\text{g kg}^{-1}$ range, with the notable exception of anthraquinone

(> 80 µg kg⁻¹), which is still often used as a wild boar repellent despite its ban several years ago. Many animals showed residues of at least two and up to seven PPPs. Apart from measurements carried out in the context of PPV or toxicovigilance on moribund or dead animals, these measurements of tissue concentrations are only very rarely linked to assessments of the toxic effects of the compounds.

Shinya et al. (2022) assessed the exposure of wild raccoons *Procyon lotor* to NNs in Japan. Acetamiprid, imidacloprid, clothianidin, dinotefuran, thiacloprid, thiamethoxam, and desmethyl-acetamiprid were detected in the urine. The results showed a high exposure prevalence: at least one of the six NNs screened or one metabolite was found in 90% of the raccoons. The concentrations were comparable to the levels reported in humans.

Krief et al. (2022) conducted a controlled experiment in a zoo on the captive chimpanzee, in which 152 organics and their metabolites belonging to 21 chemical families were measured in hair samples. The samples were collected (i) when monkeys were fed fruits and vegetables from CF coming from southern France or Spain and (ii) after a food shift when monkeys were fed 100% of fruits and vegetables originating from OF. Seventy-nine chemicals were detected in the monkeys fed with CF diet and 63 when fed with OF diet, and 20 compounds were no longer detected after the food shift. The mean number of 66.5 compounds/individual decreased to 56.3 compounds/individual when the chimpanzees were fed OF food. The concentrations of 29 compounds also decreased overall (γ-HCH, PCP, metazachlor, DETP, permethrin, mecoprop, MCPA, dichloprop, 2,4-D, prochloraz, carbendazim, oxamyl, propoxur, acetamiprid, imidacloprid, thiacloprid, oxadiazon, pyraclostrobin, propazine, terbutryn, DCPMU, DCPU, diuron, cyprodinil, pyrimethanil, trifluraline, spinosyn A, lenacil and prosulfocarb). The concentration increased between CF and OF food for five compounds: bisphenol S, tebuconazole, indoxacarb, trifloxystrobin and chlortoluron. Using the same multiresidue analysis of hair samples from chimpanzees free-living in Kibale National Park, Uganda, Krief et al. (2022) reported the detection of 60 compounds in wild chimpanzees with a mean of 40 compounds/individual. The compounds detected in wild chimpanzees included OCs (γ-HCH, PCP, and HCB), OPs (IMPy, DMP, DMTP, DEP, DETP, TCPy, PNP, and 3Me4NP), pyrethroids (permethrin, CI2CA, 3-BPA), amid PPPs and acid herbicides (mecoprop, MCPA, dichlorprop, 2,4-D, metolachlore), azoles (thiabendazole), triazines/triazinones (atrazine desethyl, propazine), NNs (imidacloprid, thiacloprid), ureas (DCPMU, DPMU, 3,3-dichloroaniline, diuron, fenuron), oxadiazines/phenylpyrazoles/strobilurins (oxadiazon, fipronil, fipronil sulfone, azoxystrobin, trifloxystrobin), carbamates/carboxamids (carbendazim, oxamyl, propoxur, boscalid), and dinitroanilines/thiocarbamates/miscellaneous PPPs (trifluraline, spinosyn A, lenacil, prosulfocarb). The concentration ranges of the compounds were similar between captive and wild chimpanzees (Krief et al. 2022).

A multiresidue analysis targeting 73 CUPs and 67 banned PPPs (including transformation products) in the hair of an omnivorous rodent (wood mouse *Apodemus ssp.*) and an insectivorous shrew (*Crocidura russula*) living in croplands revealed the presence of 32 to 65 compounds detected per

individual, among which 18 to 41 CUPs per individual. A total of 112 compounds were detected (Fritsch et al. 2022). The occurrence of CUPs was high in small mammal populations since 25 compounds were detected in more than 75% of the individuals, meaning that approximately half of the 61 detected CUPs were present in almost all the populations (75–100% of individuals). The results showed the ubiquity of exposure since PPP residues were detected in all animals, regardless of the type of habitat (hedgerows, cereal crops and grasslands) or management method (CF or OF) where they were captured. The most frequently detected CUPs (> 80% of individuals) or showing concentrations among the highest (i.e., > 10 µg kg⁻¹) were epoxiconazole, cyproconazole, propiconazole, prochloraz, azoxystrobin, carbendazim, imidacloprid, thiacloprid, TCPy, Cl2CA, 3-PBA, ClCF3CA, cypermethrin acetamiprid, metolachlor, MCPA, 2,4-D, pendimethalin, dimethachlor, mecoprop, prosulfocarb, dichlorprop, lenacil, boscalid, aclonifen, and chlortoluron. The 4 compounds detected in 70 to 80% of the samples were all fungicides, mainly azoles (prochloraz, propiconazole, cyproconazole) and pyraclostrobin (strobilurin family). The highest concentrations (> 50 µg kg⁻¹) were measured for the herbicides aclonifen, dichlorprop, diflufenican, isoproturon, MCPA, mecoprop, metolachlor and propyzamide; the fungicides boscalid, carbendazim, cyproconazole, epoxiconazole, prochloraz, propiconazole and tebuconazole; and the insecticide imidacloprid. This study demonstrates the exposure of wild mammals to chemical families of compounds that have various modes of action and different types of usage and application (e.g., spray, coating). Finally, the analyses revealed differences in the number of compounds detected, concentrations and exposure profiles to PPPs between wood mice and shrews, which might be related to their physiological traits and/or ecological traits, most notably their diet.

Recent research has focused on GLY, revealing pervasive exposure to glyphosate in several mammals in farmlands. In samples of the gastric content of the Iberian hare (*Lepus granatensis*) from Spain, Martinez-Haro et al. (2022) did not detect GLY in animals from PPP-free areas, while the frequency of detection was 9 to 22% in hunted hares and reached 45% in animals found dead from PPP-treated areas. Hair samples were collected in herbivorous and granivorous/omnivorous rodents (voles *Microtus arvalis* and *Myodes glareolus*, wood mouse *Apodemus sylvaticus* and house mouse *Mus musculus*) and insectivorous shrews (*Crocidura russula*) sampled in French arable landscapes. Screening of GLY, its main metabolite AMPA, and glufosinate in hair showed the detection of the three compounds in all species (64% of individuals for GLY, 51% for AMPA, and 44% for glufosinate) (Fritsch et al. 2023). The frequencies of detection and concentrations were lower overall in insectivorous shrews and omnivorous wild mice than in herbivorous and granivorous voles. The frequencies of detection and the concentrations were not found to be related to farming practices or proxies of PPP treatment intensity at the landscape scale in croplands, revealing the ubiquity of exposure over the agrosystem mosaic.

Chiropterans

Like in other mammals, complex mixtures of PPPs were found in bat carcasses of two species (*P. pipistrellus* and *Myotis myotis*) in Turkey, demonstrating recurrent exposure to multiple residues

(Kuzukiran et al. 2021). Different chemical families of historical and currently used insecticides, fungicides and herbicides were detected. These included pyrethroids (e.g., tau-fluvalinate, cyhalothrin, cypermethrin, deltamethrin), pyridazones (e.g., pyridaben), dinitroanilines and acid herbicides (e.g., pendimethalin, fluroxypyr), and triazoles (e.g., triticonazole, epoxiconazole, cyproconazole). Multi-residue analyses (209 PPPs and POPs) conducted on the liver of several hundred bats belonging to five species (*Eptesicus serotinus*, *M. myotis*, *Nyctalus noctula*, *P. pipistrellus*, and *Plecotus auritus*) collected across Germany revealed 28 compounds with four to 25 different AIs per individual (Schanzer et al. 2022). Among the PPPs, OCs were the most frequently detected, followed by other insecticides (i.e., deltamethrin and permethrin, chlorpyrifos, and metabolites of fipronil). Several families of fungicides have also been detected, with a total of eight AIs (i.e., azoles: difenoconazole, epoxiconazole, propiconazole, tebuconazole, and tetraconazole; strobilurins: azoxystrobin; morpholins: fenpropimorph; anilids: dimethomorph), while picolinafen (pyridine derivative) was the only detected herbicide. The authors stressed that bat contamination was homogeneous across Germany except in the case of some species with specialised ecological niches (Schanzer et al. 2022). These two studies showed the exposure of bats to banned OCs and OPs and to several CUPs with azole fungicides and pyrethroid insecticides in common, but they did not detect any NNs. In a study screening three NNs (clothianidin, imidacloprid, and thiamethoxam), carbaryl and four systemic herbicides (2,4-D, atrazine, dicamba, and glyphosate) in the hair of big brown bats (*Eptesicus fuscus*) sampled in Missouri (USA), three to eight compounds were detected in the sample pooled at the county level. All the samples were positive for the herbicides 2,4-D and glyphosate and for the insecticide imidacloprid (Hooper et al. 2022). Like nonflying small mammals, chiropterans are exposed to glyphosate, but the concentrations are greater in bats (Hooper et al. 2022).

Analyses of guano collected from maternity roosts of the lesser horseshoe bat (*Rhinolophus hipposideros*) in France showed the presence of OCs such as endosulfan and lindane in several colonies (Afonso et al. 2016). However, none of the other PPPs (CIIs, metaldehyde, anticoagulant rodenticides and approximately 10 AIs/metabolites of herbicides and fungicides) were detected. This contrasting result may be related to the matrix used (faeces) and to the residence time before sampling.

The trophic route is considered to be the main pathway of exposure of bats to insecticides via the contamination of prey (Mineau and Callaghan 2018; Hernandez-Jerez et al. 2019). Recent studies have shown exposure to insecticides and many fungicides (e.g., azoles, oxadixyl) and herbicides (e.g., 2,4-D, atrazine, glyphosate, pendimethalin), but no detailed information is available about the exposure pathways involved (Kuzukiran et al. 2021; Hooper et al. 2022, Schanzer et al. 2022). Studies and reviews mention a risk of trophic exposure of chiropterans, particularly to insecticides such as NNs, based on monitoring chiropteran activities and dosages in their prey occurring at the sites they visited (Stahlschmidt and Brühl 2012).

Reptiles

With the exception of OCs and, to a lesser extent, anticoagulant rodenticides, few *in situ* data are available on the accumulation of PPPs in reptiles. Since the 1970s, reptiles have been shown to accumulate OCs at potentially high concentrations, but few studies have been conducted since 2000. They reported low residue levels compared to those measured in the 1970s, but knowledge allowing a toxicological interpretation of tissue concentrations for reptiles is lacking (Weir et al. 2013). Maternal transfer of OCs to eggs has been shown in alligators and is thought to contribute to the low egg-laying viability observed in the populations studied (Rauschenberger et al. 2004; Rauschenberger et al. 2007). Another field study revealed the presence of OC residues in chameleon *Chamaeleo chamaeleon* eggs (Diaz-Paniagua et al. 2002). The accumulation of anticoagulants, most often biocides used to control invasive species in an island context, in reptiles has also been described (reviewed in Mauldin et al. 2020). This family of rodenticides is considered to be poorly metabolised by reptiles, which are generally not highly sensitive despite differences between taxa (Mauldin et al. 2020). Only Guillot (2017) has performed multiresidue monitoring of five snake species, mainly from France, for herbicides, fungicides and insecticides other than OCs. Analysis of 39 AIs (i.e., 26 OCs and derivatives, eight pyrethroids, four chlorophenyl, chloronitrile and oxazole fungicides, and one dinitroaniline herbicide) was performed on the fat of 175 individuals who died from different causes in the wild. Only OCs and metabolites were detected in more than 10% of the individuals analysed, and their average concentrations were greater than 10 µg kg⁻¹ ww. The concentrations of p,p' DDE were greater in aquatic species. Among the other AIs, four pyrethroids (bifenthrin, deltamethrin, cis- and trans-permethrin) and the herbicide pendimethalin were detected in two to 9% of the samples at mean concentrations between 1.4 and 7.2 µg kg⁻¹ ww. In addition, further determinations in eggs revealed low concentrations of OCs and derivatives. Guillot (2017) concluded that although average OC levels do not appear to be of concern, certain high concentrations are evidence of high local contamination. The families of PPPs other than OCs were almost exclusively measured under controlled conditions. Cypermethrin (Chen et al. 2016), diflubenzuron and flufenoxuron (Chang et al. 2018b), chlorpyrifos (Ciliberti et al. 2013) and NNs (Wang et al. 2018; Wang et al. 2019b; Wang et al. 2019c); herbicides (ammonium glufosinate, Zhang et al. 2019); and fungicides (triadimenol, Wang et al. 2014; myclobutanil, Chen et al. 2017) were detected in several organs and tissues. The results revealed different internal distributions and postexposure temporal variations depending on the AIs considered; the limited number of studies prevented generalisation. Maternal transfer to eggs was demonstrated as 77.0 ± 9.1 µg kg⁻¹ of alpha-cypermethrin were measured in eggs laid by lizard females exposed to the highest dose (Chen et al. 2019b). de Solla and Martin (2011) exposed snapping turtle (*Chelydra serpentina*) eggs to soils contaminated by 10 PPPs (atrazine, simazine, metolachlor, azinphos-methyl, dimethoate, chlorpyrifos, carbaryl, endosulfan I and II, captan, and chlorothalonil) applied at 2 or 20 times the application rate. The findings suggested that the compounds accumulated have low sorption to carbon or lipids and high-water solubility. For the most hydrophilic compounds, a high vapour

pressure would also increase uptake.

Amphibians (terrestrial stages)

In natura, amphibians accumulate complex mixtures of legacy PPPs and CUPs. In agricultural areas in the USA, multiresidue analyses of the tissues of different species have shown the presence of numerous PPPs (Smalling et al. 2013; Smalling et al. 2015; Swanson et al. 2018), with several families of insecticides, herbicides and fungicides detected. Complex mixtures involving compounds currently banned in several countries in Europe and North America (OPs, carbamates, dicarboximides, pyrethroids and triazines: bifenthrin, diazinon, iprodione, simazine, and carbofuran) and compounds still in use were found in tissues. Mixtures of 17 PPPs, including 8 fungicides, 4 herbicides and 5 insecticides, as well as the transformation products of 4 AIs, were detected in two frog species, *Pseudacris maculata* and *Lithobates pipiens* (Smalling et al. 2015). Among the CUPs, the AIs detected were herbicides such as metolachlor, propyzamide and pendimethalin; pyrethroid insecticides; and many fungicides belonging to several chemical families, including azoles (e.g., fenbuconazole, fluoxastrobin, imazalil, metalaxyl, myclobutanil, pyraclostrobin, tebuconazole). In a study conducted in Argentina, a total of 20 PPPs were detected in the tissues of two species with contrasting ecology, one semiaquatic (*Leptodactylus latrans*) and the other terrestrial (*Leptodactylus latinasus*) (Brodeur et al. 2022). Considering all the sites, regardless of their distance to cultivated areas, 12.5% to 57% of the individuals had residues of at least one PPP (up to 12 compounds/individual) (Brodeur et al. 2022). Various chemical families were detected, this included 9 insecticides (chlorpyrifos-methyl, chlorpyrifos-ethyl, pirimiphos-methyl, fenitrothion, bifenthrin, permethrin, chlorantraniliprole, imidacloprid and buprofezin), 4 herbicides (acetochlor, metolachlor, atrazine and imazethapyr), and 7 fungicides (azoxystrobin, picoxystrobin, pyraclostrobin, trifloxystrobin, metalaxyl, epoxiconazole and carbendazim).

In laboratory studies, PPPs bioaccumulate in amphibian tissues and even eggs following dermal or oral exposure to insecticides, herbicides and fungicides. Examples include the metabolite of the herbicide fenoxaprop-ethyl (Jing et al. 2017), alpha-cypermethrin and some of its transformation products (DCCA, 3-PBA) (Yao et al. 2017), pyraclostrobin and metconazole (Cusaac et al. 2016), imidacloprid, atrazine, triadimefon, fipronil, and pendimethalin, bifenthrin, metolachlor, triadimefon, propiconazole, and 2,4-D (Van Meter et al. 2015; Van Meter et al. 2018; Glinski et al. 2019). Dermal absorption was demonstrated for multiple PPPs (imidacloprid, atrazine, triadimefon, fipronil, pendimethalin, pyraclostrobin, metconazole, propiconazole, metolachlor, 2,4-D, triadimefon) with varying physicochemical characteristics. The authors emphasised that bioaccumulation could explain the high internal concentrations found in amphibians during the terrestrial stage after PPP spray treatments. Maternal transfer of fenoxaprop (a metabolite of the herbicide fenoxaprop-ethyl), as well as of cypermethrin and some of its metabolites, to eggs has been shown in the adult frog *Rana catesbeiana*, raising questions about potential toxicity for the next generation (Jing et al. 2017; Yao et al. 2017).

Several studies aimed at estimating the potential exposure of amphibians to PPPs during terrestrial stages in various crop types. They have shown a high probability of co-occurrence between the presence of animals in treated plots or in their vicinity during treatments. This co-occurrence sometimes involves high proportions of breeding populations. In a vineyard area in Germany, the authors calculated that 14-29% of common toads (*Bufo bufo*) could be present in a plot at the time of at least one PPP application, and up to 24% of the population of a water body could come into contact with PPPs in a single day (Leeb et al. 2020). By investigating the potential exposure of several species (frogs, toads and newts: *Bombina bombina*, *Rana arvalis*, *Pelobates fuscus* and *Triturus cristatus*) in different crops, Berger et al. (2013) reported the co-occurrence between amphibians and GLY treatments in up to 100% of amphibian populations. This co-occurrence was observed for the spring, summer and autumn treatments. Lenhardt et al. (2015) demonstrated that late migrant species such as *B. bombina* and *P. fuscus* could be exposed to a greater number of PPP applications than early migrant species such as *R. arvalis*. The temporal coincidence with at least one PPP application reached 86% of the breeding population in *P. fuscus* during winter. In maize, up to 17% of the *B. bombina* breeding population may encounter at least one herbicide application.

III.4. Indirect effects

Literature reviews on the impact of PPPs on wildlife point out the importance of indirect effects via trophic cascades and interspecific competition through the suppression of food resources or competing species as well as habitat alterations (Bright et al. 2008; Köhler and Triebkorn 2013; Stanton et al. 2018; Kraus et al. 2021). Some agricultural chemicals can directly impact plants and arthropods. PPP use is now recognised as a major factor involved in widespread arthropod decline (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019; Wagner et al. 2021; Brühl and Zaller 2021) and thus can limit wildlife food supplies (Møller et al. 2021, Rattner et al. 2023). The use of PPPs also impacts plant communities, leading to a decrease in weed seed abundance and a loss of host plants for insects (Bright et al. 2008; Köhler and Triebkorn 2013). The impacts of PPPs and fertilisers) dramatically impair aquatic invertebrates and thus limit the emergence of adults which are important food resources of high nutritional quality for terrestrial insectivores (Hallmann et al. 2014; Brühl and Zaller 2021; Kraus et al. 2021; Poulin et al. 2021). Contaminants, including PPPs, can cause losses in the available biomass of these prey (i.e., through induced mortality or altered emergence phenology) and reduce the energetic/nutritional quality of the available prey community (i.e., increased bioaccumulation, decreased diversity) (Kraus et al. 2021; Kolbensschlag et al. 2023). This disturbs ecosystem functioning in terms of prey biomass input from the aquatic to the terrestrial environment (prey for a large diversity of terrestrial predators such as birds or bats) (Kraus et al. 2021). Studying prairie and agricultural wetlands, Kraus et al. (2021) demonstrated a decrease in the emergence of adult aquatic insects with increasing internal insecticide concentrations. The decrease in the biomass of emerging insects was observed to reach 43-73% (Kraus et al. 2021).

The deleterious effects of PPPs on the food supply reduction on wildlife seem to be mostly caused by the ecological interactions between species (e.g., trophic interactions and competition).

The crucial role of food supply depletion as one of the drivers of the unintended impact of PPPs on wildlife has been recognised in regulation. For instance, the recently issued European technical guidance for risk assessment for birds and mammals states that “*The claim to sufficiently protect the biodiversity of birds and mammals in agricultural landscapes requires that the impacts of indirect effects by a pesticide-mediated decline in food availability (e.g., in the form of earthworms, insects and weeds) and cumulative risks of pesticide use at the landscape level are ecologically negligible*” and recommends addressing the issues of reduced food availability as much as possible within the risk assessment process of PPPs (European Food Safety Authority 2023).

Impacts of PPPs on host-parasite or -pathogen interactions are other major indirect effects that also involve biotic interactions and effects on communities. This topic has been described mainly in amphibians.

III.4.1. Effects on dietary resources

Birds other than raptors

The indirect effect of PPPs via the reduction of food resources (arthropods and seeds) is currently proposed as one of the most likely explanations for the decline of farmland granivorous and insectivorous birds (Benton et al. 2003; Boatman et al. 2004; Bright et al. 2008; Kuijper et al. 2009; Stanton et al. 2018; Rigal et al. 2023). The impacts of PPPs on wildlife populations via the reduction of trophic resources for wildlife became was revealed many years ago, with, for example, work on partridges in the 1980s (Potts 1986). Since then, several studies have demonstrated a relationship between PPP use, concomitant decline in insect and plant communities, and declining bird populations (Benton et al. 2003; Bright et al. 2008; Geiger et al. 2010; Gibbons et al. 2015; Mineau and Whiteside 2013; Møller et al. 2021; Sanchez-Bayo and Wyckhuys 2019; Stanton et al. 2018; Van Dijk et al. 2013). The negative impact of resource depletion on reproductive success has been demonstrated for many passerines with respect to insect resources, which are essential during the breeding season (Morris et al. 2005; Poulin et al. 2010; Bright et al. 2008), and to seeds or fruits (Gibbons et al. 2006; McKenzie et al. 2011; Rey 2011). For example, by decreasing arthropod food resources, insecticides applied during the breeding season have been identified as one of the factors decreasing the breeding performance of corn buntings and yellowhammers (Brickle et al. 2000; Boatman et al. 2004; Hart et al. 2006). In Canada, links between landscape-scale agricultural intensification, PPP use, insect contamination, and joint declines in insect (prey) and swallow (predator) populations have been reported (Poisson et al. 2021; Garrett et al. 2021a). Reduced prey availability may alter the foraging behaviour of adults, with implications for their reproductive success and survival, perhaps affecting long-term population trends (Stanton et al. 2016). For instance, Bouvier et al. (2022) showed that great tits preferentially foraged in organic rather than conventional orchards, leading to increased foraging distance and reduced efficiency in feeding nestlings for birds

breeding in CF, where nestling survival and the number of fledglings were lower. The use of deltamethrin and carbofuran resulted in a decrease in the proportion of grasshoppers in the diet of chestnut-collared longspur (*Calcarius ornatus*) chicks, a diversification of food with unusual items, and an increase in the distance adults travelled for feeding (Martin et al. 2000).

The reduced abundance and diversity of emergent insects associated with surface water contamination by insecticides could explain the reduction in the density of insectivorous birds (Cavallaro et al. 2019; Williams and Sweetman 2019).

While herbicides can directly impact plant resources for herbivores and granivores, they can also have an effect on invertebrate resources, possibly through toxicity but also through modification of the plant communities on which invertebrates depend (Köhler and Triebkorn 2013). For example, the application of herbicides to crops affected bird populations through changes in invertebrate food resources. Early treatments reduce plant resources (weeds) while having a marginal and insignificant effect on cereal crops (Taylor et al. 2006). Moreover, a decrease in soil arthropods has been observed in relation to a decrease in weeds. As arthropods are an important dietary component of pheasant and gray partridge chicks, their decline may affect the development of chicks through a reduction in resources (Taylor et al. 2006).

The indirect effects related to the decrease in food resources have often been studied during the spring breeding season, when food requirements are greater due to the rearing of nestlings. However, links between PPP pressure and the quantities of food available at other times of the year (autumn and winter) have been mentioned (e.g., Benton et al. 2003; Bright et al. 2008). Indeed, the use of herbicides throughout the seasons severely limits the development of plant abundance and diversity (and seed production) in treated fields and in surrounding areas, with consequences for the habitat quality for many arthropods (Brühl et al. 2021b). Thus, beyond the breeding season, declines in granivorous birds have been linked to reduced winter survival, probably due to reduced seed availability (Siriwardena et al. 2000; Bright et al. 2008; Butler et al. 2010). In autumn and winter, McKenzie and coworkers (2011) showed that skylarks fed more frequently in stubbles, which had not received PPP treatments and which had higher weed seed densities.

Borg and Toft (2000) showed in gray partridges, based on an experiment where the respective proportions of aphids and grasshoppers in the diet were controlled or self-selection by chicks, that the composition of the available prey community was important for the survival and growth of nestlings. They concluded that the increase in the proportion of aphids in the cereal arthropod fauna may be detrimental to chick survival, since high densities of aphids cannot compensate the lack of a diverse insect food to ensure nutritional quality. While the reduction of food quantity is a crucial factor that explains the effect of PPPs on bird biodiversity, the nutritional quality of prey and thus the composition of the available prey communities is also mentioned as essential for the survival and reproductive success of birds (Kuijper et al. 2009; Spiller and Dettmers 2019).

With regard to certain families of compounds, Gibbons et al. (2015) highlighted the role of indirect effects of NNs and fipronil via the reduction in the food supply in field crops. Hallmann et al. (2014)

reported significant relationships between NN surface-water contamination and insectivorous bird declines and suggested that depletion of insect food resources caused cascading trophic effects. In a forest environment, Falcone and DeWald (2010) showed that imidacloprid treatment of trees impacted prey populations (especially lepidoptera). The cultivation of herbicide-resistant genetically-modified organisms GMOs would cause an even greater likelihood of indirect effects (Gibbons et al. 2006). Biopesticides such as spinosad or those based on the use of *Bacillus thuringiensis Bt* properties can also cause indirect effects on food webs, resulting in reduced food resources for insectivores (Poulin et al. 2010; Poulin and Lefebvre 2018; Kolbenschlag et al. 2023). Apart from these AIs, most of the related studies have been carried out *in natura* by comparing areas with or without treatment. Thus, they highlight the impacts of PPP use on birds as a whole, i.e., without targeting a particular chemical family.

From a theoretical point of view, the reduction in resources due to PPPs could lead to changes in intra- and interspecific competition relationships (Clements et al. 2009; Rohr et al. 2006). This hypothesis has been proposed to explain why generalist species are less affected by intensive agricultural practices, including PPP treatments, than specialists are (Filippi-Codaccioni et al. 2009; Filippi-Codaccioni et al. 2010b; Jeliaskov et al. 2016).

Raptors

Only Naim et al. (2011) suggested possible indirect effects of PPPs on raptors via reductions in prey availability. These authors explained the lower reproductive success of barn owls in oil palm plantations treated with different anticoagulant rodenticides by the decrease in rat density, the target species of the treatments and the main prey of the barn owl. However, these conclusions are limited by the lack of monitoring of the feeding behaviour of chicks, their diet and the availability of potential alternative prey. Some raptor species are insectivorous (e.g., honey buzzard, Eurasian scops owl, *Otus scops*, lesser kestrel *Falco naumanni*), at least in some seasons. Therefore, entomofauna decline could also affect them, but no study has addressed this issue.

Mammals other than chiropterans

Studies on the indirect effects of PPPs are extremely rare for mammals, apart from bats. In a review on indirect effects, Prosser et al. (2016) cited only one experimental study showing an effect of PPP sprays on the wood mouse. After spraying herbicides at agronomic rates, a decrease in the rodent population in the treated areas was noted, while the population actually increased nearby. The decrease in resources caused migratory movements of individuals, but the authors suggest that after 3 years of monitoring, the decrease in biodiversity of plant resources could be the cause of reduced reproduction and/or survival of rodents. However, these findings do not preclude the effects of posttreatment drift on grassy verges and areas. A study in Norway investigated the indirect effect of GLY use in forests on the presence and use of woodlands by the moose *Alces alces*. After the application of this herbicide to the forest plots, the foraging resource availability was reduced by 60 and 96% in summer and winter, respectively, 4 years after the treatments. These areas were also

less frequented by mooses (Milner et al. 2013).

Chiropterans and nonflying insectivorous mammals

The phenomenon of insect food resource depletion also affects insectivores, such as chiropterans, and is considered a threat to bat populations (Williams-Guillén et al. 2016). Numerous studies in Europe and North America have shown an association between greater quantities of arthropod resources in organic crops and greater activity, abundance and specific richness in bats and shrews (Wickramasinghe et al. 2003; Wickramasinghe et al. 2004; Jennings and Pocock 2009; Put et al. 2018; Oliveira et al. 2021).

Korine et al. (2020) reported increased bat activity and species richness in cotton-growing regions located in Israel, with a peak occurring at the moment of high insect pest abundance and a positive correlation between bat activity and the abundance of cotton leafworm (*Spodoptera littoralis*). Comparing bat activity before and after chemical spraying, a decrease in activity that lasted for several nights was observed after spraying events (Korine et al. 2020). Such an effect could be related to toxicity and/or to the reduction in insect prey density. Moreover, it has been shown in semiarid ecosystems that total bat activity decreased with the use of agrochemicals both at the landscape and at the plot scales (Kahnonitch et al. 2018). The authors highlighted the long-term and landscape-scale effects of agrochemical inputs on bat activity, suggesting that such a trend could be related to the reduction in prey abundance and diversity (Kahnonitch et al. 2018).

The cultivation of GMO exhibiting insecticidal traits has been shown to affect the potential for predation by bats in croplands and may induce declines in insect prey associated possibly with deleterious effects on bats (Williams-Guillén et al. 2016).

For NNs, comprehensive data support the conclusion that chiropterans are negatively influenced by the use of these insecticides, both directly through toxicity and indirectly via a reduction in insect abundance (Mineau and Callaghan 2018).

Reptiles

Although effects due to trophic cascade have been proposed to explain the decline of reptiles (Mingo 2018), there is no evidence of the impacts of PPPs on their populations or communities via the reduction of food resources. Even if the mechanisms explaining the decline in Malagasy lizard populations following fipronil spraying have not been specifically studied, this decline is more likely due to the reduction in prey (i.e., termites) rather than to the direct toxicity of this insecticide (Peveling et al. 2003). A recent microcosm study showed that the individual effects of simazine on lizards were due to the complex articulation of the direct toxicity of this herbicide and indirect mechanisms related to predator–prey behavioural dynamics and variations in food resources (Wang et al. 2021).

III.4.2. Land use and habitat changes

Birds other than raptors

The importance of noncropped areas (e.g., hedgerows, field margins) and seminatural habitats that are used all or part of the time (e.g., grasslands, fallow land, meadows) in agricultural landscapes is one of the key elements influencing the decline of certain bird species, as they are habitats exploited for feeding, nesting and breeding or wintering (Robinson and Sutherland 2002; Traba and Morales 2019). The use of PPPs in these habitats can alter the composition and/or plant structure as well as invertebrate populations, thus affecting habitat quality (Kuijper et al. 2009). Improving habitat availability and quality is one of the main management measures proposed to restore gray partridge populations, and this improvement is partly achieved by reducing PPP use (Kuijper et al. 2009).

Studying the impact of herbicides (GLY and imazapyr) to control phragmites in marshes, Lazaran et al. (2013) detected a negative effect on the reproduction of the marsh wren (*Cistothorus palustris*), a passerine bird that depends on reed beds. Following treatments, a decrease in the density of occupied territories (2.39 to 0.54 territories ha⁻¹), a strong reduction in the density of active nests (1.43 to 0.12 nests ha⁻¹) and a significant postponement of the date of nest initiation (approximately 36 days) were observed (Lazaran et al. 2013). Altered habitat characteristics during most of the breeding season, appear to be the main driver of this impact on the breeding population. Similarly, a reduction in natural habitats and a decrease in bird populations have been reported in wetlands aerially sprayed with GLY (Ojelade et al. 2022).

In the context of forestry management, herbicide treatments to suppress or limit the growth of herbaceous and woody species at plantations induces changes in the structure and composition of the vegetation compared to naturally evolving patches. These habitat changes can lead to negative effects on birds, but the impacts are dependent on the guilds (e.g., open versus forest birds, coniferous versus deciduous stand specialists, foliage gleaners versus ground-feeding species) (Betts et al. 2013; Kroll et al. 2017; Rolek et al. 2018; Sladek et al. 2008). These effects generally diminish or disappear altogether after a few years as the vegetation regenerates, as these practices are carried out on mosaic plots in forest areas and occur only once at planting or in the first few years of plantation growth. For example, when studying herbicide treatments of increasing intensity in forestry, negative effects on the abundance and richness of early ecological successional birds were found over the 4-5 years posttreatment period, with a stronger effect on foliage-feeding species (e.g., 23-52% reduction in richness) than on species with other feeding behaviours (e.g., reduction of 8-25%) (Betts et al. 2013; Kroll et al. 2017). Decreasing the intensity of herbicide treatments also had positive effects on birds during the first few years of tree growth, particularly for species with declining population trends in the US Pacific Northwest (Kroll et al. 2017). Effects on bird communities were no longer detected 5 years after cessation of herbicide treatments, likely due to rapid regeneration of vegetation (Kroll et al. 2017).

Mammals

A study conducted in North America showed a link between herbicide use (hexazinone) in forests and the decline of an oak species, which is a preferred habitat component of the fox squirrel *Sciurus niger*. The decrease in the oak population was associated with a reduction in the squirrel population, suggesting a link between herbicide application and the depletion of this rodent through habitat alteration (with no abnormal mortality otherwise noted) (Boone et al. 2017). Considering the small mammal assemblages in forest sites, some of which were subjected to thinning management with herbicide use, declines in some populations were detected, but they recovered two years after treatment. Responses to the different management treatments were strongly dependent on the ecological traits of the small mammals, with abundant and opportunistic species being relatively unaffected by the treatments. Some species, such as open land species in herbicide-treated areas or species associated with a dense shrub layer in thinned stands, exhibited positive responses (McLaren et al. 2011).

Reptiles

While no study has shown indirect effects of PPPs by habitat modification used by reptiles, McConnell and Sparling (2010) suggest that the main risk of prothioconazole and its metabolite prothioconazole-desthio to aquatic and semiaquatic reptiles would be through habitat change related to the impacts on aquatic plants and invertebrates.

Amphibians (terrestrial stages)

Several studies performed within the context of forestry management have addressed the responses of amphibians by comparing management methods such as slash-and-burn, clear-cutting with or without herbicide treatments, or shelterwood cutting with or without herbicide treatments. Salamander populations responded in terms of abundance, demography, reproduction or activity to the various management regimes; highlighting the importance of microhabitats, temperature and humidity, and canopy openness (Homyack and Haas 2009; O'Donnell et al. 2015). Management methods are sometimes destructive, which hampers the ability to separate the effects of physical disturbances from possible chemical disturbances linked to the use of herbicides.

III.4.3. Behavioural changes and vulnerability to predation

Several authors have discussed the effects of PPPs on vertebrate behaviour (e.g., Ford et al. 2021; Saaristo et al. 2018). Recent reviews and opinions have stressed that altered behaviour is the consequence of various neurological and physiological changes that ultimately link subindividual effects to individual- and population-level impacts. Behavioural endpoints are increasingly studied in ecotoxicological studies, but significant gaps in knowledge warrant further research (Saaristo et al. 2018). Behavioural toxicology is overlooked in risk assessment procedures (Ford et al. 2021). PPPs, especially legacy ones such as carbamates, OCs and OPs, have been shown to be capable of inducing various adverse changes in behaviour, such as parental care, movements, foraging

behaviour, and reproductive behaviour (Saaristo et al. 2018). Among the consequences mentioned, an increase in the risk of predation of the exposed individual is commonly assumed. In a review on the impact of CIIIs on wildlife, Lambert et al. (2005) noted that physiological and behavioural effects can affect the biology of individuals and threaten the population. Exposure to CIIIs induces a decrease in both activity and vigilance, which could lead to increased exposure to predators. Moreover, the weakening of individuals due to the reduction in their foraging behaviour and inappetence caused by these insecticides could also enhance their predation. For bats exposed to various insecticides (OCs, OPs, pyrethroids), impaired movement and escape ability could result in increased vulnerability to predation (O'Shea and Johnston 2009). A decrease in mobility with paresis or paralysis was shown for partridges exposed to NNs, which could increase their vulnerability to predation (Millot et al. 2017). Finally, alterations in antipredation behaviour measured by the inability to recognise a snake as a potential predator have been shown in mice exposed to the herbicide haloxyfop-p-methyl ester (Mendes et al. 2018). A greater predation on contaminated prey could also lead to overexposure of predators, but this phenomenon has yet to be readily investigated.

III.4.4. Susceptibility to pathogens

Current knowledge suggests that the toxic effects of PPPs may limit the resistance of animals to pathogens and parasites via various direct and ecological pathways, including immunotoxicity and immunomodulation, endocrine disruption, metabolic and energetic disturbances and/or by promoting transmission/infection. However, little is known about the role of PPPs in altering the dynamics of pathogens or parasites and the dynamics of their hosts and vectors. This could represent aggravating or limiting factors for the potential impact of PPPs on populations. The issues of antibiotic resistance, fungicide resistance and antiparasitic resistance in pathogens and parasites are among the emerging fields of research in human and domestic animal health. The consequences of PPP selection pressures on pathogen and parasite strains and the impact on their dispersal in the environment could be an issue for wildlife health and require further research.

III.5. Effects on ecological functions and ecosystem services provided by terrestrial vertebrates

III.5.1. Synthesis of the main ecological functions related to terrestrial vertebrates

The literature on the impacts of PPPs on the ecological functions and/or ecosystem services provided by wildlife is limited. Terrestrial vertebrates are involved in many ecological functions (see Table SI1 in the supplementary information). It can thus be intuitively stated that PPPs likely weaken these functions by impacting terrestrial vertebrate populations and communities, but no quantitative study is available on this topic.

In the case of reptiles, the EFSA (Ockleford et al. 2018) has conceptually addressed this issue by defining nine types of ecosystem services associated with this taxonomic group. The EFSA

(Ockleford et al. 2018) also provides a synthesis of the potential consequences of different reptile protection options that could be chosen by PPP risk managers and regulators on the ecosystem services they provide.

In a large study in Europe, Geiger et al. (2010) showed that insecticide and fungicide use had a consistent negative effect on biodiversity (wild plants, carabids, and ground nesting birds), and insecticides also reduced the potential for biological control of pests; however, the proportion of this reduction related to bird decline was not quantified.

A review focused on regulating ecosystem services and disservices provided by wildlife (invertebrates and vertebrates). It presented the main available knowledge about the role of animal populations as sources of services and causes of disservices and the potential impacts of agricultural intensification on the provision of these services/disservices in temperate and tropical zones (Gutierrez-Arellano and Mulligan 2018). The terrestrial vertebrates mentioned in this review are birds, rodents, small mammals (including chiropterans), and reptiles. The wildlife services listed include the maintenance of pollinator-dependent wild plant communities and crops (function: pollination and seed dispersal), the regulation of population size and the control of herbivore occurrence/abundance in crops (biological pest regulation) (function: population growth regulation) and the reduction of the risk of pathogen transmission to humans (via host diversity) (function: disease transmission). Disservices include disruption of native plant–animal relationships, spread of invasive plants, induction of unanticipated ecological associations, loss of wild plant populations and damage to crops and livestock and increased risk of zoonotic disease transmission (via overexploitation of vectors and increased human–wildlife interactions). This review suggested (i) an increase in the provision of the cited services in relation to species richness and wildlife abundance due to the increase in functional diversity and complementarity that broadens the range of services provided, and (ii) the increase in the intensity and spatial distribution of service provision since abundance determines the occurrence of services. Thus, ecosystems with low species abundance or richness may have little or no service provision. According to this review, agricultural intensification has negative effects on service providers and favours the development of population imbalances that may cause the disappearance of key species, reduce services and increase disservices. While the contribution of PPPs is not quantified, the authors suggest that PPPs play a role through their negative effects on the abundance and diversity of wildlife populations. The impact of PPPs on services and disservices in agrosystems related to the ecological functions of terrestrial vertebrates is often overlooked and certainly represents an emerging and crucial area of research in the future.

III.5.2. Impact on protected or threatened species and on cultural and natural heritage

The effects of PPPs on populations or individuals of protected and/or threatened terrestrial vertebrates (e.g., raptors, bats, amphibians) have been presented in the previous sections. These

threats may occur during the breeding or wintering seasons or during other critical periods, such as migration. This implies impacts on heritage and cultural services not only over the ranges of breeding populations but also in migratory stopovers (biodiversity reservoir, nature tourism, protected or classified sites; e.g., RAMSAR) (Yildirim and Ozcan 2007; Krief et al. 2017).

On the other hand, some PPPs can be used for the conservation of threatened species. The use of rodenticides for the control of invasive rodent populations on islands around the world has been documented in numerous papers. Aerial or terrestrial application of brodifacoum (the main AI used) has been successful in eradicating rat populations on several islands, mainly in the intertropical zone. It is generally shown that the use of rodenticides can, initially and depending on the local conditions of use, have an adverse effect on native species, but assessments made after several months or years demonstrate the favorable impact on local/native/endemic terrestrial vertebrate populations (Howald et al. 2007). In other contexts, rodenticides have been associated with negative effects on populations of protected and threatened species. We can cite, for example, the case of red kites (Berny and Gaillet 2008) or that of the endemic Réunion harrier (Coourdassier et al. 2019).

III.5.3. Biological control and regulation (predation) and provisioning

Among the ecological functions potentially modified by PPPs, only predation has been the subject of extensive study. The example of predator/prey interactions when the latter are exposed to anticoagulant rodenticides demonstrates the important role of the contamination of voles by these rodenticides. The transfer of residues through ingestion of contaminated prey can reduce the populations of predators (Jacquot et al. 2013), leaving the subsequent regulation of vole populations to the action of PPPs. While this topic has been modelled (Baudrot et al. 2020), it is also the subject of numerous articles based on field data.

The decline in the bat population in the USA due to white-nose syndrome, a disease in which PPP contamination is potentially involved, has been estimated to allow 1,320 tons of insects each year to elude predation (Williams-Guillén et al. 2016). The cultivation of *Bt* cotton has been shown to result in a reduction in the value of the pest control services provided by bats (Williams-Guillén et al. 2016). Some studies have focused on both the joint measurement of services and dysservices produced by vertebrates (Tschumi et al. 2018). With respect to small mammals, rodents can cause damage to crops, as is the case for herbivorous voles. By studying weed seed removal (service) and wheat grain consumption and crop damage (dysservice) associated with rodents, Fischer et al. (2018) found that vole abundance (but not field mice) and crop damage were associated. Crop damage decreased with decreasing plot-scale seeding density and increasing wheat height, both of which are associated with OF practices. Vole abundances and crop damage were highest in CF fields and in some regions of the country of study (Germany).

In a study assessing the relationship between wood production, biodiversity conservation and ecosystem services, Stokely et al. (2021) examined the species richness of several taxa (flora, insect pollinators, birds and wild ungulates) and assessed 13 parameters corresponding to cultural,

provisioning and regulatory services. Herbicide use increased the allocation of the net primary production of cultivated trees, the expected timber volume and the harvest income at 40 and 60 years of age, while flora with heritage/cultural value decreased by 71%. Forage production (i.e., food resources for wild ungulates) was reduced by 41%, bird richness by 25%, and floral resources by 42%, the latter proxy was associated with 38% fewer pollinator species. However, herbicide use did not appear to influence blueberry pollination, bird control of herbivorous arthropods, wild ungulate abundance, or regulatory services related to forest production. The authors indicate that despite an herbicide-induced reduction in plant diversity on logged sites, posttreatment vegetation growth appears to allow these sites to serve as foraging habitats for ungulates, birds and some pollinators within logged forest landscapes. Another forest study showed that birds reduced arthropod abundance by 16% and plant damage by 14% and that some forestry pests were severely restricted, with reductions of up to 30% (Harris et al. 2020). Although plant abundance was reduced by 67% and plant diversity by 55% in the most intensive herbicide treatments, the intensity of the bird effects on arthropods and plant damage was not altered. In this study, the pest control service of birds was not affected by herbicide, while avifaunal richness was affected (Harris et al. 2020).

III.6. Aggravating or mitigating factors

III.6.1. Exposure routes and bioavailability

The oral route, especially via food, is recognised as the major route of contaminant exposure for wildlife, and the contributions of the respiratory and dermal routes are insufficiently studied to quantify them precisely. The latter are not taken into account in most risk assessment procedures, which is commonly considered a shortcoming that may bias exposure estimates. For example, Mayer et al. (2020) identified the oral route related to grooming activities as a major source of exposure of hares to PPPs in field crops (uptake by foraging assessed as 7-fold lower than uptake via overspray/oral grooming), which is transposable to other mammals. Mineau (2002) demonstrated that the ratio of dietary to dermal exposure was a better predictor of induced mortality than was the dietary route alone. In addition, the cutaneous uptake of PPPs modifies their metabolism, circumventing the digestive system (including the liver) and thus the first-pass effect, which is generally responsible for the capture/degradation of a more or less important part of the AI. Several studies on insecticides (carbamates, OPs and NNs) have highlighted the presence of PPP residues on skin and/or feathers, highlighting the potential role of aerial sources in the exposure of wildlife via dermal and/or respiratory and/or oral routes (Vyas et al. 2007; Graves et al. 2019). Finally, for some vertebrate groups (notably herptiles and chiropterans), the dermal route appears to play an important role in exposure (Ockleford et al. 2018, Yao et al. 2017). Thus, the relative contributions of the different exposure routes may differ according to (i) the physiological, biological, phenological and ecological characteristics of the taxa, (ii) the physicochemical properties of the AI (e.g., K_{ow} , K_{oa}), (iii) the persistence and fate of the AI and its transformation products in abiotic compartments, (iv) the modalities of application (e.g., spraying, seed coating) and type of formulation (e.g., emulsifiable

concentrate, slow-release capsule suspension), and (v) other environmental parameters related to climate and meteorology.

Although it is well known that soil characteristics influence the bioavailability of PPPs, only a few studies have questioned whether they also contribute to the exposure of vertebrates, for which direct contact with the soil is rarely considered. However, some studies have shown that soil parameters influence both the bioaccumulation and effects of PPPs on herptiles. For instance, Van Meter et al. (2016) showed that a low organic matter content (3%) promotes the uptake of imidacloprid, atrazine, triadimefon, fipronil, and pendimethalin in toads compared to soil with a higher content (14%). The authors noted that agricultural soils generally have rather low organic matter content.

III.6.2. Sensitivity related to ecophysiology and ecological traits

Interspecies variability in physiological sensitivity to PPPs is not as well documented for wildlife as for plants or terrestrial and aquatic arthropods. The differences in sensitivity between species are a source of major uncertainty, as only a few species have been tested (e.g., rats, mice, mallards, and bobwhite quails). In the absence of comparative data, species diversity likely encompasses taxa that may be more sensitive than laboratory species. Despite the application of safety factors in ERA, the most sensitive species might be at risk, as demonstrated for NNs (Ockleford et al. 2018). The comparison of acute toxicity thresholds between data from regulatory dossiers and independent studies on species that are sometimes very closely related highlights variations of factors of 10 to 100 (Gibbons et al. 2015).

The ecological traits of species condition and their exposure and/or responses to PPPs:

- Diet may be a critical factor for some species. The numerous articles on birds and chiropterans generally highlight the increased risk for insectivorous and granivorous birds towards direct (consumption of contaminated resources including coated seeds) and/or indirect (reduction of seed and arthropod resources) effects. For example, because of the dehusking of consumed seeds (Avery et al. 1997; Prosser and Hart 2005), the exposure of some passerines and rodents (Fringillidae, wood mouse) to AIs used in seed coating might be decreased (Brühl et al. 2011; Morris and Thompson 2011). The issue of secondary poisoning via food webs is also relevant for raptors with anticoagulant rodenticides and banned PPPs such as carbamates because of foraging and feeding behaviors involving scavenging and preference for target rodents (Nakayama et al. 2019; Christensen et al. 2012; Badry et al. 2020; Hindmarch and Elliott 2018). In amphibians, terrestrial feeding habits during inactive resting periods may increase exposure.
- Some biological and ecological characteristics of chiropterans appear to be exposure risk factors, such as gregariousness, social "grooming" within a group, intense energy metabolism and high food requirements.
- For poikilothermic vertebrates such as herptiles, low temperatures are the cause of reduced metabolism and thus lower consumption and a reduction in exposure. This also leads to a decrease in the biotransformation capacity of AIs, which can increase the risk from non

metabolised substances such as pyrethroids or glufosinate ammonium (Wang et al. 2019c; Zhang et al. 2020). These higher-than-expected contaminated animals could be in turn sources of greater PPP levels for their predators through trophic exposure.

- In herptiles, direct dermal contact with soil and soil burrowing behaviours (e.g., sheltering in amphibians, nesting in reptiles) may enhance exposure to PPPs when individuals are present and stay in treated fields (Ockleford et al. 2018). Furthermore, the high permeability of the amphibian skin favours transdermal absorption and toxic effects of PPPs when exposed via water or contaminated soils and when exposed directly to sprays. Amphibians also have an immune system with an important cutaneous component compared to that of other vertebrates, and disruption of this system by contaminants can increase their vulnerability to lethal infections. Finally, this group is considered to be particularly sensitive to endocrine disruption that can be induced by certain PPPs (see section III.2.2).
- Territoriality associated to small home range is an additional risk factor associated with a likelihood of repeated exposure to PPPs without any possibility of escaping (e.g., herptiles, Ockleford et al. 2018; birds, Lopez-Perea et al. 2015). Conversely, high mobility (mammals and birds) in a landscape with intensive PPP agricultural practices may enhance exposure to mixtures of PPPs (Fritsch et al. 2022; Mayer et al. 2020). In amphibians, seasonal movements may also lead to exposure.
- The life span of species modulates exposure and increases the vulnerability of long-lived species to chronic exposure, cumulative exposure, multiple coexposure events over time, and long-term effects of contaminants.

III.6.3. Mixtures of PPPs and other toxicants

While many studies have assessed the toxicity of a single AI, exposure of wildlife and frequent accumulation of mixtures of toxic compounds (including PPPs) are well-established realities (see III.3). Coexposure may be due to the cooccurrence of multiple substances from the same source and/or to the occurrence of more than one substance from different sources. Notably, coexposure also refers to the temporality of exposure, which implies that animals may be exposed to mixtures even if contact with various substances does not occur simultaneously (Beronius et al. 2020). The characteristics of the mixtures may be inherent in the commercial formulations used, some of which have multiple AIs and/or coformulants that may modulate the toxicity of the AIs.

The assessment of mixture effects on individuals and populations is hampered by the limited knowledge on (i) the nontarget toxic mechanisms of action and associated sublethal effects of the compounds on organisms and (ii) their interactions underlying possible “cocktail effects” (i.e., additivity, antagonism or synergy of effect) (Thompson 1996; Hernandez-Jerez et al. 2019) and (iii) the large variety of mixture compositions in terms of AI combinations and concentrations that wildlife may experience *in natura*, which complicates the design of reliable laboratory experiments. For instance, a synergistic oestrogenic effect of a PPP mixture (prothiofos / pyriproxyfen and

thiabendazole / orthophenylphenol) has been demonstrated with rat cell cultures, the effect of the mixture being more than 10 times greater than that of each PPP separately (Manabe et al. 2006).

Exposure to mixtures can facilitate the uptake of PPPs or, on the contrary, a reduction in PPP uptake via competition depending on the substances and mixture considered. These processes have been highlighted in amphibians exposed to soils contaminated by herbicides and/or insecticides and/or fungicides alone or in mixture, where the bioaccumulation of the compounds increased or decreased (Glinski et al. 2019; Van Meter et al. 2018). Different nonexclusive mechanisms could be involved in these phenomena: sorption/desorption processes in soils, passive/active uptake in organisms, metabolism and detoxification, and excretion. However, further research is needed to better understand and quantify these processes in AI bioaccumulation (Van Meter et al. 2018). Moreover, the modes of action of PPPs may change depending on the interactions between the AIs present in the mixture, modulating the effects on organisms independently of variations in bioaccumulation due to multiexposure (Van Meter et al. 2018). It is important to stress that some PPPs or combinations of PPPs with the greatest impacts are not necessarily those with the highest tissue bioaccumulation (Van Meter et al. 2018).

III.6.4. Landscape

Numerous works have shown the major influence of the composition and structure (spatial arrangement and connectivity) of seminatural habitats in agricultural landscapes on wildlife abundance and diversity as well as on ecosystem functioning and services (Benton et al. 2003; Michel et al. 2006; Robinson and Sutherland 2002; Rusch et al. 2016; Tschardt et al. 2005; Stote et al. 2001). Landscape features and PPP use intensities are often correlated, and the most intensive practices involving the highest use of PPPs are generally carried out in simplified landscapes (Norton et al. 2009). This implies (i) a major difficulty in quantifying the respective impact of the different practices used in production systems, including the use of PPPs specifically, and (ii) that landscape features and PPP use interact in agroecosystems, with organisms being subjected to these pressures jointly. It has been suggested that the unintentional effects of PPPs could be mitigated or additively or even synergistically amplified by landscape features and should be considered within a "multistressor" framework (Hole et al. 2005). Spatial issues and processes occurring at the landscape scale are increasingly recognised as crucial factors shaping the unintended effects of PPPs on wildlife and are increasingly considered in both research studies and by regulatory agencies (Morrissey et al. 2023; European Food Safety Authority 2023). The literature suggests that the beneficial effect of farming systems that do not use CUPs (i.e., essentially OF) on biodiversity (e.g., increased species richness and increased abundance of taxa) varies depending on the landscape features around the cropped plots and even at the farmland scale. Field studies conducted at regional, national or continental scales on taxa, including birds and small mammals, have shown that differences in biodiversity between the OF and CF systems are influenced by interactions with factors acting at the plot level (e.g., crop type, plot size/cropping area, hedges,

rotations, and PPP use) and at the landscape scale, featuring a habitat mosaic (e.g., surfaces under OF and landscape features such as seminatural habitats within a radius of several km) (Filippi-Codaccioni et al. 2010a; Gabriel et al. 2010; Fischer et al. 2011; Winqvist et al. 2011; Kirk et al. 2020). Meta-analyses have described an overall positive role of OF on biodiversity compared to CF, but landscape features shape organismal responses to such cropping systems where synthetic PPPs are not used (Bengtsson et al. 2005; Tuck et al. 2014). The beneficial effect of OF is generally greater in landscapes dominated by so-called "intensive" practices (with high proportions of cropping) than in complex and/or heterogeneous landscapes comprising cultivated plots and many other biotopes. But this effect reaches a tipping point after which biodiversity and food web functioning may be too altered to allow OF to compensate for the deleterious impacts of PPP use in the surroundings and landscape simplification (e.g., Winqvist et al. 2011). These works also highlight the combined role of PPP use practices and habitat heterogeneity in the landscape on ecological functions and ecosystem services (e.g., biological regulation potential). In particular, the 'simplification' or 'homogenisation' of the landscape seems to play a major role (Filippi-Codaccioni et al. 2010a; Gabriel et al. 2010; Fischer et al. 2011; Winqvist et al. 2011). More complex landscapes (i.e., more patch heterogeneity, smaller cropped patches, more seminatural habitats, greater connectivity between habitats) likely allow for functioning with source and refuge habitats that locally compensate for some of the effects of intensification practices at the plot scale. Tscharrntke et al. (2005) noted that in simplified landscapes, local habitat allocations (land-use management choices) were more important (in terms of biodiversity consequences) than in complex landscapes, which are otherwise globally threatened by global landscape homogenisation/simplification. Similarly, the impacts of PPPs in forest ecosystems may depend on the woodland mosaic which supports biodiversity and ecosystem functioning (Stoleson et al. 2011).

Modelling studies (Topping et al. 2005; Dalkvist et al. 2013; Topping et al. 2016) conducted on different species (e.g., birds, voles, hares) and types of PPPs (e.g., insecticides, fungicides) have shown that the severity of PPP effects varies according to landscape characteristics in terms of composition and spatial configuration. The essential spatial features were (i) the location and position of different treated crop plots versus untreated habitats that strongly influence wildlife exposure due to both spray drift and movements of animals (e.g., foraging activities) and (ii) the connectivity between untreated habitats within the landscape mosaic that can facilitate the dispersal of individuals and thus improve the possibility and speed of recovery of the population impacted by the PPP treatments.

Climate change and other global change stressors have now been added to the pressure related to the intensification of agricultural practices such as PPP use and landscape changes. This context of multiple stressors composes the real-world situation that free-living wildlife is facing, and "true" control situations without any disturbances become rare if they still exist. Currently, gaps in knowledge look greater than insights from the scientific literature to allow quantifying the impacts on biodiversity within such a complex interplay of drivers.

III.6.5. Cropping systems and related agricultural practices at the plot level

Few vertebrate taxa have been studied in this area of research, and studies have relied mainly on empirical comparisons of plots or farms with or without PPP use (e.g., between OF and CF systems) or gradients of PPP use (treatment frequency indicator). Various studies have compared the effects of cropping systems on bird or small mammal communities, mainly in terms of abundance, species composition or diversity or by focusing on functional groups (e.g., specialists or generalists or aerial versus terrestrial hunters or foliar insect gleaners). The results are sometimes contradictory between regions or countries for a given crop. For instance, it has been reported that specialist birds (habitat and diet specialisation) benefit from OF practices (Filippi-Codaccioni et al. 2009; Geiger et al. 2010; Guerrero et al. 2012; Kirk and Lindsay 2017); however, depending on the context and group studied, this pattern was not always observed (Chamberlain et al. 2010).

In field approaches comparing several cropping systems for a given habitat, other agri-environmental factors covarying with the use of PPPs (e.g., fertilisers, crop rotation, % seminatural habitats, etc) may be responsible for the community responses. For example, the differences observed between OF and CF farms in Canada are more related to land use than to PPP treatment intensity, even if the latter remains significant (Kirk and Lindsay 2017).

Soil management practices

The hypothesis often put forward is that conservation tillage farming, unlike OF or CF, could maximise the resources accessible throughout the year due to the reduction or absence of soil disturbance, even if the higher use of herbicides limits such a beneficial output. There are closely related trade-offs between soil tillage and herbicide use, which makes difficult disentangling of their respective effects. Brühl et al. (2021b) stated that *“herbicide impacts cannot be separated from confounding with soil management practices such as tillage”*. Thus, soil management practices (e.g., tillage, hoeing) are rarely studied in interaction with other factors of interest, such as PPPs or landscapes (Jeliazkov et al. 2016; Flohre et al. 2011). At the scale of French cereal systems, the impacts of different herbicide uses and tillage practices were compared by monitoring chiropteran activity or abundance (Barré et al. 2018) or bird diversity and community specialisation indices (Filippi-Codaccioni et al. 2009; Chiron et al. 2014; Jeliazkov et al. 2016). For bats, the results showed greater activity and species richness in the OF plots and in the nonploughed plots treated with low amounts of herbicides than in the other conventional systems. This finding indicates the positive effects of both the absence of PPP treatments and of the absence of tillage. The results for birds were more variable and depended on the indicator. Jeliazkov et al. (2016) observed (i) a greater bird community specialisation index in plots with low chemical use and low tillage and (ii) a positive effect of no tillage and a negative effect of herbicide treatments on total and specialist bird abundances and diversity. Conservation tillage practices seem to favor invertivores more than omnivores, and over the years after conversion, these practices are increasingly favorable to granivores (Filippi-Codaccioni et al. 2009; Chiron et al. 2014). Overall, these studies reveal an adverse effect of

herbicide treatments, and the authors stress that nonploughing in favour of intensified herbicide use is not an effective practice for bird conservation.

Chemical fertiliser use

There are limited data on this topic. However, many technical itineraries propose successive treatments with chemical fertilisers and PPPs over short periods in autumn and spring. This leads to a strong correlation between their uses in CF and makes it difficult to disentangle their effects *in natura*. In a controlled study, the additive effects of PPPs and fertilisers were shown on snapping turtle eggs exposed to treated soils, with the toxicity principally caused by ammonia treatment (de Solla and Martin 2011).

Sowing practices

Goulson (2013) computed the minimum quantity of treated seeds ingested likely to induce wildlife mortality based on the acute toxicities of several PPPs in different species. He estimated that the probability of reaching a toxic threshold is high given the amount of seeds left on the soil surface after sowing. Wheat or winter barley seeds are less hazardous than maize due to the lower concentration of AIs in pellets (Goulson 2013; Millot et al. 2017). Some mitigating factors to reduce the risks related to the consumption of coated seeds have been proposed (e.g., European Food Safety Authority 2008):

- Optimal seed burial is recommended (de Snoo and Luttik 2004; McGee et al. 2018).
- The use of repellents to limit seed ingestion (Avery et al. 1994; Avery et al. 1997). For instance, thiram and ziram (fungicides) are used as bird repellents (Werner et al. 2010). However, the efficiency of repelling depends on other factors, such as the availability of alternative food resources and food requirements (Lopez-Antia et al. 2014; Millot et al. 2017).

III.6.6. Climatic factors and climate change

The effects of PPPs can be modulated by harsh weather conditions through several processes. First, the increased use of certain PPPs such as fungicides during rainy springs or interactions between the impacts of PPPs and unfavourable climatic conditions can affect the reproductive success of vertebrates (Odderskaer et al. 1997; Garrett et al. 2021b). These unfavorable weather conditions are aggravating factors in addition to the direct effects of PPPs on wildlife and the indirect effects of habitat and food limitations due to agricultural intensification. The negative effects of weather under climate change could therefore exacerbate the consequences of PPPs and habitat degradation on the reproductive success of birds in “intensive” agrosystems (Burns et al. 2016; Stanton et al. 2018; Spiller and Dettmers 2019; Garrett et al. 2021b). The possible consequences of climate change are generally considered to increase the effects of PPPs, as 83% of studies that combined temperature increase and PPP exposure showed a synergistic effect of these factors (Köhler and Triebkorn 2013).

Stratospheric ozone depletion and global warming are accompanied by an increase in UV radiation,

which can contribute to the effects of PPPs (Blaustein et al. 2003) through various phenomena, such as the degradation or photoactivation of AIs or additional or synergistic effects in sensitive taxa, such as amphibians. This research topic has not been adequately addressed, and additional knowledge is needed to analyse the generality of these phenomena in other taxonomic groups.

IV. SUMMARY AND RECOMMENDATIONS

IV.1. Main conclusions

Unintentional effects of PPPs have been reported on terrestrial vertebrates via both direct and/or indirect effects. This is particularly true for birds, for which there is extensive literature, and to a lesser extent for other taxa.

For populations, guilds or communities, direct acute toxicity of PPPs has been documented *in natura* on raptors and carnivorous mammals, notably with occasional massive poisoning events. Since 2000, these phenomena have involved mainly anticoagulant rodenticides in the context of legal use or misuse and CII (OPs and carbamates), most of which are banned or of restricted use in many parts of the world but are still used illegally. Overall, under authorised use, reported cases of acute poisoning are becoming less frequent due to bans or regulatory changes. Illegal poisoning of carnivores with CII remains a serious threat to the conservation of certain (groups of) species on several continents. Although cases of mortality in granivorous birds due to the consumption of seeds coated with NNs or carbamates have been reported, their consequences on populations are not precisely known. Acute toxicity effects have also been reported for many PPPs at recommended application rates in amphibians in the terrestrial phase under experimental conditions.

Growing concerns are emerging about the detrimental impacts on wildlife of chronic exposure to current-use insecticides (especially NNs, OPs, and pyrethroids), of herbicides (notably GLY), and of fungicides (especially triazoles). The literature available on wildlife is too limited to identify which other CUPs (e.g., SDHI, 2,4-D, butenolids and sulfoxamines) may impact biodiversity through sublethal effects. At the individual and subindividual levels, numerous studies have documented direct sublethal effects of different AIs generally tested alone. Insecticides have been the most studied, followed by fungicides and herbicides. The responses measured were life history traits and behavioural, physiological or cellular alterations. The results obtained show that various substances including CUPs affect the health of individuals, their behaviour and reproductive success at environmentally relevant doses of exposure and, therefore, possibly impact populations or even communities. However, the absence of explicit links with higher levels of organisation in experiments as well as simplified and sometimes unrealistic exposure contexts limit the interpretation of quantitative consequences on biodiversity *in natura*. New questions are raised about the involvement of PPPs in the emergence and prevalence of infectious and parasitic diseases in wildlife.

Over the last decade, evidence of the indirect effects of PPPs on wildlife populations has been published. Conducted mainly in Europe and North America, these studies have shown correlations between the use or contamination of the environment by PPPs, especially insecticides, and population declines or reproductive performance of insectivorous birds explained by the quantitative and/or qualitative reduction of their food resources. These studies mainly concern the global use of insecticides or certain families or substances such as NNs or bioinsecticides (*Bt* toxins used in nonagricultural contexts, i.e., forestry or mosquito control, spinosad) and their impacts on insectivorous birds. In addition, other PPPs, such as fungicides, especially those that also have insecticidal effects, are reported to impact insect-dependent taxonomic groups, such as chiropterans and birds. Several studies have also demonstrated the effects of herbicides on terrestrial vertebrate populations and communities through the negative impact on the support functions provided by plant communities (habitats, food resources, etc.) for the vertebrates themselves and for the invertebrates that constitute their prey. Therefore, the substitution of PPPs having a high acute toxicity by AIs that are less toxic to terrestrial vertebrates does not necessarily represent an effective alternative for reducing or preventing undesirable effects. The massive use of PPPs or biopesticides over time and space can alter invertebrate and plant communities, which may change the relationship between terrestrial vertebrates and their environment and lead to cascading effects in food webs that impact wildlife via direct and/or indirect mechanisms. Due to the reduction in the use of the most toxic and persistent PPPs, the trend of a predominant effect of PPPs on wildlife through impacts on food supply and processes related to food web functioning is becoming increasingly established in the literature. The drivers of indirect effects rely more on ecological processes than on modes of action of PPPs.

Although withdrawal from the market of AIs induce unacceptable risks constitutes a primordial option and sounds like an efficient solution to limit the impacts of PPPs on biodiversity, its benefit may ultimately be limited. Our review shows that despite the positive effects of regulatory bans, such a nonsystemic single solution may not fully allow to reach the goals of biodiversity conservation and raise further concerns. For instance, the recent ban on NNs as PPPs in Europe has raised the question of possible alternative solutions. The available chemical alternatives identified by the French Agency for Food, Environmental and Occupational Health & Safety (ANSES) based on registered AIs in Europe are mainly pyrethroids (e.g., beta-cyfluthrin but banned since, cypermethrin, deltamethrin, lambda-cyhalothrin, tau-fluvalinate, esfenvalerate), some OPs (chlorpyrifos-methyl but banned since, phosmet) and carbamates (pirimicarb, fenoxycarb but banned since) and other compounds belonging to other chemical families (ANSES 2018). A comparative assessment showed that several of these alternative AIs (alone or in mixtures) present a greater risk to birds and/or mammals than NNs (ANSES 2018). Furthermore, while there is no information on terrestrial vertebrates other than acute toxicity data for most of these alternative substances, our synthesis shows that pyrethroids are likely to induce direct adverse effects on individuals or populations of most of the groups studied, and exposure has been proven *in situ*. Indirect effects via reduced food availability or behavioural alterations leading to increased susceptibility to predation have also been

shown or suggested for pyrethroids. Thus, if chemical alternatives (pyrethroids or others) to NNs are retained or even preferred for all or part of the uses, their consequences for terrestrial vertebrates through potential direct and/or indirect effects will have to be carefully evaluated.

Some studies have highlighted mostly positive, sometimes neutral or even adverse effects of OF on communities or populations of terrestrial vertebrates, depending on the landscape context. The methodological approaches used rarely make it possible to identify the factors responsible for the effects and have led to controversy over the relative contributions of PPPs versus other environmental modifications often linked to CF (landscape modifications, habitats, tillage practices, fertilisers, etc). For the most studied groups (e.g., insectivorous birds), population declines are frequently described as multifactorial, and while it is difficult to rank the various causes, the involvement of PPPs can be considered very likely based on the weight of evidence provided by current knowledge. Landscape factors can intervene, modulate exposure or direct and indirect effects of PPPs on wildlife. Moreover, landscape changes linked to CF practices have deleterious effects on biodiversity that amplify the impacts of PPPs.

Several studies have demonstrated the exposure of terrestrial vertebrates to mixtures of PPPs using measurements within the environment or direct residue analysis of tissues or body fluids. However, information is principally available on legacy or banned compounds (OCs, anticoagulants), whereas there are limited data for CUPs. There are multiple potential exposure routes, and their relative contributions are poorly understood or quantified depending on the AIs and taxa. The available data show that vertebrates be exposed to a wide variety of legacy PPPs, CUPs and transformation products, including those assumed to be not persistent and not bioaccumulative. The effects of mixtures of PPPs on individuals, populations and communities are currently poorly quantified and understood.

Our review shows that landscape heterogeneity, including the presence of seminatural habitats and agroecological infrastructures, is a necessary but not sufficient condition for ensuring the protection of biodiversity and ecological functions in agroecosystems where adverse impacts of PPPs occur. This also applies to the unintended effects of PPPs, where the reduction of use both at the cultivated plot and at the landscape level is an essential but insufficient measure to achieve the objectives of biodiversity conservation and the ecological functioning of agroecosystems if landscape features are still disturbed. Management measures should thus consider these two options jointly and in a complementary manner. However, management actions entailing agroecological infrastructures must be cautiously designed and applied since PPPs and their transformation products can locally accumulate (e.g., buffer strips, hedgerows) in habitats that are attractive for wildlife. Further research is warranted to understand and predict the potential role of agroecological infrastructures as “ecotoxicological traps” in agrosystems where PPPs are intensively applied.

Finally, the effects on ecosystem services provided by terrestrial vertebrates are generally discussed

in a speculative manner due to the diversity of services provided but are poorly measured and not characterised causally. Similarly, the effects on the functions that support ecosystem services are poorly understood or not characterised.

IV.2. Priorities to fill knowledge gaps and perspectives

1 - Towards a better characterisation of the eco-exposome

The information available on the contamination of terrestrial ecosystems by PPPs, particularly for CUPs, remains incomplete. Recent developments in chemical analytical methods (target or nontarget screening) have made it possible to acquire multiresidue data on PPP concentrations in different environmental media for characterizing the AIs and mixtures most frequently detected *in situ*, their concentrations, and their variability at different spatial and temporal scales. The technical itineraries of farming and spatial ecology features of the species should be considered when defining the sampling strategy for such a survey. Moving toward the “eco-exposome” looks promising and is needed for the path forward in wildlife toxicology (Morrissey et al. 2023). In addition to characterising internal exposure, which requires wildlife sampling and possibly modelling, multimedia and multicomponent external exposures could be addressed by using integrated passive samplers (Morrissey et al. 2023). Moreover, wildlife sampling strategies can benefit from advances in minimally invasive methods and new approach methodologies (NAMs) or and Non-Animal Technologies (NATs) (Morrissey et al. 2023; Rattner et al. 2023). Finally, a better characterisation of the contamination of the environment and organisms by PPPs would make it possible to compare this information with the toxic thresholds (NOAEL, toxicological reference values, etc.) available especially for mammals (rats or mice) and, to a lesser extent, for birds. However, interpreting the toxicological significance of coexposure would require toxic thresholds established from exposure to mixtures or other methods allowing multiple compound effect assessments, which might be the case for adverse outcome pathways (AOP, Scholz et al. 2022) and developing modelling methodologies (e.g., toxicokinetic-toxicodynamic models “TK-TD”).

2 – Identification of priority PPPs and in natura monitoring

This review shows that defining which AIs, commercial formulations or mixtures should be monitored or be the subject of risk mitigation for wildlife remains a challenge. Among the AIs identified as at high risk, most are banned or of limited use (anticoagulant rodenticides, CIIIs, NNs, OCs). For CUPs, a ranking would be inherently biased against the most studied AIs. Two complementary approaches to prioritisation could be implemented.

(i) *a priori* identification of priority PPPs can be based on methods aggregating the identity and quantities of AIs used in a given territory and their toxicity (de Montaigu and Goulson 2020). Such an approach is immediately operational if the requested data are available but it does not consider the time course of treatments, physico-chemical properties controlling the fate of compounds and exposure, sublethal toxicity or indirect effects. The resulting hierarchy can therefore be used only to

guide short-term surveillance strategies. In the midterm, individual-based models and spatially explicit modelling adapted to different contexts and agricultural practices, different species and integrating technical itineraries would help to prioritise and manage the risk posed by AIs and their mixture.

(ii) *a posteriori* identification complements *a priori* approaches and can be based on field monitoring of environmental contamination and effects on individuals and populations (EFSA 2023; Vijver et al. 2017). The monitoring strategy for contamination may focus on *a priori* identified AIs, or an *a posteriori* option may be chosen based on monitoring covering a wide spectrum of AIs (see IV.2.1). The characterisation of the exposome for several model or focal species would contribute to PPV strategies and to assessing the *a priori* risk according to more realistic multiexposure scenarios. The monitoring of effects by means of indicators, including both endpoints and sentinel/focal species, should also be considered. These paradigms are evolving toward trait-based approaches to improve the choice of which taxa to prioritise or which features to focus on (Morrissey et al. 2023). Epidemiological approaches correlating large-scale population monitoring and PPP treatment intensities and approaches based on weight of evidence (e.g., Hill's criteria) could also help to identify *a posteriori* which agricultural production systems, AIs, commercial formulations or mixtures are the riskiest for certain taxonomic and/or ecological groups.

3 - Towards a better characterisation of direct effects: Establishing relationships between environmental contamination, tissue concentrations and toxic effects from individuals to population

We report numerous cases of PPP accumulation in wildlife for which no relationship has been established between internal concentrations and effects, which prevents interpretation of the risk they represent. Even if their meaning is limited, we recommend the definition of critical concentrations relating to sublethal effects for CUPs or those frequently detected in wildlife. These concentrations should be measured in tissues whose sampling does not require the sacrifice of animals. The responses to be measured to define these critical concentrations should consider the mechanisms of action of the AIs and/or provide information on the state of health of the individuals and the life-history traits involved in population dynamics (Rattner et al. 2023). If the establishment of these "internal concentration–effect" relationships requires experimental approaches, the exposure contexts and environmental conditions should be sufficiently realistic to allow extrapolation to field situations.

Upscaling from molecular initiating events to demographic consequences at the population level is challenging and requires the combination of approaches and endpoints, including behavioural responses that are often overlooked despite their role in survival, fitness and transgenerational outcomes (EFSA 2023; Saaristo et al. 2018; Ford et al. 2021). Avenues for the improvement of experimental and field designs to assess toxicological effects in wildlife and to make links with exposure have been proposed recently in reviews (Morrissey et al. 2023; Bean et al. 2023, Rattner

et al. 2023).

4 - Addressing both direct and indirect effects in a multiple stressor context: Identifying the mechanisms responsible for population declines in situ

Assessments of the effects of CUPs on terrestrial vertebrates suffer from a lack of causal links between the responses measured at the individual and subindividual levels, most often under experimental conditions, and those observed on populations or communities *in natura*. Understanding the direct and indirect mechanisms involved in population declines requires greater integration of measured responses by combining monitoring population trends with those of exposure, individual (life-history traits) and subindividual responses. To achieve the goal of protecting wildlife biodiversity, indirect effects must be explicitly considered in combination with direct toxic effects (EFSA 2023, Rattner et al. 2023).

For several decades, ecosystems have undergone a combination of changes, mainly of anthropogenic origin, which are referred to as global change. Global change includes climate, landscapes and habitats, introduction of invasive species or emergence of pathogens and the physical and chemical composition of the environment. Regardless of whether these changes are the direct result of agricultural activity, they are likely to interact in complex ways to modify the structure and function of biological and ecological systems. Therefore, these changes should be taken into account as additional pressures in ecotoxicological experimental designs.

The implementation of ambitious field designs is essential for identifying the influence of different factors on wildlife responses to PPPs and on the postregistration effects of contaminants in nature (Morrissey et al. 2023). This involves defining a sufficient number of sites selected to present orthogonal gradients of the variables of interest, in which population trends, the health of individuals and their demographic performance, and the quality of the environment (landscape, habitat, food, pathogens, agricultural practices, etc) are simultaneously measured. These correlative approaches can allow for semiexperimental conditions if properly designed. The design of operational and sustainable systems should be based on existing platforms at the international and national levels, such as the Long-Term Ecological Research Network (LTER). Like in epidemiological approaches to human health, we recommend developing long-term holistic approaches to understanding the consequences of multiple stressors on individual health, population dynamics and the functioning of communities and ecosystems. The relationships between climate change and ecotoxicological impacts could be tested via models that integrate the influence of climate on the fate of production systems and agricultural practices at the regional and international levels, related PPP uses, the distribution and phenology of species, and modifications of ecological communities.

5 - Considering landscape, spatial scales and temporality

With regard to terrestrial vertebrates, many taxa exploit the environment over the range of landscape mosaics, i.e., over areas larger than crop fields only. PPPs are used to treat cultivated plots on a

repeated and regular basis within and between years at the farm scale, at the regional scale, nationwide, and globally. These scales of use imply the chronic release of numerous AIs into the environment over large areas and pseudopersistence (i.e., “*gradual accumulation in the environment as their degradation is slower than their input*” (Hvezdova et al. 2018). In addition, treatments can affect surrounding untreated habitats through different mechanisms, which are influenced by landscape features (e.g., edge effects altering drift, roughness affecting atmospheric deposition, grasslands and riparian zones buffering runoff). The understanding of wildlife responses must be carried out at a relevant spatial scale integrating the main underlying processes. It would be necessary to strengthen the studies of exposure and effects at landscape scales (i.e., larger than the plot and its adjacent environment: from 1 to several km²) by integrating the composition and spatial pattern as well as the function (e.g., refuges, corridors) of landscape components. The concomitant and interactive effects of landscape features and PPP use on wildlife responses should be an area of research focus.

There is a need to improve the consideration of duration, chronicity and repetition of exposure. The temporality of agricultural practices (e.g., intra- and interannual frequency of treatment), of individuals or populations (e.g., phenology and activity rhythms) and of the processes leading to effects (e.g., potentiation or carry-over effect, Harrison et al. 2011) is essential when assessing the impact of PPPs. The exposure schedule with respect to critical life stage windows of vulnerability and of transgenerational impacts in effects assessment via both laboratory tests and *in natura* monitoring should be better addressed because many wildlife species are long-lived taxa and because exposure can occur throughout life, from the early stages *in utero/in ovo* to adulthood. Further research is needed to better understand the toxicokinetics and toxicodynamics of AIs in the context of chronicity, pulse and repetition of exposure.

Various tools are available when *in situ* experiments are logistically complicated or for prospective ERA to achieve such research aims. Spatially and temporally explicit modelling is considered a promising approach for integrating complexity, heterogeneity and multiscale processes in research and testing management and mitigation scenarios (EFSA 2023; Topping et al. 2020; Morrissey et al. 2023). Population models, especially spatially explicit models, have been developed during recent decades and improved upon, allowing scenario-based assessments and early application in ERA but requiring additional research, database building, and validation studies (Rattner et al. 2023). This would benefit management measures at the scale of farms and farm networks to reach the objectives of biodiversity conservation. Considering landscape ecotoxicology concepts and spatial ecology frameworks is important because of the gaps in the knowledge about the impacts of PPPs on ecological functions and ecosystem services.

6 – Assessment of the effects of PPPs on ecological functions associated with terrestrial vertebrates, ecosystem functioning and ecosystem services

Acquiring knowledge and developing tools for quantifying the effects of PPPs on the ecological

functions and services provided by wildlife are fundamental for understanding, preventing and managing the unintended effects of PPPs on ecosystem functioning. The main ecological functions and associated (dys)services provided by wildlife species/functional groups can be identified from the available literature. Thus, to provide fewer speculative elements than at present, a short-term challenge lies in the definition of operational indicators allowing the quantification of these functions/(dys)services and in their implementation in future monitoring schemes. Studying the links between PPP use and functions/(dys)services at the scale of the landscape mosaic would make it possible to detect the responses of organisms in cultivated plots and in other habitats where other functions/(dys)services may be involved. This approach is crucial for considering all functions and the extent to which they are involved, but also for considering possible trade-offs or synergies between functions/(dys)services and ecosystem multifunctionality. With regard to management objectives, landscape characteristics and agroecological infrastructures should be considered policy levers for promoting ecosystem services for agriculture to limit the need for PPPs to ensure the necessary conditions for the health and conservation of wildlife.

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Supplementary Information (SI)

Text SI1. Detailed queries

Table SI1. Ecological functions associated to terrestrial vertebrates

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- SUPPLEMENTARY INFORMATION -

Text SI1. Presentation of the list of keywords and the query.	2
Table SI1. Ecological functions associated to terrestrial vertebrates	4

TEXT S11. PRESENTATION OF THE LIST OF KEYWORDS AND THE QUERY.

The query was run on the Web of Science the December, 18th 2020. Only the references published from January, 1st 2000 onwards were included.

FINAL QUERY: (#1 OR #5) AND #2 AND (#3 NOT #4) NOT #6

1 : TI=(pesticid* OR "plant protection product\$" or PPP or "phytosanitary product\$" or phytopharmaceutic\$ or agrochemical\$ or herbicid* or insecticid* or nematocid* or helminticid* or fungicid* or molluscicid* or "active substance\$" or Acaricide\$ or Algicide\$ or Attractant or Desiccant or Elicitor or "Plant activator" or "Plant growth regulator" or Repellent\$ or Rodenticid* or neonic* or triazin* or phenylur* or organochlorine or organophosph* or carbamat* or pyrethroid* or "Basic substance*" or "Low risk active substance*" or "active substance*" or "active ingredient*" OR "seed treatment\$" OR "treated-seed\$" OR "coated seed\$" OR "Dressed seed\$" OR "seed coating") OR AB=(pesticid* OR "plant protection product\$" or PPP or "phytosanitary product\$" or phytopharmaceutic\$ or agrochemical\$ or herbicid* or insecticid* or nematocid* or helminticid* or fungicid* or molluscicid* or "active substance\$" or Acaricide\$ or Algicide\$ or Attractant or Desiccant or Elicitor or "Plant activator" or "Plant growth regulator" or Repellent\$ or Rodenticid* or neonic* or triazin* or phenylur* or organochlorine or organophosph* or carbamat* or pyrethroid* or "Basic substance*" or "Low risk active substance*" or "active substance*" or "active ingredient*" OR "seed treatment\$" OR "treated-seed\$" OR "coated seed\$" OR "Dressed seed\$" OR "seed coating") OR AK=(pesticid* OR "plant protection product\$" or PPP or "phytosanitary product\$" or phytopharmaceutic\$ or agrochemical\$ or herbicid* or insecticid* or nematocid* or helminticid* or fungicid* or molluscicid* or "active substance\$" or Acaricide\$ or Algicide\$ or Attractant or Desiccant or Elicitor or "Plant activator" or "Plant growth regulator" or Repellent\$ or Rodenticid* or neonic* or triazin* or phenylur* or organochlorine or organophosph* or carbamat* or pyrethroid* or "Basic substance*" or "Low risk active substance*" or "active substance*" or "active ingredient*" OR "seed treatment\$" OR "treated-seed\$" OR "coated seed\$" OR "Dressed seed\$" OR "seed coating")

2 : TI=(ecotoxic* OR toxicity OR poison* OR intoxication\$ OR "side effect\$" OR "adverse effect\$" OR "indirect effect\$" OR "negative effect\$" OR decline OR "QSAR" OR "risk assessment" OR bioaccumulation OR exposome OR exposure OR residue\$ OR "transformation product\$" OR metaboli* OR "non-intentional effect\$" OR "unintentional effect\$" OR "biological impairment" OR "physiological impairment" OR "ecological impairment" OR toxic* OR mixture\$ or endpoint\$ OR biomarker* OR bioindicator* OR "bio indicator*") OR AB=(ecotoxic* OR toxicity OR poison* OR intoxication\$ OR "side effect\$" OR "adverse effect\$" OR "indirect effect\$" OR "negative effect\$" OR decline OR "QSAR" OR "risk assessment" OR bioaccumulation OR exposome OR exposure OR residue\$ OR "transformation product\$" OR metaboli* OR "non-intentional effect\$" OR "unintentional effect\$" OR "biological impairment" OR "physiological impairment" OR "ecological impairment" OR toxic* OR mixture\$ or endpoint\$ OR biomarker* OR bioindicator* OR "bio indicator*") OR AK=(ecotoxic* OR toxicity OR poison* OR intoxication\$ OR "side effect\$" OR "adverse effect\$" OR "indirect effect\$" OR "negative effect\$" OR decline OR "QSAR" OR "risk assessment" OR bioaccumulation OR exposome OR exposure OR residue\$ OR "transformation product\$" OR metaboli* OR "non-intentional effect\$" OR "unintentional effect\$" OR "biological impairment" OR "physiological impairment" OR "ecological impairment" OR toxic* OR mixture\$ OR endpoint\$ OR biomarker* OR bioindicator* OR "bio indicator*")

3 : TI=(vertebrat* OR wildlife OR amphibia* OR reptile\$ OR herpetofauna* OR bird\$ OR avian OR avifauna OR raptor\$ OR eagle\$ OR passerine\$ OR songbird\$ OR anatid* OR shorebird\$ OR "wild game" OR ungula* OR galliform* OR lagomorph* OR rodent\$ OR insectivor\$ OR hare\$ OR deer\$ OR mammal\$ OR wolf\$ OR lynx OR badger\$ OR fox OR foxes OR Mustelid* or "hedgehog*" OR bat OR bats OR chiropter* OR shrew\$ OR snake\$ OR lizard* OR tortoise* OR frog\$ OR salamander\$ OR waterbird\$ OR waterfowl\$) OR AB=(vertebrat* OR wildlife OR amphibia* OR reptile\$ OR herpetofauna* OR bird\$ OR avian OR avifauna OR raptor\$ OR eagle\$ OR passerine\$

OR songbird\$ OR anamid* OR shorebird\$ OR "wild game" OR ungula* OR galliform* OR lagomorph* OR rodent\$ OR insectivor\$ OR hare\$ OR deer\$ OR mammal\$ OR wolf\$ OR lynx OR badger\$ OR fox OR foxes OR Mustelid* or "hedgehog*" OR bat OR bats OR chiropter* OR shrew\$ OR snake\$ OR lizard* OR tortoise* OR frog\$ OR salamander\$ OR waterbird\$ OR waterfowl\$) OR AK=(vertebrat* OR wildlife OR amphibia* OR reptile\$ OR herpetofauna* OR bird\$ OR avian OR avifauna OR raptor\$ OR eagle\$ OR passerine\$ OR songbird\$ OR anamid* OR shorebird\$ OR "wild game" OR ungula* OR galliform* OR lagomorph* OR rodent\$ OR insectivor\$ OR hare\$ OR deer\$ OR mammal\$ OR wolf\$ OR lynx OR badger\$ OR fox OR foxes OR Mustelid* or "hedgehog*" OR bat OR bats OR chiropter* OR shrew\$ OR snake\$ OR lizard* OR tortoise* OR frog\$ OR salamander\$ OR waterbird\$ OR waterfowl\$)

4 : TI=(zebrafish* OR "bird cherry" OR xenopus OR "snake* venom" OR seal OR seals OR whale OR whales OR dolphin\$ OR porpoise\$ OR "sea lion\$") OR AB=(zebrafish* OR "bird cherry" OR xenopus OR "snake* venom" OR seal OR seals OR whale OR whales OR dolphin\$ OR porpoise\$ OR "sea lion\$") OR AK=(zebrafish* OR "bird cherry" OR xenopus OR "snake* venom" OR seal OR seals OR whale OR whales OR dolphin\$ OR porpoise\$ OR "sea lion\$")

5 : TI=(biopesticid* OR "bio pesticid*" or BTI OR thuringiensis OR "microbial agent*" OR semiochemical* or "semio chemical*" or "natural* extract*" or "plant extract*" or "natural substance*" or "plant substance*" or biocontrol* or "bio control*" OR "pest* control*" or "weed* control*") OR AB=("microbial agent*" OR biopesticid* OR "bio pesticid*" or BTI OR thuringiensis OR semiochemical* or "semio chemical*" or "natural* extract*" or "plant extract*" or "natural substance*" or "plant substance*" or biocontrol* or "bio control*" OR "pest* control*" or "weed* control*") OR AK=("microbial agent*" OR biopesticid* OR "bio pesticid*" or BTI OR thuringiensis OR semiochemical* or "semio chemical*" or "natural* extract*" or "plant extract*" or "natural substance*" or "plant substance*" or biocontrol* or "bio control*" OR "pest* control*" or "weed* control*")

6 : TS=(medical OR "human health" OR biomedical OR pharmacol* OR "cell* line\$" OR "in vitro" OR "cell* toxicit*" OR "cell* viability" OR "cell* culture*" OR P450 OR antimicrobi* OR antibacterial OR ivermectin* OR avermectin* OR restore OR disruptive OR cytotoxicit* OR "animal model*" OR "gene* expression") OR TS=("flame retardant*" NEAR "organophosph*")

TABLE S11. ECOLOGICAL FUNCTIONS ASSOCIATED TO TERRESTRIAL VERTEBRATES

N.B.: The bibliographic references are provided at the end of the table.

Ecological function	Description or process	Case or example
Biological control: pest control and regulation of prey or predator dynamics through trophic cascades (top-down and bottom-up regulation)	Consumption/predation of different types of crop pests or weeds in various agrosystems	<p>Passerine birds, small mammals and bats in croplands (cereals, vineyard, orchards, gardening and horticulture, forestry, livestock farming) predate on crop pests and weed seeds.</p> <p>Raptors, top-predators and mesocarnivores predate on pest small mammals in grasslands and croplands</p> <p>Examples of trophic cascades involving predatory mammals including key predators</p> <p>Inversely, examples of vertebrate species considered as pests in agriculture or silviculture: corvids, pigeons, passerines, and ungulates</p>
Regulation of disease transmission (infectious and parasitic diseases)	Predation of pathogen vectors by insectivores	Amphibians, birds, and bats consume and control the population of pathogen insect vectors
Transmission of parasites and pathogens	<p>Host or vector of communicable disease to human or livestock</p> <p>The biodiversity of vector or host communities and of predators as well as population dynamics can modify the transmission of pathogens following a “dilution” pattern (“dilution hypothesis”) or an intensification pattern (“rescue hypothesis” or “amplification effect”).</p>	<p>Leptospirosis (rodents), alveolar echinococcosis (rodents and canids), rabies (carnivores), Lyme disease (mammals), haemorrhagic fever renal syndrome (rodents), plague (rodents), avian influenza (birds), swine fever (wild boar)</p> <p>Small mammal and bird hosts or vectors and mammalian predators play a role in transmission dynamics (e.g., Lyme disease, alveolar echinococcosis)</p>
Clean water and environment (environmental purification)	<p>Contribution to self-purification capacity of ecosystems via scavenging behaviour.</p> <p>Stimulation of organic matter decay and decomposition, reduction of methane production, clean-up of waste and landfills or sewage sludges.</p>	<p>Raptors and other mammalian or avian scavengers, some mesopredators</p> <p>Ducks, swans, and waterbirds, opportunistic feeding birds</p>

<p>Food provision</p>	<p>Resources: many vertebrates are the main preys of numerous carnivorous species among which some are threatened.</p> <p>Constitute resources that drive bottom-up control in numerous ecosystems and the numerical response of various predators.</p> <p>Facilitation: their activities allow or foster the access of other species to food or nesting resources.</p> <p>Mutualistic relationships.</p>	<p>Rodents and lagomorphs</p> <p>Some birds foster access to food for other for instance through “beaters - followers” interactions or via feeding activities (example: wells of sape)</p> <p>Birds (waterbirds, raptors, woodpeckers, kingfishers, ictorids, drongos)</p>
<p>Structuration of communities and biodiversity</p>	<p>Biodiversity: genetic and specific richness, abundance of vertebrates themselves.</p> <p>Biodiversity: increase in genetic or specific richness of invertebrates and plants.</p> <p>Limit the increase of other facultative opportunistic scavengers (ex. rats, stray dogs)</p>	<p>All vertebrates, threatened or endangered species</p> <p>Rodents and lagomorphs</p> <p>Predators, amphibians, scavengers</p>
<p>Dynamics of vegetation communities</p>	<p>Stimulation of plant growth and biomass.</p> <p>Effects on primary production: positive, neutral or negative.</p> <p>Influence on the structure, the dynamics or the trajectory and long-term trends of vegetation communities: direct role via or indirect role via the predation of herbivorous species</p>	<p>Rodents and lagomorphs, birds</p> <p>Large herbivores</p> <p>Predators</p>
<p>Propagule dispersal</p>	<p>Dispersal of propagules (via the faeces, food stocks, zoochory on feathers or hair or skin)</p> <p>Enhancement of germination success and of vegetation production.</p> <p>Mutualistic interactions.</p>	<p>Tropical bats.</p> <p>Rodents and lagomorphs, large herbivores</p> <p>Canids.</p> <p>Birds: corvids, passerines, waterbirds</p>
<p>Pollination</p>	<p>Pollination</p>	<p>Tropical bats, birds</p>
<p>Dynamics and structure of habitats and microhabitats</p>	<p>Engineer species: tunnels and galleries in soils, dams on watercourses, cavities in trees, tunnels and holes in banks, nest structures, etc.</p>	<p>Small mammals (rodents and lagomorphs, insectivores such as moles), marge or meso-mammals such as beavers</p> <p>Birds: nests represent various resources, in particular micro-habitats for other organisms (creation of cavities and galleries, cup or dome nests with materials allowing thermoregulation)</p>

Modification of soil properties	Increase of moisture and permeability, decrease of soil erosion	Rodents and lagomorphs
Nutrient cycling	Contribution to nutrient cycling, increase of available nitrogen, increase of phosphorus. Acceleration or slowdown of nutrient cycling, enrichment, translocation of nutrients through moving at local and landscape scales (i.e., flux between patches within the landscape mosaic) and at large, global scale (e.g., migrations, breeding colonies)	Rodents and lagomorphs, amphibians, large mammals, terrestrial birds, seabirds, waterbirds
Water cycle	Increase of moisture and permeability, decrease of soil erosion, siltation control. Engineer species: bioturbation, export of nutrients, creation of microhabitats for instance at edges of wetlands.	Rodents and lagomorphs, amphibians Waterbirds
Buffering of climate change impacts	Control of herbivores Role in community structure via top-down and bottom-up control, trophic interactions, competition	Grey wolf, top-predators
Ecosystem resistance/resilience	Ecosystem resistance to invasion, increase of resilience following wildfire “Early warning signals” and “sentinel species”	Large and small herbivores Raptors, passerines, and herptiles

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