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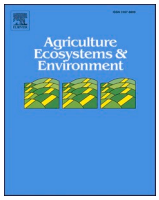

On the ambivalence of granivorous carabids: Weed seed bank regulators, potential crop pests or both?

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ABSTRACT

Carabids have long been beloved by collectors and have recently gained much attention in research as beneficial natural enemies of pests and weeds. With agricultural transformation towards lower herbicide use, carabids are expected to help carry the burden of weed regulation. While there is good evidence to found these expectations on, relying on seed-consuming carabids for natural weed regulation also has clear limitations. One of these is the fact that many carabids can be crop pests themselves, often in addition to their beneficial roles as natural enemies of pests or weeds. In a qualitative review, we gathered the available evidence for 72 carabid species acting as crop pests in 27 crops by damaging crops or consuming their seeds. Based on selected examples from different crops, we portray the historical impact and current state of carabids as crop pests. Due to the scarcity of recent reports, we expect that most carabids acting as crop pests are not a currently relevant economic problem across regions and crops, with beneficial ecosystem services provided by carabids outweighing possible damages. Yet, given the abundance of historical evidence and the current trajectory of agriculture towards a more sustainable management that aims to decrease chemical crop protection and increase carabid populations, we see a need to consider that carabids can, under certain conditions, act as crop pests. In this context, it will be crucial to get a better understanding of potential carabid crop pests around the globe, to identify under which conditions carabids switch roles from ecosystem service provides to ecosystem disservice providers and to understand how this role switching will be affected by climate change and agricultural transformation.

1. Introduction

Carabids are beneficial to agricultural production as they provide natural pest and weed regulation and have hence been studied intensively by ecologists in the last decades (Lövei and Sunderland, 1996). While they were mainly regarded as natural enemies to arthropod pests in the past, the impact of seed-consuming species on natural weed regulation has gained increasing attention in recent years (Fig. 1). That certain seed-consuming species can and do also act as pests on crops has, however, largely been neglected by the scientific community so far.

Carabids are the most influential arthropod weed regulators, consuming hundreds of seed per day and per square metre under field conditions (Kulkarni et al., 2015). Seed-consuming carabids are widespread in temperate agroecosystems and carabid communities are often dominated by species that are at least facultative weed seed consumers, e.g., *Pterostichus melanarius*, *Poecilus cupreus* or *Harpalus rufipes* (Carbonne et al., 2020; Boetzl et al., 2024). While reported seed predation rates vary strongly across weed species, for some species, carabids can reduce the number of seeds entering the soil seed bank by almost 90 percent for some weeds (Honěk and Martinkova, 2005). Carabid seed preferences are generally driven by body-size (Honěk et al., 2007; Kulkarni et al., 2015) and a positive relationship is commonly found between the density of large species and weed seed predation rates on sentinel prey cards (see e.g. Trichard et al. 2013 or González et al. 2020). Besides post-dispersal seed predation on the soil surface, many carabids also climb plants and feed on seeds pre-dispersal, often during seed ripening (Sasakawa, 2010), or move within the soil and consume buried seeds depleting the seed bank (Klimeš and Saska, 2010). While the evidence for long-term seedbank regulation by carabids is scarce, field experiments showed that the density of seed-consuming

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carabids can shape and reduce soil seedbanks across one growing season (Bohan et al., 2011; Carbonne et al., 2020). With the transformation towards more sustainable cropping systems in which biodiversity mediated ecosystem services replace conventional inputs (Bommarco et al., 2013), natural weed regulation provided by carabids is expected to partially substitute herbicide inputs and conventional deep tillage.

Carabid mediated weed regulation, however, also has its limitations. Only few carabid genera are believed to be strictly granivorous (e.g., some species of the genera *Ophonus*, *Amara* or *Zabrus*) while the majority of seed-consuming carabids and the species dominating carabid communities are facultative granivores (Larochelle, 1990; Honěk et al., 2007). Weed seed consumption in these omnivorous species depends on the availability and sometimes preference for alternative prey and is reduced when the availability of alternative prey is high (Carbonne et al., 2020, 2023; Petit et al., 2023). In addition, the presence of larger-sized predators decreases the activity of their prey, including smaller-sized carabid seed consumers, by both intraguild predation and via a non-consumptive landscape of fear resulting in reduced weed seed predation in field experiments, which will be a challenge when natural pest and weed regulation are aimed to be enhanced simultaneously (Prasad and Snyder, 2004; Carbonne et al., 2023). Vertebrate seed predation is commonly found to be much more important than invertebrate seed predation in comparative studies (see e.g. Meiss et al. 2010 or Schumacher et al. 2020). Further, not weed seed consumption per se is important for agricultural production, but specifically the regulation of economically relevant weed species with perennial life cycles that are difficult to control without herbicide use (Armengot et al., 2015). Carabids have so far not been shown to be capable of reliably regulating these weeds with seed preferences and consumption rates varying across studies (Brust, 1994; Honěk et al., 2007; Saska, 2008). In general, existing evidence indicates that weed diversity and/or abundance promotes granivorous carabids, i.e., the carabid-weed relationship is likely to be driven bottom-up rather than top-down (Diehl et al., 2012; Boetzl et al., 2024).

Though these limitations may indicate an overestimation of carabid weed seed regulation, they are not necessarily detrimental. Yet, some carabid species can also act as crop pests. Here, we review the past and present impact of carabids acting as crop pests based on a qualitative review of the available literature. We assess their current impact, discuss future trajectories in the light of ecological intensification of contemporary agricultural systems aimed for within the framework of the European Green Deal (European Union, 2020) and similar sustainability strategies and point towards emerging knowledge gaps.

2. Methods

We conducted a systematic literature search for reports of carabid beetles acting as crop pests using the ISI Web of Science Core Collection, the CABI international archives, google scholar and google. We regarded carabids as acting as crop pests if larvae or adults damage crop seeds, seedlings, plants or their parts leading to a direct reduction in absolute crop yield or the failure of the crop. We searched for 'carabid*', 'ground beetle*'and 'pest', 'damage' or 'crop' in any combination of these words in English and German. The initial search was conducted on 19 September 2023, the search was repeated several times and the final query was made on 16 February 2024. We searched for publications with no limitations on dates or languages. In addition we asked colleagues in the field for further publications and searched the reference lists in all identified publications for further, previously undetected reports. We filtered all publications found by the following criteria: (i) The carabid species was identified, (ii) the crop type was stated and (iii) crop damage was reported and (iv) the observation was made under realistic field conditions (i.e. we excluded all reports of acceptance of crop or crop seeds by carabids under lab conditions). We only included published reports that can be found online or in archives. This methodology yielded a total of 102 literature references for carabids acting as crop pests. Their full bibliography is given in Supplementary Material, Table S1.

Much of the detected evidence for carabids acting as crop pests was hidden in the so called 'grey literature', mostly in older publications and often in discontinued journals that are not indexed in the ISI Web of Science Core Collection. These observations were made by plant pathologists, agronomists, entomologists or even amateur collectors and mostly published as technical reports, in faunistic or in taxonomic publications in various languages. During our search, we detected further, mostly very old references (prior 1920) that could not be obtained for review but are reviewed in Larochelle (1990). According to this publication, these references do not contain any additional species × crop type interactions that we could have missed.

3. Results

We found evidence for 72 carabid species recorded as pests of at least 27 crops, with 90 % of the species reported from the Palaearctic realm,

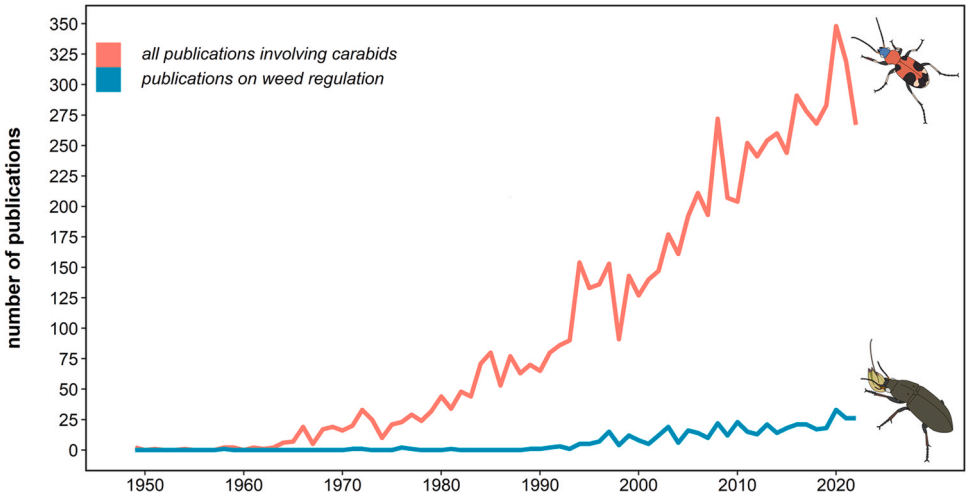

Fig. 1. Publications listed in the ISI Web of Science core collection per year for the search terms 'carabid*' (7370 publications; red line) and 'carabid*' AND 'weed' OR 'granivore*' OR 'seed' (453 publications; blue line). The search was performed on 08 January 2024 and publications with publication year 2023 were excluded as not all publications may have been listed yet for this year. This search does not resemble the search performed in our review and is presented purely for illustration purposes.

predominantly the agricultural areas in Europe, and only 2 species reported from the global south (Fig. 2 & Supplementary Material, Table S1). These species are all but rare – they account for approximately 48 percent of all carabid individuals in crop fields across 28 studies from Europe reported in Boetzl et al. (2024).

On cereals, 36 carabid species were reported as pests, with a majority belonging to the subfamily Zabrini. The corn ground beetle, *Zabrus tenebrioides*, is a well-known example. While adults feed on ripening seeds of grasses as well as various winter cereals (Fig. 3A) their larvae feed on the tillering winter cereal plants in autumn and can cause drastic damages with each larva consuming roughly 100 cm^2 of leaf area during development, the area of approximately 25 winter wheat plants (Fig. 3B) (Wetzel and Epperlein, 1978). In favourable years, mass reproduction can lead to densities up to and above 100 000 larvae per ha and result in the defoliation of entire fields (Tiebas et al., 1992; Popov and Bărbulescu, 2007; Panuta et al., 2018). In such years, the species has destroyed significant shares of winter cereal fields, e.g. 70 % in Italy (Nicosia et al., 1996) and 90 % in France (Chabanel et al., 2008) with reported absolute annual crop losses ranging up to 250 000 ha in Romania (Georgescu et al., 2017). In many regions, especially in southern and south-eastern Europe, insecticides are currently being used against *Z. tenebrioides* demonstrating its status as economically relevant crop pest (Nicosia et al., 1996; Popov et al., 2010). At least 28 carabid species were reported as pests on strawberries (Fig. 2; Supplementary Material, Table S1) and especially the strawberry seed beetle, *Harpalus rufipes* (Carabidae, Harpalini), can cause considerable damage: Adults feed on the nuts (achene), thereby injuring the fruits (Fig. 3C) opening a gateway for infections with *Botrytis cinerea* and other fungal pathogens that reduce the marketability of fruits or lead to direct yield losses (Kirchner, 1939; Lindroth, 1992). Historic yield losses due to *H. rufipes* ranged up to 95 % and the species was actively controlled using traps and insecticide soaked baits (Zolk, 1932; Mühle, 1939). While reports of damages were almost absent after the mid-1970s (Supplementary Material, Table S1), the species is still occasionally relevant, causing 30 % yield loss in tunnel-produced strawberries in a recent report (Thoss, 2020). On Brassicas, several species of the genus *Amara* (Carabidae, Zabrini) have been observed feeding on seeds, with at least *A. similata* being a specialised seed predator of this family (Lindroth, 1992; Luka et al., 1998; Klimeš and Saska, 2010). *A. similata* and *A. ovata* have been observed feeding on ripening oilseed rape seeds in the field but economic assessments are lacking (Luka et al., 1998). Several species of the genus *Ophonus* (Carabidae, Harpalini) are specialised seed predators on umbellifers (Apiaceae), e.g. *O. subsinuatus* that is a specialist on dill (Veselý and Resl, 2021). This could affect the seed production for the many vegetable crops in this family (e.g. caraway, carrot, celery, coriander etc.) but reports of economic relevance are absent.

But not only ripening seeds are attacked by carabids: Various carabid species have also been observed feeding on freshly sown seeds, growing crop seedlings or their roots (18 species; Supplementary Material, Table S1). For instance, the Palaearctic species *Clivina fossor* (Carabidae, Clivinini) has been reported as pest on seedlings of sugar beet and chicory, in some cases resulting in complete crop failure (Proft, 2000; Mielke and Schöber-Butin, 2002; Jossi et al., 2004). In North America, several species of the genus *Stenolophus* (Carabidae, Harpalini) are pests on germinating seeds and seedlings of maize, sugar beets, sorghum and millet and have in the past occasionally caused losses of entire fields and

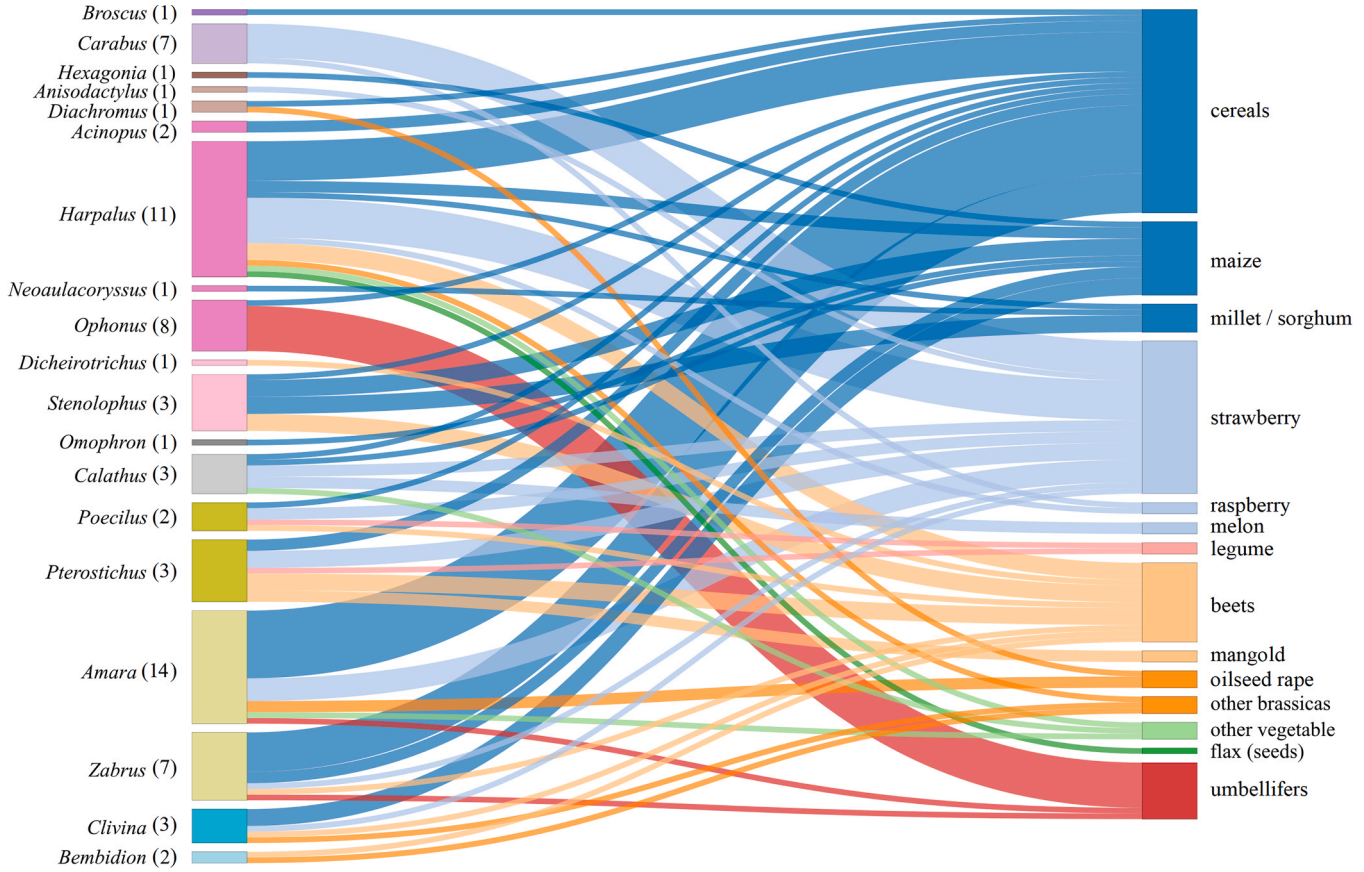

Fig. 2. Interaction between carabid genera (left; the number of species is indicated behind the genus name) and different crop types on which species of these genera were observed acting as pests (either by feeding on plant tissue or by consuming the seeds of crops). Colours indicate relatedness: genera within the same tribes in carabids (left) and closely or functionally related crop types (right). The width of the links represents the number of species of the genus that were observed as pests on the respective crop and the colouration of the link follows the respective crop type. For the species and crop interactions that are the basis of this figure, see Supplementary Material, Table S1.

Fig. 3. Examples of carabids acting as crop pests: Adult of the corn ground beetle, *Zabrus tenebrioides*, feeding on ripening wheat grains (A) and its larva next to a damaged wheat tillers (B) and the adult of the strawberry seed beetle, *Harpalus rufipes*, feeding on the nuts of a ripening strawberry, thereby damaging the protecting exocarp and opening a gateway for an infection with *Botrytis cinerea* (as seen on the fruit on the left). Pictures made available to us by courtesy of Tomasz Klejdysz (A & B) and Hagen Thoß (C).

made chemical control necessary (Kirk, 1975; Pausch, 1979). All interactions between carabids and different crops are displayed in the Supplementary Material in Table S1 with references and accompanied by a more detailed description of some carabid species acting as pests and their economic implications.

4. Discussion

4.1. The current impact of carabids as pests

Despite the recent focus of carabids as beneficial weed seed regulators, their role as potential crop pests has obtained only negligible attention in recent research, especially in the 21st century. Our qualitative literature review highlights that many seed-consuming carabid species do occasionally act as crop pests which implies that the beneficial services performed by carabids can be context-dependent. Carabids are, however, usually not considered major insect crop pests and even the most serious documented historical crop losses to carabids were typically limited to certain areas and shorter timeframes (e.g., Georgescu et al., 2017). In contrast to many economically relevant multivoltine crop pests, carabids reproduce only once per year and carabid populations thus have limited growth potential restricting their impact as crop pests (Ziter et al., 2012).

With the exception of some species of the genus *Zabrus* that are economically relevant pests in the Mediterranean and Eastern Europe, recent reports of crop damages caused by carabids were generally scarce or lacking. We found few recent reports of carabids causing relevant yield losses or requiring insecticide applications. The absence of perceived crop damages due to carabids despite the increasing amount of research performed in temperate agricultural landscapes, indicates that under the current agricultural management regime, most carabids are not economically relevant pests. It is possible that seed-consuming carabids that can act as pests are not abundant enough to have a noticeable economic impact as they are passively controlled by the widespread use of systemic insecticides against various insect crop pests. That some historically relevant carabid crop pests have been pushed onto regional or national red lists in the last decades, e.g., *Zabrus tenebrioides* in Bavaria (Lorenz and Fritze, 2020), presumably due to current agricultural management and intensified cultivation methods could be an indication for this.

For the moment, economic assessments of the potential impact of carabids as pests are lacking for most agricultural systems. We assume that while carabid crop pests contribute to overall crop losses, their current impact is likely negligible compared to other, more dominant and specialised crop pests or weeds (Oerke, 2006). It is likely that current damages caused by carabids are in most cases so low that they will not be detected, are attributed to other pests or are below economic thresholds. In addition, we assume that carabid mediated pest and weed regulation services currently outweigh carabid caused crop damages in most cases. Nevertheless, we see the potential that the importance of carabid pests could increase in the future if carabid populations increase and insecticide pressures are simultaneously removed. Therefore, we see a clear need to quantify carabid crop damage potentials and potential effects of climate change and the transformation towards more sustainable and biodiversity-friendly agricultural production on these.

4.2. Sustainable agriculture – disservices through the backdoor?

Scientists have recognised the pressures of intensified agricultural management on farmland biodiversity and have consequentially called for a policy shift. New and refined policies such as the European Green Deal aim for a fundamental transformation of agricultural systems to the benefit of biodiversity and biodiversity-mediated ecosystem services, specifically pollination, pest and weed regulation and nutrient cycling (Ekroos et al., 2014; European Union, 2020). However, the risk of simultaneously supporting crop pests and ecosystem disservices is rarely discussed (Zhang et al., 2007).

In Europe, policymakers aim for a drastic reduction of pesticide use over the coming decades (European Union, 2020; Jacquet et al., 2022) with certain insecticides (e.g., several neonicotinoids) being banned entirely due to their harmful effects on human health and the environment (Sánchez-Bayo, 2014). While reduced pesticide use will inadvertently free many pests from efficient pest control (Jacquet et al., 2022), it is expected to simultaneously benefit natural enemies as insecticides affect natural enemies on higher trophic levels by both sub-lethal and lethal effects via the food chain (Douglas et al., 2015; Greenop et al., 2020). It is likely that carabids currently suffer from insecticide use, either directly when acting as crop pests or indirectly by consuming affected prey. The impact of carabids acting as pests could thus increase when pesticide pressure is reduced. Yet, problems with carabids as pests have apparently not been recognised in organic agriculture, which is in line with results for other pests in these systems (Muneret et al., 2018). If and to which degree current pesticide use mediates crop damage caused by carabids remains to be determined.

Apart from pesticide reduction, current policies focus on increasing farmland biodiversity, mainly via the establishment of near-natural and non-crop habitats in agri-environmental schemes (Ekroos et al., 2014; Boetzl et al., 2021). Some of these habitats are especially intended to

build up carabid populations via the provision of continuous food resources and undisturbed habitat for sheltering and overwintering, with such habitats sometimes even referred to as 'beetlebanks' (e.g. Collins et al. 2003). Biodiversity supporting measures can also benefit taxa classically identified as crop pests (Sutter et al., 2018; Lundin et al., 2023), but in previous assessments, carabids were never considered as potential pests. At the moment, it remains unclear how carabid populations and communities will be affected by the agricultural transformation and which species may benefit. We hence see the necessity of a more comprehensive evaluation of biodiversity supporting measures.

4.3. Emerging knowledge gaps and open research questions

Both current and future impacts of carabids acting as pests on crops are understudied. In case relevant impacts are detected, establishing effective pest management without simultaneously harming farmland biodiversity or hampering beneficial pest and weed regulation services provided by carabids would be challenging. Such management would require targeting selected, potentially problematic carabid species instead of the entire community and potentially by shifting community compositions towards desired ecosystem service outcomes. This requires a deeper understanding of carabid ecology, habitat requirements and the context-dependence of realised ecosystem functions on the species level.

Further, it is unclear how carabids and especially potential carabid pests will be affected by climate change. For the cereal pest *Zabrus tenebrioides*, recent outbreaks were linked to favourable hot and dry climatic conditions that will become more common with climate change in temperate agricultural landscapes in the foreseeable future (Georgescu et al., 2017; Panuta et al., 2018). It seems likely that some species could regain relevance as a crop pests in the future.

Another knowledge gap is the global south, where agricultural systems and many of their specific pests and problems are generally insufficiently studied. While natural pest regulation and especially carabids have recently gained some attention (see e.g. Vogel et al. 2023), we are not aware of any studies on seed-consuming carabids in tropical smallholder systems (but see Birkhofer et al. 2024 for overall seed predation). In our review, we only found reports for two carabid species of the Afrotropical and Neotropical realms acting as crop pests despite carabid communities in the global south containing many species of the same families that have historically caused crop losses in temperate regions. Research is needed to identify weed regulation potentials and potential carabid pests in tropical smallholder systems.

4.4. Context dependency of seed predation in carabids

The concept of ecosystem services and disservices is based on the human valuation of ecosystem functions or processes. Within an ecosystem, species do not have certain predefined roles but their realised roles depend on the respective context (Saunders et al., 2016). Perceived services like weed seed regulation can become perceived disservices under changing conditions when crop seeds are targeted. Most of the carabid species discussed here are indeed ambivalent, fulfilling several functional roles simultaneously as natural enemies to crop pests, as natural weed seed bank regulators but also, under certain conditions, as crop pests. For instance, a generalist omnivorous carabid species like *P. melanarius* can feed on crop pests and weed seeds but also become a crop pest itself, feeding on crops, developing seeds or grain (Supplementary Material, Table S1). In addition, the predation of germinating crop seeds itself can be detrimental in one year but beneficial in the following year when the same crops would be volunteers in a different crop. The realised role of many carabid species is, at any time, somewhere within the continuum between these aspects and functional roles can thus not simply be pinned to certain species. This makes it difficult to determine the realised impact of different species on agroecosystems. It is currently unclear if there is a species-specific equilibrium between all these functional roles and where this equilibrium is located in different species and assemblages and under which internal and external conditions functional roles shift or become predominant over others. More research is needed to investigate when and under which conditions carabid species switch roles from providing ecosystem services to providing ecosystem disservices (and vice versa) in order to manage carabid assemblages towards beneficial ecosystem services and ensure consistent natural pest and weed regulation in future agroecosystems.

Author contributions

FAB conceptualised the study and conducted the literature search, FAB and MK wrote the first version of the manuscript, revised the manuscript and both authors gave final approval for publication.

CRediT authorship contribution statement

Fabian Alexander Boetzl: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Michal Knapp:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Data availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109226.

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