Resilience and function: Beetles as critical drivers of global ecological processes

- 3 Jacob Muinde^{1, 2, 3*}, Caren Ochieng^{1,2,3}
- ⁴ Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
- ²National Museums of Kenya, Museum Hill, Nairobi P.O. Box 40658-00100, Kenya
- ³University of Chinese Academy of Sciences, Beijing 100049, China
- 7 *Correspondence: mulwamuinde2000@gmail.com

8

9

10

11 12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

1

2

Abstract

Beetles (Coleoptera), among the most diverse and ecologically significant insect groups, play vital roles in ecosystem functioning and service provision. With over 300,000 described species, their adaptability - driven by traits such as elytra and diverse feeding habits enables them to occupy nearly all terrestrial niches. Beetles contribute to nutrient cycling, pollination, seed dispersal, pest regulation, and decomposition, directly supporting ecological balance and human well-being. However, climate change and anthropogenic activities - including land-use shifts, pollution, and habitat fragmentation - threaten beetle populations, disrupting their ecological functions. Despite their exceptional diversity and critical roles in ecosystem functioning, beetles (Coleoptera) remain disproportionately understudied compared to more charismatic insect orders such as bees and butterflies, which have long been focal points in ecological research due to their recognized pollination services. Additionally, most studies examine single stressors, neglecting the compounded effects of co-occurring global change drivers. Long-term monitoring and conservation strategies are urgently needed to mitigate biodiversity decline and preserve beetles as ecosystem engineers. This review synthesizes current knowledge on beetle-mediated ecosystem services, highlights threats from anthropogenic pressures, and proposes future research directions to safeguard their ecological contributions.

1. Introduction

A functionally intact ecosystem comprises an interactive tapestry of living organisms and their immediate surroundings, driven by synergies, relationships, and dependencies developed over millions of years (Verma et al., 2023). Insects play an integral role in maintaining ecological

balance, influencing diverse spheres of the Earth's functioning (Schowalter, 2012; Scudder, 2017). Ubiquitous in nature, they contribute to nutrient cycling, pollination, decomposition, herbivory, predation, mutualism, and parasitism (Eggleton, 2020; Crespo-Pérez et al., 2020). These ecological functions are critical for trophic interactions and regulation, which are essential for ecosystem stability (Wu et al., 2024). Species diversity is a key determinant of ecosystem health and resilience (Tilman et al., 2014). The coexistence of diverse insect species reduces herbivory, suppresses diseases, enhances nutrient cycling, promotes interspecific complementarity, and optimizes resource use, ensuring stable energy flow (Greenop et al., 2021; Zhou et al., 2023).

Beetles (Coleoptera) are among the most diverse and widely distributed organisms, with approximately 300,000-450,000 described species (Stork et al., 2015; Muinde & Katumo, 2024). They inhabit nearly every terrestrial environment, including Antarctica (Ashworth & Erwin, 2016). Their remarkable diversification is attributed to the evolution of elytra, which protect them from predation, external pressures, and environmental stress. Some studies suggest that their close evolutionary relationship with flowering plants also contributed to their diversity. However, this raises questions about whether beetles merely track biogeochemical patterns controlled by plants rather than actively driving them (Yang & Gratton, 2014; Sota et al., 2022). Beetles exhibit diverse feeding habits including omnivory, carnivory, fungivory, florivory, detritivory, coprophagy and scavenging, highlighting their critical role in terrestrial food webs (Lee et al., 2020). Their broad dietary flexibility may have facilitated their colonization of nearly all ecological niches (Bradford et al., 2013; Wislocki, 2021).

Beetles mediate crucial ecosystem functions, including nutrient cycling, bioturbation, plant growth enhancement, seed dispersal, parasite suppression, pollination, and trophic regulation (Manning et al., 2016). They also provide essential ecosystem services that directly benefit human well-being, such as food provision, decomposition of fecal matter (reducing pest fly populations), nitrogen retention (maintaining forage productivity), soil conditioning, crop productivity enhancement, and cultural services (Doube, 2018; Bao et al., 2019; Servín-Pastor et al., 2021). Their economic value is substantial; for example, dung beetles save the UK cattle industry approximately US\$497.8 million (£367 million) annually in conventional and organic systems (Beynon et al., 2015). Similarly, their introduction in Southwestern Australia increased cattle revenue from US\$14.3–21.8 to per hectare annually (Viera, 2024). Additionally, beetles serve as

bioindicators, signaling environmental disturbances or changes under ecosystem stress (McGeoch, 2007; Ghannem et al., 2017).

However, climate change and anthropogenic activities in the 21st century have severely disrupted insect-mediated ecological functions and ecosystem services, including those provided by beetles (Noriega et al., 2018). This poses challenges in quantifying and valuing ecosystem services, particularly amid global changes that alter biogeochemical patterns, biodiversity distribution, and ecological stability.

While bees and butterflies have dominated ecological research due to their charismatic appeal and recognized pollination roles, beetles remain understudied despite their unparalleled diversity and ecological significance. This review synthesizes existing knowledge on beetlemediated ecosystem services, advocating for their inclusion in ecological research and conservation agendas. By doing so, we aim to stimulate further investigation into how beetles support ecosystem stability and resilience in the face of global environmental change.

2. Ecosystem functions

2.1 Beetles as Decomposers

Decomposition involves the biogeochemical cycle of nutrients through the biosphere. This process is aided by soil invertebrates that breakdown vertebrate excreta and dead plant materials into simpler forms that are absorbed back to the plants (Crowther et al., 2019; Pausas & Bond, 2020). Plants and animal tissues enter the detritus pool ass litter and excreta/carrion respectively. The rate at which decomposition occurs is influenced by several factors including the detritus quality, the environmental factors such as temperature and water availability as well as the activities of the soil invertebrates (Wu et al., 2021; Favila, 2024). The role of macro and microinvertebrates in litter decomposition is majorly noted between 0-38 days after which fungi and bacteria facilitate further decomposition (Cárdenas & Dangles 2012; Cárdenas et al. 2017). The earliest wood-boring beetles likely emerged as decomposers of decaying plant material and fungi dates back to early cretaceous period 125-66 MYA (Schmidt et al., 2020; Peris et al., 2021). Carrion and dung beetles mediate the nutrient cycling through decomposition of freshly deposited vertebrate excreta and carcasses of dead animals (Nadeau et al., 2015; Sun et al., 2023). Some of the beetle families associated with dung decomposition belong to the Hydorophilidae,

Scarabaeidae, Geotrupidae, Cryptophagidae, Staphylinidae, Histeridae, Hybosoridae and Trogidae. Beetle families associated with carcass decomposition includes Silphidae, Staphylinidae, Histeridae and Dermestidae (Nadeau et al., 2015; Engasser et al., 2021; See table. 1).

Table 1. Summary of the beetle families that play different ecological functions in the ecosystem.

Ecological functions	Family	References
Decomposition	Scarabaeidae, Geotrupidae, Silphidae, Trogidae, Cerambycidae, Passalidae, Staphylinidae, Tenebrionidae, Curculionidae, Dermestidae, Hydorophilidae, Cryptophagidae, Histeridae, Hybosoridae Anobiidae, Bostrichidae, Brentidae, Buprestidae, Cerambycidae, Lymexylidae & Zopheridae	Crawford 1981; Schuster & Schuster 1985; Hansen, 1997; Scott 1998; Bang et al. 2005; Watson & Carlton 2005; Nichols et al. 2008 & Ulyshen, 2018
Bioturbation	Scarabaeidae, Carabidae, Tenebrionidae & Staphylinidae	Krell et al., 2003; Brown et al., 2010; Wharton 2011; Eyre et al. 2013; Johnson et al., 2016 & Wyatt et al. 2012
Trophic regulation	Carabidae, Coccinellidae, Staphylinidae, Rhipiphoridae, Meloidae, Chrysomelidae & Curculionidae	Obrycki & Kring 1998; Farrell, 1998 Kromp, 1999; Bologna & Pinto 2002; Blossey et al. 2001 & Louda et al., 2003
Bioindicators	Scarabaeidae, Lucanidae, Carabidae, Elmidae, Coccinelidae, Tenebrionidae & Staphylinidae	Ranius et al. 2005; Thomaes et al., 2018; Gontijo 2019; Knapp et al., 2020; Bauernfeind & Moog 2020; Nervo et al., 2021 & Saito et al. 2022
Pest control	Coccinellidae, Carabidae, Elateridae, Staphylinidae & Tenebrionidae	Roy et al., 2016; Gurr et al. 2017; Mani & Krishnamoorthy 2020; Frank et al., 2022; Andersen et al., 2023; Jeffs & Lewis 2023
Pollination	Nitidulidae, Curculionidae, Scarabaeidae, Mordellidae, Oedemeridae, Ptiliidae, Mordellidae, Elateridae, Lagriidae, Cleridae, Coccinellidae, Cryptophagidae, Corylophidae, Anthicidae, Hybosoridae, Calliphoridae, Hydrophilidae, Histeridae, Bostrichidae, Cantharidae, Cetoniidae & Rutelidae	Ollerton et al., 2020; Terry et al., 2021; Liu et al. 2022; Steenhuisen et al., 2022; Kawakita & Kato 2023; Muinde & Katumo, 2024.

Based on their nesting strategies, the dung beetles are categorized into Paracoprid (tunnelers), Telocoprid (ball-rollers) and Endocoprid (dwellers). The Tunneller dung beetles bury freshly depositing wastes by vertebrates below ground surface within the vicinity of the original

deposition, the ball-rollers move the nutrient-rich organic materials to distance away and bury it below the earth surface while the dwellers feed and brood in the dung at the original site of deposition (Cheng et al., 2022; Anderson et al., 2024). Each of these categories of the dung beetles have implication on their ecological functions. Burying dung by the tunnelers below earth surface reduce emission of greenhouse gases into the atmosphere, prevent nitrogen volatilization hence increasing the available nitrogen for reabsorption by the plants (Cheng et al., 2022). On the other hand, moving the dung by ball-rollers to a new location instigate microorganisms and chemical changes on upper soil layers (Shah & Shah, 2022). The dwellers breakdown the vertebrate excreta at the original deposition site hence enriching the original site (Ambrožová et al., 2021;). Contrastingly, the carrion beetles feed on carcasses where just like the dweller dung beetles they feed on the original site and brood in it. Their larvae also feed on the carcass and further break it into simpler forms releasing the nutrients to the soil (Englmeier et al., 2023). The decomposition efficiency of carrion and dung beetles is influenced by several factors such as altitude, seasons, habitat specificity, soil contents, predation, competition, temperature, sunlight exposure and food quantity and quality (Büchner et al., 2024).

It is worth noting that dung beetle species and functional diversity jointly sustain the process of dung decomposition, with even limited beetle species but functionally diverse assemblages maintaining high activity (Dangles et al., 2012). In addition, the large dung beetle species disproportionately face the threat of human-driven extinctions, however positive interactions among functional groups play a great role in maintaining biodiversity-ecosystem functioning relationships (França et al., 2020). Lastly, partial and temporal variability further modulate decomposition effectiveness (Labidi et al., 2012).

Unlike carrion and dung beetle decomposition, dead wood decomposition can take years to fully to decompose (Ekström et al., 2021). Dead wood is among the major and readily available detritus and represents 20–30% of total forest biomass in temperate and tropical ecosystems providing resources for organisms (Weedon et al., 2009; Zumr et al., 2024). Some of the factor that influence the decomposition of dead wood includes temperature, oxygen, moisture, wood size and quality, number of decomposing organisms and carbon dioxide (Wijas et al., 2024). Saproxylic beetles depend on dead wood during some stages of their life cycle (Traylor et al., 2023). Some of the saproxylic beetle families includes Scolytidae, Cerambycidae, Buprestidae, Bostrichidae,

Brentidae, Curculionidae, Staphylinidae, Cleridae, Nitidulidae, Histeridae, Rhizophagidae, Monotomidae, Ciidae, Cucujidae, Erotylidae, Leiodidae, Trogossitidae (Nadeau et al., 2015; Deregowski, 2024). Moreover, each of these families contribute uniquely to the decomposition, for instance, Scolytidae (bark and ambrosia beetles), accelerate wood decay by introducing symbiotic fungi (e.g., *Ophiostoma* spp.) that break down lignin and cellulose, Passalidae (bess beetles) mechanically fragment decaying wood while enhancing microbial activity and Cerambycidae (longhorn beetles) through larval tunneling, they increases wood surface area for fungal colonization, (Stokland et al., 2012; Ulyshen, 2016, 2018).

Globally, the impact of beetles as decomposers and their role in nutrient cycling has attracted a considerable attention from the scientific community (Nichols et al., 2008; Torabian et al., 2024). Beetles have contributed significantly to the ecosystem maintenance in the Australian Alps which is inhabited by a wide range of pest animals and is vulnerable to climate change and mass mortality events has detrimental effects to the ecosystem (Stone et al., 2023). Similarly, introduction of dung beetles in Australian ecosystem through Dung beetle project helped clear the dung accumulation problem due to introduction of livestock in absence of native-ruminant adapted dung beetle fauna (Nichols et al., 2008). The ecological importance of beetles as decomposers have also been reported in Antipodes and North America (Pokhrel et al., 2021), South America (Maldaner et al., 2024), and Mexico (Barragán et al., 2021). Globally, decomposer services provided by beetles and other organisms were estimated at \$17 trillion annually, underscoring their critical role in maintaining ecosystem function (Costanza et al., 1997). Additionaly, dung beetles in particular enhance soil fertility and pasture productivity for example, in Veracruz, Mexico, their burial activity generated US\$149.1 to us\$423.6 per animal unit in economic benefits by improving forage availability (Lopez-Collado et al., 2017).

2.2 Beetles as Pollinators

Beetle pollinator-plant interactions date back to early cretaceous period (Bao et al., 2019). Some beetle families such as Chrysomelidae, Curculionidae, Tenebrionidae and Scarabaeidae are among the early insects that interacted with early angiosperms around 140-100 mya (Thien et al., 2009; Muinde & Katumo, 2024). Previous studies have highlighted the role of beetle as pollinators, Sayers et al., (2019) reported beetles as the fourth among insect pollinators and second major pollinator of the plants in the tropics. Beetles have also been reported as the prominent and

pollinators of angiosperms such Magnoliaceae, Annonaceae, Cyclanthaceae, Calycanthaceae, Araceae and Aracaceae (Paz et al., 2021; Muinde & Katumo, 2024). While the global economic value of beetle pollination remains difficult to quantify due to limited research, recent studies have identified key economically important plants dependent on beetles, including magnolia, nutmeg, sugar palms, custard apples, and sugarcane (Sabino et al., 2022). The success to pollination is the individual beetle pollinator- plant interaction (Macgregor & Scott-Brown, 2020). Therefore, both the beetles and plants have evolved some mechanisms that facilitates the pollination process. Such mechanisms range from floral scent (Pereira et al., 2014; Maia et al., 2021), floral morphology (Etl et al., 2022), thermogenic sensitivity (Seymour et al., 2009; Wang et al., 2017), and floral mimicry (Gottsberger et al., 2021). Beetles also evolved traits to exploit floral resources such as comb of setae on the mandibles, palps and forelegs, antennal and mandible pouches, conspicuous eyes and snout mandibles (Krenn et al., 2005; Muinde & Katumo, 2024). The question of beetle pollination being a secondary outcome of the flower visitations still remains unresolved since most of the flower visiting beetles exhibit both florivory and herbivory behaviors and the effectiveness of the pollination is barely understood.

2.3 Trophic regulation

All living organisms regardless of their size play a very significant in the trophic interactions (Verma et al., 2023). The multifaceted interactions between organisms such as mutualism, symbiosis, parasitism, competition and predation are crucial in maintaining ecological equilibrium (Didham et al., 1998). The research on interspecific and intraspecific interaction of beetles and other organisms is still at its infancy. Some of the recent studies includes the mutualism interaction between ambrosia beetles and ambrosia fungi which is one of the well explored beetlefungal interactions, the adaptation allows beetles to store and transport their nutrition while the pathogens depend on the beetle for dispersal and cultivar maintenance (Hulcr & Stelinski, 2017; Gugliuzzo et al., 2022).

Beetles also tend to host diverse microbial symbionts that play crucial roles in their growth, survival and reproduction (Favila, 2024; Salazar-Rivera et al., 2024). This includes beetle-bacteria symbiosis where the bacteria (obligatory and beneficial microbial symbionts) contribution ranges from plant biomass digestion, conferring defense against predators and pathogens, defense against plant secondary pathogens, detoxifying enzymes and nutrient supplementation (Fukumori et al.,

2022). Noteworthy, the beetle-bacterial symbioses occur at both intracellular and extracellular level. For instance, Nutrition supplementation symbionts target the gut while the defense symbionts target the extracellular walls (Maire et al., 2020; Salem & Kaltenpoth, 2022). Cassidinae beetles (Chrysomelidae) are associated with *Stammera* bacteria, located in the host foregut, whose genome influence production of pectin-degrading enzymes that assist the beetle in digestion of food (Fukumori et al., 2022). Additionally, bacterium *Nardonella* found weevils release tyrosine for cuticle hardening (Anbutsu et al., 2017).

Competition is a common phenomenon that arise over space availability, food resource and potential mates (Renahan & Sommer, 2021). Intra and inter-competition in beetles is well exhibited in decomposition function where decomposers compete over carrion or dung (Matuszewki & Bielewicza, 2021). Trumbo & Sikes, (2021) reported that interspecific competition between decomposers appears minimal due to utilization of non-overlapping resources as well as variation in carcass utilization strategies. Negative competition between beetles and blowflies is reported in the way both species colonize the carrion, with blowfly's larvae feeding on carcass much earlier than beetle larvae which have a longer life cycle. Therefore, enabling the blowflies to monopolize the greater part of the detritus pool (Charabidze et al., 2021). To reduce the competition dung beetles have adopted a Sit-and-wait strategy that enable the beetles to reserve time and energy by flying at perching at strategic position where they can easily perceive the smell of fresh dung. This strategy ensures optimal foraging of whenever available (Vulinec et al., 2007; Sabu & Nithya, 2016). Competition for food is common exhibited in interspecific interactions while competition for mates is restricted to conflict with species (Nichols et al., 2008). When competition limits beetles from getting the high quality and quantity share for available resources, beetles tend to plastically respond in morphology (colors and size), life history traits and behaviors (dietary habits and lifestyles) (Renahan & Sommer, 2021; García-Atencia et al., 2024).

Beetles experience significant vertebrate predation pressure across ecosystems (Young, 2015). As a result, beetles have evolved anti-predatory respond in morphology such as improved sensory traits (Nervo et al., 2023), cryptic and aposematic coloration (Doktorovová et al., 2019), development of sound emitting stridulatory organs (Giulio et al., 2014), defensive secretion (Laurent et al., 2003), aggregation strategies (Kowles et al., 2012), change of diel activity (Lobo & Cuesta, 2021) and geographical shift (Ge et al., 2023). Furthermore, Scholtz et al. (2009)

proposed that the evolution of distinct nesting strategies in beetles may represent an adaptive response to larval predation pressures. Lady birds as biological control agents are the epitome of predation in beetles. They are entomophagous insects that voraciously feed on other insects, thereby regulating the prey-predators interact and maintaining ecological balance (Rondoni et al., 2021).

2.4 Bioturbation

Beetles are considered critical players in maintaining soil biota populations and increasing soil aeration and porosity (Tarhan, 2018). The success of beetles in bioturbation is due to their diverse nesting strategies that contribute to displacement and mixing of the sediment particles during burrowing (Leiva & Sobrino-Mengual, 2023). Beetle's nesting strategies impact the soil ecosystem through excavation and translocation of soil, formation of nests, chambers and galleries, and incorporation of dead organic matter deep into the soil (Hsieh et al., 2023). Tunnelers and ball-rollers produce a higher level of bioturbation due to aggressive digging to bury dung, leading to deposition of tunnel soil particles on the surface. This displacement may bury large-sized seeds filtered from dung pats, protecting them from predation and desiccation (Leiva & Sobrino-Mengual, 2023). However, due to limited research in this area, this argument remains hypothesized.

Recent review proposes three mechanisms by which soil fauna, including beetles, could shape POM (Particulate organic matter) and MAOM (Mineral-associated organic matter) formation, this includes transformation of organic matter, translocation of materials, and grazing on microorganisms, which alters microbial abundance and composition (Angst et al., 2024). Beetles likely contribute to all three, particularly through bioturbation-driven translocation and microbial community shifts via dung burial (Natta et al., 2024). Quantifying these mechanisms in beetles could resolve unanswered questions about their impact on soil aeration, nitrogen mobilization, and porosity.

For instance, Natta et al. (2024) reported that tunneling and dung translocation by beetles significantly affect oxygen concentrations. Dwellers' bioturbation of dung pats increases surface oxygen, favoring aerobic decomposition (Brune et al., 2000). Bioturbation also alkalinizes soil pH, particularly at dung deposition sites (Laverock et al., 2013). Phytophagous beetles, known as

agricultural pests in adulthood, contribute to bioturbation as rhizophagous larvae (Johnson et al., 2015). Subterranean nesting adaptations-body size (deCastro-Arrazola et al., 2023), strong jaws (Álvarez et al., 2018), and reinforced mandibles (Farji-Brener et al., 2024) also facilitate these processes.

Life stages further modulate bioturbation: larvae exhibit lower activity compared to adults, which disrupt larval tunnels and construct wider dung-preservation galleries (Wislocki, 2021; Piccini, 2018). Notably, pupation stages contribute little to the bioturbation process. Cross-disciplinary studies combining isotopic tracing, physical fractionation, and microbiological assays are needed to test how beetle ecological strategies directly influence soil organic matter stabilization, a critical gap for modeling soils as carbon sinks and nutrient stores.

2.5 Seed dispersal

247

248

249

250

251

252

253

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

271

272

273

Beetles mediates both endozoochory and diplochory, processes that are important for plant recruitment and establishment into new localities hence reducing rodent seed predation, pathogen infection and provision of favorable conditions for germination (Pedersen & Blüthgen, 2022; Leiva & Sobrino-Mengual, 2023). Diplochory is clearly exhibited in dung beetles where they move and bury seeds that are embedded in vertebrate fecal deposition (Andresen & Levey, 2004; Manns et al., 2020). Secondary seed dispersal increases the survival and germination chances. Vulinec, (2002), reported that tunnel burying of dung decreased seed predation by 95-98%. Biophysical attributes of the seeds also determine their success in dispersal since dung beetles filter seeds by size. Pubescent seeds have hairly surface that hold thin layer of dung hence trick beetles into burying them like dung balls (Pedersen & Blüthgen, 2022). Beetle size also influences seed dispersal success, large-bodied dung beetles move greater quantities of food hence dispersing more seeds (Nichols et al., 2008). There is limited evidence on the endozoochory in beetles, which can be attributed to seed size that limit ingestion by beetles. Nonetheless, Vega et al., (2011) observed endozoochory in *Pimelia costata* that feed on *Cytinus hypocistis* fruits and later defacating the fully intact seeds. Unlike diplochory, endozoochory is reported to increase the chance of seed predation due to the release of dung odors that attract seed predators (Sousa-Lopes et al., 2019).

2.6 Pest control

274

275

276

277

278

279

280

281

282

283

284

285

286

287

288

289

290

291

292

293

294

295

296

297

298

299

300

301

302

303

Accumulation of carcass and vertebrate excreta detritus pool overtime pollute the environment with foul smell and provide breeding sites for pests and parasites (Pokhrel et al., 2021). This detritus pool attracts diverse groups of beetles that mediates the decomposition process through breakdown into simpler forms that can easily get reabsorbed into the soil (Wetherbee et al., 2021). Beetles are among the main contributors of the breakdown of plant and vertebrate detritus pool (Seibold et al., 2021). During this process, beetles disrupt the breeding habitat for pest and parasites by mechanical damage of pest eggs, introduction of competition for food with the pest larvae and disturbance of the micro-habitat that support pest growth (Nichols et al., 2008; Nichols & Gomez 2014). Beetles also reduce the spread of soil-borne human pathogens (Jones et al., 2019).

Exotic ladybirds (Coccinelidae) are entomophagous insects and effective biological pest control agents worldwide (Segura et al., 2024). Globally, it has been used in in control in aphids, mealybugs, cottony cushion scale, pysllids and whiteflies (Soares et al., 2018). The efficiency of exotic ladybird is attributed to its close co-evolutionary history to its prey. For instance, exotic ladybird *Iberorhyzobius rondensis*, Eizaguirre was reported to achieve its full development only when fed with its pest prey Matsucoccus feytaudi which forage on Pinus pinaster (Rondoni et al., 2012). In the 1950s, the use of exotic ladybirds for biological control reached its peak because of their high effectiveness and alternative to chemical pesticides (Rondoni et al., 2012). However, there has been concern on their commercialization due to the potential effect on non-target insects (Rondoni et al., 2024). In some cases, exotic ladybirds lead to loss of native ladybird populations thereby threatening taxonomic and functional diversity. Notably, most countries have agreed to assess the risk involved and for balancing benefits and risks before the release of the exotic ladybirds (van Lenteren et al., 2008; Loomans, 2021). Therefore, it is imperative to ensure proper assessment and impact of the exotic lady birds to the native species and the surrounding ecosystems (Grez & Zaviezo, 2024). Globally, the success of introduction of exotic ladybirds as biological control agents includes Rodolia cardinalis from Australia to California (U.S.A) (Soares et al., 2018), Coccinella undecimpunctata L. in New Zealand (Michaud, 2012), Rodolia cardinalis from Australia to Portugal (Amaro, 1999), Harmonia axyridis to South Africa (Stals & Prinsloo, 2007) and *Harmonia axyridis* (Asian lady beetle) to Britain (Majerus et al., 2006).

2.7 Beetles as pest and disease vectors

Larval and adult beetles are considered as both pests and vectors of plant pathogens since they directly feed on plants and act as host to plant pathogens that they deliver to plants during foraging (Zhao et al., 2019;). Notably, beetle-plant pathogens coexist symbiotically whereby beetles play the host while the pathogens release effectors, proteins and small molecules that manipulate plant defense response to beetle feeding (Gedling et al., 2018). The beetle-pathogens interaction is a complex phenomenon such that beetles vectors have developed preference for pathogen-infected plants (Bhat & Rao, 2020). This is due to the influence of the pathogens on the vector's host plants to produce plant volatile organic compounds that attract beetle vectors. Moreover, pathogens can also have a direct effect on beetle sensory behavior to phenotypic changes of host plants (Chesnais et al., 2020).

According to Smith et al (2017), beetles is a successful vector to approximately 11% of insect-mediated viruses and with over 70 beetle species in Meloidae, Chrysomelidae, Coccinelidae and Curculionidae families transmitting viruses to economically important vegetables and grain crops. Transmission of virus via beetle vectors can be attributed to the fact that beetles are pests to infected plants, therefore as they feed on plants they come into contact with viruses and ingested to the gut region or get into the hemolymph region through chewing wounds (Gedling et al., 2018). Similarly, transmission of bacteria occurs during the feeding process when beetles ingest bacterial infested host plants and the bacteria is retained in insect gut and later deposited as fecal droppings into wounds of other plants (Krawczyk et al., 2021).

Some of the plant diseases mediated by beetle vector - bacterial interactions include bacterial wilts of cucurbits transmitted via *Acalymma vittatum* and *Diabrotica barberi* (Chrysomelidae) and account for upto 80% losses in cucurbit yields (Mitchell & Hanks, 2009). Stewart's bacterial wilt in maize is transmitted via Chrysomelidae, Elateridae and Scarabaeidae (Bae et al., 2015). Beetle vector-fungus transmission occurs when beetles feed on plants that are infected with fungus or its spores. The fungus is ingested and transmitted to other host plants either directly or via mycangia (Mayers et al., 2020; Rodrigues et al., 2023). Some of the beetle-mediated fungus diseases include vascular wilt disease of elm trees caused by *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* and transmitted by bark beetles (Willsey et al., 2017). Black-stain root

disease affecting conifers is caused by *Leptographium wageneri* that is transmitted by *Hylastes macer* and *Hylastes nigrinus* (Cannon et al., 2016). Moreover, *Epitrix papa* (Chrysomelidae) is vector of *Pytophtora infestans* which cause potato blight (Margus & Lindström, 2022).

2.8 Beetles as Bioindicators

Bioindicators are organisms that are utilized in screen the health of natural ecosystem in the environment (Parmar et al., 2016; Ali et al., 2021). They range from biodiversity, ecological, environmental and pollution bioindicators (Holt & Miller, 2011; Chowdhury et al., 2023). Beetles are major biondicators of environmental disturbance and biodiversity loss in terrestrial ecosystem (Maksimovich et al., 2023). For instance, Saproxylic beetles, one of the most speciose, functionally diverse groups is used as bioindicator of forest health and biodiversity, this is due to their high sensitivity to environmental disturbance (Doerfler et al. 2018; Karpiński et al., 2021). Groundbeetles are great soil heath bioindicators due to their action to soils such as soil aeration and water porosity (Nichols et al., 2008). The impact of agricultural intensification on biodiversity and ecological structures cannot be overestimated, therefore beetles as bioindicators are crucial in assessing the environmental health and sustainability (Maksimovich et al., 2023).

Globally, anthropogenic activities have led to pollution of both land an aquatic ecosystem (Häder et al., 2020; Priya et al., 2024). Notably, most of the pollutants on land end up in water bodies and threatening the aquatic biota systems (Okorondu et al., 2022; Mukherjee et al., 2023). The severity of different pollutants on aquatic biota is based on the extent to which it can be taken up into organisms and its consequences in the food web (Nilsen et al., 2019). Diving beetles (Dytiscidae) and whirligig beetles (Gyrinidae) are key players in monitoring the accumulation level of pollutants in aquatic ecosystem. This is due to their abundance and speciose nature as well as ingestion of the pollutants during predation (Roth et al., 2020; Jasrotia et al., 2024).

3. Ecosystem services

Ecosystem services are the benefits obtained from ecological interactions and have direct or indirect ties to the quality of human life such as food, fiber, water, pest and disease control, improved pasture growth and nutrient cycling (Dangles & Casas, 2019; Brock et al., 2021). Ecosystem services offered by insects are grouped into four categories; (i) provision of services, (ii) regulation of services, (iii) supporting services and (iv) cultural services (Ahammad et al.,

2019). The economic valuation of insects is essential for conservation efforts and effective resource allocation (Hanley et al., 2015). Over time, quantification and economic valuation and quantification of ecosystem services provided by insects has received a considerable concern from scientific community. Previous studies have estimated the ecosystem services by insects to be at least US\$361 to 577 billion per year (Lautenbach et al. 2012), with insect pollination services accounting for US\$584 million of crop production in UK (Smith et al., 2011) and US\$57 billion per year in the United States (Lonsdorf et al., 2011). Despite the limited knowledge on the economic valuation of beetle pollination, recent studies have highlighted their roles in pollination of some economically important crops (Khalifa et al., 2021; Sabino et al., 2022). While research on the economic value of beetles remains limited, some studies have measured the worth of dung beetles in various regions around the world. Using a combination of economic analysis, modelling and field experiments, Beynon et al., (2015) dung beetles save the UK cattle industry an estimate of US\$498.5 million per year and highlighting a potential increase by US\$54.6 million per year if significant conservation efforts is implemented.

The role of beetles in nutrient cycling cannot be overestimated. Through nutrient cycling crops are replenished with nutrients thus increasing their health and productivity (Tully & Ryals, 2017). Similarly, livestock pastures also benefit from the nutrient cycling process which improve grass quality and quantity. The economic benefit of dung degradation by dung beetles to livestock industry in Mexico was estimated at US\$176,709.76 per year (Huerta et al., 2013), US\$1.4 million per year in Florida, United States and US\$380 million per year in United States (Losey & Vaughan, 2006; Stanbrook-Buyer at al., 2024). The role of beetles in providing ecosystem services is well documented in Australian ecosystem. Through their ecological services, dung beetles increased the income of livestock farmers in Western Australia by approximately US\$ 29.4-1307 per hectare per year (Vieira, 2024). The decomposition of vertebrate excreta by soil invertebrates among them beetles decrease the livestock parasites which is a serious threat to livestock health and cost the Australian livestock farmers around US\$ 228.7 million per year (Hansen et al., 2022). Beetles are major players in secondary seed dispersal contribute to re-establishment of plants leading to reforestation and restoration of threatened plant species which in turn contribute to timber products as well as food (Nichols et al., 2008).

4. Effects of global change on beetle-driven ecosystem functions and services

Global change is a complex phenomenon driven by co-occuring and correlated factors such as climate change and anthropogenic disruptors which includes land-use changes, agricultural intensification, land fragmentation, biological invasions, urbanization, industrialization (Magura et al., 2017; Romiti et al., 2021; Rivera & Monteros, 2023). These factors are the leading drivers of global insect decline (Sanchez-Bayo & Wyckhuys, 2021; Rabitsch & Zulka, 2024). Beetles are major players in ecosystem service provision, therefore research on their response to global change is critical for the conservation (Gotcha et al., 2021). Climate change is a key driver of global change and its direct and indirect effects on beetles is particularly significant (Colares et al., 2021). Climate change can have serious effects on the structure and dynamic of ecosystems, biodiversity, interspecific and intraspecific interactions of beetles, male reproductive sterility, abundance and distribution, population fitness, growth rates metabolism morphology and behavior (Fisher et al., 2021; Gotcha, 2022).

Beetles are ectotherms and change in temperature subject beetles to unprecented stresss affecting their performance and efficiency in providing ecosystem services and to adapt to these changes can result in reduced biological performance and, in severe cases, death (Tseng et al., 2021; Liu et al., 2023). Notably, tropical beetles may be the most affected by temperature due to global warming since they exposed to temperature that are close to their upper thermal limits thus affecting their fitness and ecological roles (Gotcha et al., 2021, 2022; Machekano et al., 2021). Previous studies have revealed the role of temperature in mediating body size of organisms. Increased temperature leads to decreased body-sizes of beetles, a phenomenon that is highly pronounced in large-sized beetles (Tseng et al., 2018). Reduced body size in beetles have a notable implication in ecosystem function at multiple scales such as competition and dung movement in ball rolling beetles (Keller et al., 2021). Increased temperature plays as crucial role in beetle pollination. With increase in temperature, the volatile organic compounds (VOCs) increase attracting beetles (Riddick, 2020). Although knowledge on the effects of low temperature on insects is still scanty, recent study by Gotcha et al., (2021) has highlighted the impact of low temperature on morphology and fitness of beetles in temperate regions.

Global change has caused change in rain patterns hence changing water availability, which is a crucial component that influence activity and biodiversity of insects (Khaliq et al., 2014). Beetles exhibit wide variation in moisture in respect to their immediate environment, as such increase and decrease in moisture may have varying impacts on performance and fitness of beetles (Zajicek et al., 2021). For instance, increased moisture due to canopy cover in terrestrial ecosystem favor the habitat cosmopolitan foragers (Ahuatzin et al., 2019).

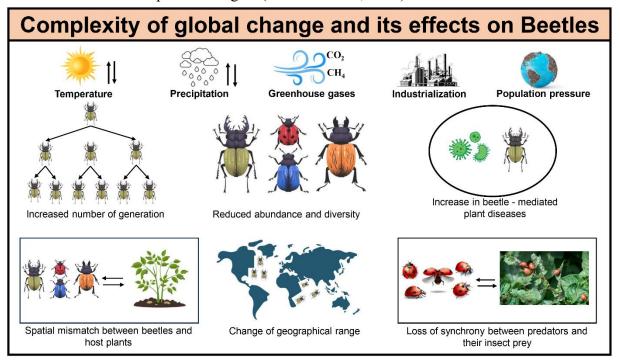


Fig 1. Schematic outline of putative effects climate and anthropogenic activities on ecosystem functions of beetles

High precipitation benefits aquatic beetles by maintaining essential water bodies, while increased detritus deposition along shorelines provides additional food resources (Deacon et al., 2019). Conversely, reduced moisture levels lead to desiccation stress, impairing beetle performance and survival (Nervo et al., 2021).

The exponential growth of human populations has become a primary driver of global change. Conversion of natural habitats for industrial and agricultural development significantly alters beetle communities and species composition (Estrada et al., 2017). Excessive land fragmentation reduces dung and carrion availability, negatively impacting beetle ecosystem functions like secondary seed dispersal (Deppe & Fischer, 2023). Climate change combined with

habitat fragmentation creates spatial-temporal mismatches between beetles and host plants (Tigreros et al., 2023). Spatial mismatches threaten specialist species through differential range shifts, while temporal mismatches disrupt ecological synchrony due to varying adaptation rates (Vitali et al., 2023; see fig.1).

Agricultural intensification has transformed natural landscapes, with forests and grasslands increasingly converted to croplands (Aune et al., 2018). This habitat loss particularly threatens specialist beetles through the elimination of host plants (Shi et al., 2024). Monoculture practices and pesticide use have caused unprecedented declines in beetle abundance and diversity, compromising their ecosystem services including pollination, pest control, and nutrient cycling (Rathoure, 2024). However, some agricultural systems may support generalist beetle diversity through introduced vegetation (Raderschall et al., 2022). Agricultural diversification strategies, including compositional and configurational heterogeneity, show promise for balancing conservation and productivity (Kleijn et al., 2019; Aguilera et al., 2020).

Urbanization and industrialization have dramatically altered ecosystems through impervious surface development, creating environments largely inhabitable to insects (Vaz et al., 2023). These processes now represent major drivers of biodiversity change in developing nations. Urban expansion generates heat islands that modify microclimates and hydrology while industrial activities alter soil chemistry through pH changes, metal accumulation, and structural degradation (Asha et al., 2022). Such environmental stressors force ecological shifts and local extinctions among beetle populations. Ground beetles are among the widely studied groups of insects in urbanization studies. This is due to their speciose nature and well-known taxonomy, ecology and sensitivity to environmental changes (Vaz et al., 2023). Globally, most of the cities have maintained relics of urban forests and introduction of decorative plants to increase their anesthetic nature (Laurian et al., 2022). Nevertheless, studies on other insect groups have reported the negative effect of urbanization and industrialization especially on poor dispersers and habitat specialists, however research on the impacts of these relic forests and decorative plants on biodiversity and ecosystem functioning of beetles is still lacking (Vaz et al., 2023).

4.1 Strategies to mitigate threats to beetles and their ecosystem services

- i. Promote citizen science initiatives, such as iNaturalist, to monitor beetle distribution and
- 465 population declines.

463

- 466 ii. Establish ecological networks (e.g., urban green corridors) to facilitate beetle migration in
- response to climate change.
- 468 iii. Integrate beetle-friendly landscapes into urban planning, including green roofs and native
- vegetation, to conserve habitat for native species.
- 470 iv. Implement long-term monitoring programs to assess beetle diversity and distribution,
- identifying threatened or declining species.
- v. Foster collaboration among beetle experts across regions to synchronize data, share
- technologies, and improve species tracking.
- vi. Increase research funding especially in developing countries to support beetle diversity surveys
- and digitization of museum/research records.
- vii. With 60-80% of beetle species remaining undescribed (Smith et al., 2022), urgent investment
- 477 in taxonomic training, digitization, and accelerated description protocols is critical to address this
- 478 fundamental biodiversity knowledge gap.

5. Conclusion

479

- Beetles mediate critical ecological functions that support, regulate, and maintain ecosystem
- balance in both natural and human-modified habitats. The services they provide including food
- provision, pest regulation, nutrient cycling, and cultural benefits are vital for human well-being.
- 483 However, in the 21st century, climate change and anthropogenic activities have emerged as major
- drivers of insect decline. Their combined and co-occurring effects exacerbate biodiversity loss
- 485 across temporal and spatial scales. Land-use changes have increased pollutant emissions,
- 486 accelerating global warming, while urbanization and industrialization drive habitat fragmentation
- and agroecosystem degradation. Pollution and urban heat islands further alter beetle ecology.

Historically, research on beetle-mediated ecosystem functions has disproportionately focused on dung beetles (Scarabaeidae) and their role in nutrient cycling, creating a knowledge gap regarding other beetle families. This bias underscores the need for expanded studies on the ecosystem services provided by diverse beetle groups. Notably, beetle pollination, a crucial yet understudied contribution to crop production remains poorly understood. Additionally, most studies examining global change impacts on beetles address individual anthropogenic stressors in isolation, neglecting their synergistic effects. The rapid acceleration of human activities in the 21st century has led to complex, often counterintuitive disruptions in beetle ecological functions and services. In developing countries, anthropogenic changes increasingly outpace research capacity to document their impacts, raising concerns about unforeseen ecological consequences.

To address these challenges, we must intensify efforts to mitigate climate change while managing unavoidable anthropogenic impacts. Although studies highlight the global reorganization of biological communities and associated biodiversity declines, future implications and solutions remain uncertain. Given the inevitability of ecosystem shifts in the Anthropocene, scientists must prioritize long-term monitoring projects to assess the extent of these changes and develop evidence-based conservation strategies to protect these essential ecological engineers.

References

- Aguilera, E., Díaz-Gaona, C., García-Laureano, R., Reyes-Palomo, C., Guzmán, G.I., Ortolani, L., Sánchez-Rodríguez, M. & Rodríguez-Estévez, V. (2020). Agroecology for adaptation to climate change and resource depletion in the Mediterranean region. A review. *Agricultural Systems*, *181*, 102809.
- Ahammad, R., Stacey, N., & Sunderland, T. C. (2019). Use and perceived importance of forest ecosystem services in rural livelihoods of Chittagong Hill Tracts, Bangladesh. *Ecosystem services*, *35*, 87-98.
- Ahuatzin, D.A., Corro, E.J., Jaimes, A.A., Valenzuela Gonzalez, J.E., Feitosa, R.M., Ribeiro, M.C., Acosta, J.C.L.,
 Coates, R. and Dáttilo, W. (2019). Forest cover drives leaf litter ant diversity in primary rainforest remnants
 within human-modified tropical landscapes. *Biodiversity and Conservation*, 28, 1091-1107.
- Ali, A., Mudasir, S., Ganie, S.A., Mir, M.U.R., Bilal, S., Hamadani, H., Shah, F. & Majid, S. (2021). Biomonitoring and Bioindicators. In *Freshwater Pollution and Aquatic Ecosystems* (pp. 185-204). Apple Academic Press.
- Ambrožová, L., Sládeček, F. X. J., Zítek, T., Perlík, M., Kozel, P., Jirků, M., & Čížek, L. (2021). Lasting decrease in functionality and richness: Effects of ivermectin use on dung beetle communities. *Agriculture, Ecosystems & Environment*, 321, 107634.
- Anbutsu, H., Moriyama, M., Nikoh, N., Hosokawa, T., Futahashi, R., Tanahashi, M., Meng, X.Y., Kuriwada, T., Mori,
 N., Oshima, K. and Hattori, M (2017). Small genome symbiont underlies cuticle hardness in
 beetles. Proceedings of the National Academy of Sciences, 114(40), E8382-E8391.

- Anderson, D. J., Berson, J. D., Didham, R. K., Simmons, L. W., & Evans, T. A. (2024). Dung beetles increase plant growth: a meta-analysis. *Proceedings of the Royal Society B*, 291(2019), 20232885.
- Andresen, E., & Levey, D. J. (2004). Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, *139*, 45-54.
- Angst, G., Potapov, A., Joly, F. X., Angst, Š., Frouz, J., Ganault, P., & Eisenhauer, N. (2024). Conceptualizing soil fauna effects on labile and stabilized soil organic matter. *Nature Communications*, *15*(1), 5005.
- Asha, G., Manoj, K., Rajesh, T. P., Varma, S., Ballullaya, U. P., & Sinu, P. A. (2022). Dung beetles prefer used land over natural greenspace in urban landscape. *Scientific Reports*, *12*(1), 22179.
- Ashworth, A. C., & Erwin, T. L. (2016). *Antarctotrechus balli* sp. n. (Carabidae, Trechini): the first ground beetle from Antarctica. *ZooKeys*, (635), 109.
- Aune, S., Bryn, A., & Hovstad, K. A. (2018). Loss of semi-natural grassland in a boreal landscape: Impacts of agricultural intensification and abandonment. *Journal of Land Use Science*, *13*(4), 375-390.
- Bae, Y.M., Jo, Y.H., Patnaik, B.B., Kim, B.B., Park, K.B., Edosa, T.T., Keshavarz, M., Kojour, M.A.M., Lee, Y.S. & Han, Y.S. (2021). *Tenebrio molitor* spätzle 1b is required to confer antibacterial defense against gramnegative bacteria by regulation of antimicrobial peptides. *Frontiers in Physiology*, 12, 758859.
- Bao, T., Zhang, X., Walczyńska, K. S., Wang, B., & Rust, J. (2019). Earliest mordellid-like beetles from the Jurassic of Kazakhstan and China (Coleoptera: Tenebrionoidea). *Proceedings of the Geologists' Association*, 130(2), 247-256.
- Barragán, F., Labastida, J., & Ramírez-Hernández, A. (2021). Response of dung beetle diversity to three livestock management systems in drylands of central Mexico. *Journal of Arid Environments*, *193*, 104598.
- Bétard, F. (2021). Insects as zoogeomorphic agents: an extended review. *Earth Surface Processes and Landforms*, 46(1), 89-109.
- Beynon, S. A., Wainwright, W. A., & Christie, M. (2015). The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. *Ecological Entomology*, 40, 124-135.
- Bhat, A. I., and Rao, G. P. (2020). "Virus transmission through pollen," in Characterization of Plant Viruses (New York: Humana Press), 61-64.
- Bradford, T. M., Humphreys, W. F., Austin, A. D., & Cooper, S. J. (2013). Identification of trophic niches of
 subterranean diving beetles in a calcrete aquifer by DNA and stable isotope analyses. *Marine and Freshwater Research*, 65(2), 95-104.
- Brock, R. E., Cini, A., & Sumner, S. (2021). Ecosystem services provided by aculeate wasps. *Biological Reviews*, 96(4), 1645-1675.
- Brune, A., Frenzel, P., & Cypionka, H. (2000). Life at the oxic–anoxic interface: microbial activities and adaptations. *FEMS Microbiology Reviews*, 24(5), 691-710.
- Büchner, G., Hothorn, T., Feldhaar, H., von Hoermann, C., Lackner, T., Rietz, J., Schlüter, J., Mitesser, O., Benbow,
 M. E., Heurich, M., & Müller, J. (2024). Ecological drivers of carrion beetle (Staphylinidae: Silphinae)
 diversity on small to large mammals. *Ecology and Evolution*, 14, e70203. https://doi.org/10.1002/ece3.70203
- Cannon, P. G., Angwin, P., & MacKenzie, M. (2016). Diseases of conifers in California. *Insects and Diseases of Mediterranean Forest Systems*, 549-582.

- Cárdenas, R. E., & Dangles, O. (2012). Do canopy herbivores mechanically facilitate subsequent litter decomposition in soil? A pilot study from a Neotropical cloud forest. *Ecological research*, *27*(5), 975-981.
- Cárdenas, R. E., Donoso, D. A., Argoti, A., & Dangles, O. (2017). Functional consequences of realistic extinction
 scenarios in Amazonian soil food webs. *Ecosphere*, 8(2), e01692.
- Charabidze, D., Trumbo, S., Grzywacz, A., Costa, J. T., Benbow, M. E., Barton, P. S., & Matuszewski, S. (2021).
 Convergence of social strategies in carrion breeding insects. *BioScience*, 71(10), 1028-1037.
- Cheng, L., Tong, Y., Zhao, Y., Sun, Z., Wang, X., Ma, F., & Bai, M. (2022). Study on the relationship between richness
 and morphological diversity of higher taxa in the darkling beetles (Coleoptera:
 Tenebrionidae). *Diversity*, 14(1), 60.
- 568 Chesnais, Q., Caballero Vidal, G., Coquelle, R., Yvon, M., Mauck, K., Brault, V., & Ameline, A. (2020). Post-569 acquisition effects of viruses on vector behavior are important components of manipulation 570 strategies. *Oecologia*, 194, 429-440.
- Chowdhury, S., Dubey, V.K., Choudhury, S., Das, A., Jeengar, D., Sujatha, B., Kumar, A., Kumar, N., Semwal, A. and
 Kumar, V. (2023). Insects as bioindicator: A hidden gem for environmental monitoring. Frontiers in
 Environmental Science, 11, 1146052.
- Colares, C., Roza, A.S., Mermudes, J.R., Silveira, L.F., Khattar, G., Mayhew, P.J., Monteiro, R.F., Nunes, M.F.S. &
 Macedo, M.V. (2021). Elevational specialization and the monitoring of the effects of climate change in insects: Beetles in a Brazilian rainforest mountain. *Ecological Indicators*, 120, 106888.
- Costanza, R., & Folke, C. (1997). Valuing ecosystem services with efficiency, fairness and sustainability as goals. *Nature's services: Societal dependence on natural ecosystems*, 49-70.
- Crespo-Pérez, V., Kazakou, E., Roubik, D. W., & Cárdenas, R. E. (2020). The importance of insects on land and in water: a tropical view. *Current opinion in insect science*, 40, 31-38. https://doi.org/10.1016/j.cois.2020.05.016.
- Crowther, T.W., Van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C. & Maynard, D.S. (2019).

 The global soil community and its influence on biogeochemistry. *Science*, *365*(6455), eaav0550.
- Dangles, O., & Casas, J. (2019). Ecosystem services provided by insects for achieving sustainable development goals. *Ecosystem services*, *35*, 109-115.
- deCastro- Arrazola, I., Andrew, N. R., Berg, M. P., Curtsdotter, A., Lumaret, J.-P., Menéndez, R., Moretti, M., Nervo,
 B., Nichols, E. S., Sánchez- Piñero, F., Santos, A. M. C., Sheldon, K. S., Slade, E. M., & Hortal, J. (2023). A
 trait- based framework for dung beetle functional ecology. *Journal of Animal Ecology*, 92, 44–65. https://doi.org/10.1111/1365-2656.1382
- de Vega, C., Arista, M., Ortiz, P. L., Herrera, C. M., & Talavera, S. (2011). Endozoochory by beetles: a novel seed dispersal mechanism. *Annals of botany*, *107*(4), 629-637.
- Deacon, C., Samways, M. J., & Pryke, J. S. (2019). Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts. *Freshwater Biology*, *64*(9), 1643-1654.
- Deppe, F., & Fischer, K. (2023). Landscape type affects the functional diversity of carabid beetles in agricultural landscapes. *Insect Conservation and Diversity*, 16(4), 441-450.
- 596 Deregowski, U. (2024). Response of saproxylic beetle communities twenty years after clearcut and partial cut harvests 597 in the eastern boreal mixedwood forest.

- 598 Di Giulio, A., Fattorini, S., Moore, W., Robertson, J., & Maurizi, E. (2014). Form, function and evolutionary 599 significance of stridulatory organs in ant nest beetles (Coleoptera: Carabidae: Paussini). *European Journal* 600 of Entomology, 111(5), 692.
- Didham, R. K., Hammond, P. M., Lawton, J. H., Eggleton, P., & Stork, N. E. (1998). Beetle species responses to tropical forest fragmentation. *Ecological Monographs*, 68(3), 295-323.
- Doerfler, I., Gossner, M. M., Müller, J., Seibold, S., & Weisser, W. W. (2018). Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biological Conservation*, 228, 70-78.
- Doktorovová, L., Exnerová, A., Hotová Svádová, K., Štys, P., Adamová-Ježová, D., Zverev, V., Kozlov, M.V. &
 Zvereva, E.L. (2019). Differential bird responses to colour morphs of an aposematic leaf beetle may affect variation in morph frequencies in polymorphic prey populations. *Evolutionary Biology*, 46, 35-46.
- Doube, B. M. (2018). Ecosystem services provided by dung beetles in Australia. *Basic and Applied Ecology*, *26*, 35-610 49.
- Eggleton, P. (2020). The state of the world's insects. Annual Review of Environment and Resources, 45(1), 61-82.
- Ekström, A. L., Bergmark, P., & Hekkala, A. M. (2021). Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles?. *Forest Ecology and Management*, *490*, 119107.
- Engasser, E. L., Stone, R. L., & Jameson, M. L. (2021). Habitat associations of carrion beetles (Coleoptera: Silphidae) across a full annual cycle. *Environmental Entomology*, *50*(3), 605-614.
- Englmeier, J., Mitesser, O., Benbow, M.E., Hothorn, T., von Hoermann, C., Benjamin, C., Fricke, U., Ganuza, C.,
 Haensel, M., Redlich, S. & Riebl, R. (2023). Diverse effects of climate, land use, and insects on dung and
 carrion decomposition. *Ecosystems*, 26(2), 397-411.
- Englmeier, J., von Hoermann, C., Rieker, D., Benbow, M.E., Benjamin, C., Fricke, U., Ganuza, C., Haensel, M.,
 Lackner, T., Mitesser, O. & Redlich, S. (2022). Dung-visiting beetle diversity is mainly affected by land use,
 while community specialization is driven by climate. *Ecology and evolution*, 12(10), e9386.
- Farji-Brener, A. G., Enríquez, M., Rosey, D., Arroyo-Gerala, P., & Arroyo-Rodríguez, V. (2024). What determines the antipredator strategy in antlion larvae? Burrowing ability decreases the duration of post-contact immobility. *Ecological Entomology*.
- Favila, M. E. (2024). The chemical ecology of dung beetles and the potential applications of their bioactive compounds. *Studies in Natural Products Chemistry*, 82, 405-423.
- Fisher, M. C., Moore, S. K., Jardine, S. L., Watson, J. R., & Samhouri, J. F. (2021). Climate shock effects and mediation in fisheries. *Proceedings of the National Academy of Sciences*, *118*(2), e2014379117.
- França FM, Ferreira J, Vaz-de-Mello F.Z, et al. El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes. *Biotropica*. 2020; 52:252–262
- Fukumori, K., Oguchi, K., Ikeda, H., Shinohara, T., Tanahashi, M., Moriyama, M., Koga, R. & Fukatsu, T. (2022).
 Evolutionary dynamics of host organs for microbial symbiosis in tortoise leaf beetles (Coleoptera: Chrysomelidae: Cassidinae). *MBio*, *13*(1), e03691-21.
- 634 García-Atencia, S., Bonilla-Gómez, M. A., & Moreno, C. E. (2024). Ecosystem functions and functional traits for the 635 study of phytophagous scarab beetles (Coleoptera: Scarabaeidae). *Ecological Entomology*, 49(4), 463-475.

- Gasca Álvarez, H. J., Zunino, M., & Deloya, C. (2018). The ninth brachypterous *Onthophagus* Latreille (Coleoptera:
 Scarabaeidae: Scarabaeinae) of the world: a new species from Mexico. *Journal of Natural History*, 52(33-34), 2121-2132.
- 639 Ge, X., Newman, J. A., & Griswold, C. K. (2023). Geographic variation in evolutionary rescue in a predator-prey system under climate change: an example with aphids and ladybird beetles. *bioRxiv*, 2023-03.
- 641 Gedling, C. R., Smith, C. M., LeMoine, C. M., & Cassone, B. J. (2018). The Mexican bean beetle (*Epilachna varivestis*) regurgitome and insights into beetle-borne virus specificity. *Plos one*, *13*(1), e0192003.
- 643 Ghannem, S., Bejaoui, M., Gahdab, C., & Boumaiza, M. (2017). Biodiversity of Ground Beetles (Coleoptera: Carabidae) from Northern Tunisia. *Journal of the Kansas Entomological Society*, 90(1), 31-43.
- 645 Gotcha, N. (2022). Dung beetles' responses to changing environments; implications on ecosystem service delivery.
- Gotcha, N., Machekano, H., Cuthbert, R. N., & Nyamukondiwa, C. (2021). Low-temperature tolerance in coprophagic
 beetle species (Coleoptera: Scarabaeidae): implications for ecological services. *Ecological Entomology*, 46(5), 1101-1112.
- Gottsberger, G., Gottsberger, B., Silberbauer-Gottsberger, I., Stanojlovic, V., Cabrele, C., & Dötterl, S. (2021).
 Imitation of fermenting fruits in beetle-pollinated *Calycanthus occidentalis* (Calycanthaceae). *Flora*, 274,
 151732.
- Greenop, A., Woodcock, B.A., Outhwaite, C.L., Carvell, C., Pywell, R.F., Mancini, F., Edwards, F.K., Johnson, A.C.
 & Isaac, N.J. (2021). Patterns of invertebrate functional diversity highlight the vulnerability of ecosystem services over a 45-year period. *Current Biology*, 31(20), 4627-4634.
- Grez, A., & Zaviezo, T. (2024). Landscape simplification, urbanization, biological invasions, and climate change: a
 review of the major threats to native coccinellids in Central Chile. *Entomologia Experimentalis et Applicata*, 172(6), 460-466.
- Gugliuzzo, A., Aiello, D., Biondi, A., Giurdanella, G., Siscaro, G., Zappalà, L., Vitale, A., Garzia, G.T. and Polizzi,
 G. (2022). Microbial mutualism suppression by Trichoderma and Bacillus species for controlling the invasive
 ambrosia beetle *Xylosandrus compactus*. *Biological Control*, *170*, 104929.
- Häder, D. P., Banaszak, A. T., Villafañe, V. E., Narvarte, M. A., González, R. A., & Helbling, E. W. (2020).
 Anthropogenic pollution of aquatic ecosystems: Emerging problems with global implications. *Science of the Total environment*, 713, 136586.
- Hanley, N., Breeze, T. D., Ellis, C., & Goulson, D. (2015). Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosystem services*, *14*, 124-132.
- Hansen, B.D., Leonard, E., Mitchell, M.C., Easton, J., Shariati, N., Mortlock, M.Y., Schaefer, M. & Lamb, D.W.
 (2022). Current status of and future opportunities for digital agriculture in Australia. *Crop and Pasture Science*.
- Hartkopf-Fröder, C., Rust, J., Wappler, T., Friis, E. M., & Viehofen, A. (2012). Mid-Cretaceous charred fossil flowers reveal direct observation of arthropod feeding strategies. *Biology Letters*, *8*(2), 295-298.
- Holt, E. A., & Miller, S. W. (2011). Bioindicators: Using organisms to measure. *Nature*, 3, 8-13.
- Hsieh, S., Łaska, W., & Uchman, A. (2023). Intermittent and temporally variable bioturbation by some terrestrial invertebrates: implications for ichnology. *The Science of Nature*, *110*(2), 11.

- Huerta, C., Martínez, M. I., de Oca, E. M., Cruz-Rosales, M., & Favila, M. E. (2013). The role of dung beetles in the
 sustainability of pasture and grasslands. WIT Transactions on State-of-the-art in Science and
 Engineering, 64.
- Hulcr, J., & Stelinski, L. L. (2017). The ambrosia symbiosis: from evolutionary ecology to practical management. *Annual review of entomology*, 62(1), 285-303.
- Jasrotia, R., Jasrotia, S., Dhar, M., Gupta, P., Jamwal, N., & Langer, S. (2024). Aquatic Insect Ecosystems: Diversity, Role, and Conservation. *Insect Diversity and Ecosystem Services: Volume 1: Importance, Threats,* Conservation, and Economic Perspectives.
- Johnson, S. N., & Rasmann, S. (2015). Root-feeding insects and their interactions with organisms in the rhizosphere. *Annual review of entomology*, 60(1), 517-535.
- Jones, M.S., Wright, S.A., Smith, O.M., Besser, T.E., Headrick, D.H., Reganold, J.P., Crowder, D.W. & Snyder, W.E. (2019). Organic farms conserve a dung beetle species capable of disrupting fly vectors of foodborne pathogens. *Biological Control*, *137*, 104020.
- Karpiński, L., Maák, I., & Wegierek, P. (2021). The role of nature reserves in preserving saproxylic biodiversity: using
 longhorn beetles (Coleoptera: Cerambycidae) as bioindicators. *The European Zoological Journal*, 88(1),
 487-504.
- Keller, M. L., Howard, D. R., & Hall, C. L. (2021). The thermal ecology of burying beetles: temperature influences reproduction and daily activity in Nicrophorus marginatus. *Ecological Entomology*, *46*(6), 1266-1272.
- Khalifa, S.A., Elshafiey, E.H., Shetaia, A.A., El-Wahed, A.A.A., Algethami, A.F., Musharraf, S.G., AlAjmi, M.F., Zhao, C., Masry, S.H., Abdel-Daim, M.M. and Halabi, M.F. (2021). Overview of bee pollination and its economic value for crop production. *Insects*, 12(8), 688.
- Khaliq, A. M., Javed, M., Sohail, M., & Sagheer, M. (2014). Environmental effects on insects and their population dynamics. *Journal of Entomology and Zoology studies*, 2(2), 1-7.
- Kleijn, D., Bommarco, R., Fijen, T. P., Garibaldi, L. A., Potts, S. G., & Van Der Putten, W. H. (2019). Ecological intensification: bridging the gap between science and practice. *Trends in ecology & evolution*, 34(2), 154-66.
- Kowles, K. A., & Switzer, P. V. (2012). Dynamics of aggregation formation in Japanese beetles, *Popillia japonica. Journal of insect behavior*, 25, 207-221.
- Krawczyk, B., Wityk, P., Gałęcka, M., & Michalik, M. (2021). The many faces of *Enterococcus* spp.—commensal, probiotic and opportunistic pathogen. *Microorganisms*, *9*(9), 1900.
- Krenn, H. W., Plant, J. D., & Szucsich, N. U. (2005). Mouthparts of flower-visiting insects. Arthropod structure & development, 34(1), 1-40.
- Labidi, I., Errouissi, F., & Nouira, S. (2012). Spatial and temporal variation in species composition, diversity, and structure of Mediterranean dung beetle assemblages (Coleoptera: Scarabaeidae) across a bioclimatic gradient. *Environmental entomology*, 41(4), 785-801.
- Lachat, T., Wermelinger, B., Gossner, M. M., Bussler, H., Isacsson, G., & Müller, J. (2012). Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators*, 23, 323-331.
- Laurent, P., Braekman, J. C., Daloze, D., & Pasteels, J. (2003). Biosynthesis of defensive compounds from beetles and
 ants. *European Journal of Organic Chemistry*, 2003(15), 2733-2743.

- Lautenbach, S., Seppelt, R., Liebscher, J., & Dormann, C. F. (2012). Spatial and temporal trends of global pollination benefit. *PloS one*, 7(4), e35954.
- Laverock, B., Kitidis, V., Tait, K., Gilbert, J. A., Osborn, A. M., & Widdicombe, S. (2013). Bioturbation determines
 the response of benthic ammonia-oxidizing microorganisms to ocean acidification. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1627), 20120441.
- Leiva, M. J., & Sobrino-Mengual, G. (2023). Cattle dung and bioturbation by dung beetles improve oak seedling establishment in Mediterranean silvopastoral ecosystems. *New Forests*, *54*(2), 289-309.
- Liu, T., Liu, H., Wang, Y., & Yang, Y. (2023). Climate change impacts on the potential distribution pattern of *Osphya* (Coleoptera: Melandryidae), an old but small beetle group distributed in the Northern Hemisphere. *Insects*, 14(5), 476.
- Lobo, J. M., & Cuesta, E. (2021). Seasonal variation in the diel activity of a dung beetle assemblage. *PeerJ*, 9, e11786.
- Lonsdorf, E., Ricketts, T., Kremen, C., Winfree, R., Greenleaf, S., & Williams, N. (2011). Crop pollination services. *Natural capital: theory and practice of mapping ecosystem services*, 168-187.
- Loomans, A. J. (2021). Every generalist biological control agent requires a special risk assessment. *BioControl*, 66(1), 23-35.
- Lopez-Collado, J., Cruz-Rosales, M., Vilaboa-Arroniz, J., Martínez-Morales, I., & Gonzalez-Hernandez, H. (2017).
 Contribution of dung beetles to cattle productivity in the tropics: A stochastic-dynamic modeling approach. *Agricultural Systems*, 155, 78-87.
- Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, 56(4),
 311-323.
- Macgregor, C. J., & Scott-Brown, A. S. (2020). Nocturnal pollination: an overlooked ecosystem service vulnerable to environmental change. *Emerging Topics in Life Sciences*, *4*(1), 19-32.
- Machekano, H., Zidana, C., Gotcha, N., & Nyamukondiwa, C. (2021). Limited thermal plasticity may constrain ecosystem function in a basally heat tolerant tropical telecoprid dung beetle, *Allogymnopleurus thalassinus* (Klug, 1855). *Scientific Reports*, *11*(1), 22192.
- Magro, A., & Hemptinne, J. L. (1999). The pool of coccinellids (Coleoptera: Coccinellidae) to control coccids (Homoptera: Coccoidea) in Portuguese citrus groves. *Bol. San. Veg. Plagas*, 25(31), 1-320.
- Magura, T., Lövei, G. L., & Tóthmérész, B. (2017). Edge responses are different in edges under natural versus anthropogenic influence: a meta-analysis using ground beetles. *Ecology and evolution*, 7(3), 1009-1017.
- Maia, A. C. D., do Amaral Ferraz Navarro, D. M., Núñez-Avellaneda, L. A., Carreño-Barrera, J., Iannuzzi, L.,
 Cardona-Duque, J., & Nantes, W. A. G. (2021). Methyl acetate, a highly volatile floral semiochemical mediating specialized plant-beetle interactions. *The Science of Nature*, 108(3), 21.
- Maire, J., Blackall, L. L., & van Oppen, M. J. (2021). Intracellular bacterial symbionts in corals: challenges and future
 directions. *Microorganisms*, 9(11), 2209.
- Majerus, M., Strawson, V., & Roy, H. (2006). The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology*, *31*(3).
- Maksimovich, K. Y., Dudko, R. Y., Shatalova, E. I., Tsakalof, A. K., Tsatsakis, A. M., Golokhvast, K. S., & Novikov, E. A. (2023). Species composition and ecological structure of ground beetles (Coleoptera, Carabidae)

- 752 communities as biological indicators of the agro-environmental sustainability. *Environmental Research*, *234*, 116030.
- Maldaner, M. E., Costa-Silva, V. D., & Vaz-de-Mello, F. Z. (2024). Dung beetles in South American pasturelands. *Biota Neotropica*, 24(1), e20231567.
- Manns, S., Holley, J. M., Hemmings, Z., & Andrew, N. R. (2020). Behavioral ecology and secondary seed dispersal by two roller dung beetles, *Sisyphus rubrus* (Paschalidis, 1974) and *Sisyphus spinipes* (Thunberg, 1818) (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*, 74(4), 849-859.
- Margus, A., & Lindström, L. (2022). Regional overview of potato pest problem in EU. In *Insect Pests of Potato* (pp. 339-347). Academic Press.
- Matuszewski, S., & Mądra-Bielewicz, A. (2021). Heat production in a feeding matrix formed on carrion by communally breeding beetles. *Frontiers in Zoology*, 18, 1-11.
- Mayers, C. G., Harrington, T. C., Mcnew, D. L., Roeper, R. A., Biedermann, P. H., Masuya, H., & Bateman, C. C. (2020). Four mycangium types and four genera of ambrosia fungi suggest a complex history of fungus farming in the ambrosia beetle tribe *Xyloterini*. *Mycologia*, *112*(6), 1104-1137.
- McGeoch, M. A. (2007). Insects and bioindication: theory and progress. *Insect conservation biology*, 7, 144-174.
- Mitchell, R. F., & Hanks, L. M. (2009). Insect frass as a pathway for transmission of bacterial wilt of cucurbits. *Environmental entomology*, 38(2), 395-403.
- Muinde, J., & Katumo, D. M. (2024). Beyond bees and butterflies: The role of beetles in pollination system. *Journal for Nature Conservation*, 77, 126523.
- Mukherjee, S., Rizvi, S. S., Biswas, G., Paswan, A. K., Vaiphei, S. P., Warsi, T., & Mitran, T. (2023). Aquatic
 Ecosystems Under Influence of Climate Change and Anthropogenic Activities: Potential Threats and Its
 Mitigation Strategies. Hydrogeochemistry of Aquatic Ecosystems, 307-331.
- Nadeau, P., Thibault, M., Horgan, F. G., Michaud, J. P., Gandiaga, F., Comeau, C., & Moreau, G. (2015). Decaying matters: Coleoptera involved in heterotrophic systems. *Beetles: Biodiversity, ecology and role in the environment*, 123-174.
- Natta, G., Merl, T., Laini, A., Roggero, A., Rolando, A., Palestrini, C., Koren, K. & Marzocchi, U. (2024). Use of planar optode technology to assess oxygen and pH dynamics in soils bioturbated by dung beetles. In *Book of Abstracts* (pp. 64-64). Università di Pisa.
- Nervo, B., Laini, A., Roggero, A., Palestrini, C., & Rolando, A. (2024). Spatio-temporal modelling suggests that some dung beetle species (Coleoptera: Geotrupidae) may respond to global warming by boosting dung removal. *Science of The Total Environment*, 908, 168127.
- Nichols, E., & Gomez, A. (2014). Dung beetles and fecal helminth transmission: patterns, mechanisms and questions. *Parasitology*, *141*(5), 614-623.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E., & Network, T. S. R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological conservation*, 141(6), 1461-1474.
- Nilsen, E., Smalling, K. L., Ahrens, L., Gros, M., Miglioranza, K. S., Picó, Y., & Schoenfuss, H. L. (2019). Critical review: Grand challenges in assessing the adverse effects of contaminants of emerging concern on aquatic food webs. *Environmental Toxicology and Chemistry*, 38(1), 46-60.

- Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J., Del Toro, I., Goulson, D., Ibanez, S.,
 Landis, D.A. & Moretti, M. (2018). Research trends in ecosystem services provided by insects. *Basic and applied ecology*, 26, 8-23.
- Okorondu, J., Umar, N. A., Ulor, C. O., Onwuagba, C. G., Diagi, B. E., Ajiere, S. I., & Nwaogu, C. (2022).

 Anthropogenic Activities as Primary Drivers of Environmental Pollution and Loss of Biodiversity: A Review.
- Parmar, T. K., Rawtani, D., & Agrawal, Y. K. (2016). Bioindicators: the natural indicator of environmental pollution. *Frontiers in life science*, *9*(2), 110-118.
- Pausas, J. G., & Bond, W. J. (2020). On the three major recycling pathways in terrestrial ecosystems. *Trends in ecology* & *evolution*, *35*(9), 767-775.
- Paz, F. S., Pinto, C. E., de Brito, R. M., Imperatriz-Fonseca, V. L., & Giannini, T. C. (2021). Edible fruit plant species in the Amazon forest rely mostly on bees and beetles as pollinators. *Journal of economic entomology*, *114*(2), 710-722.
- Pedersen, K. M., & Blüthgen, N. (2022). Seed size and pubescence facilitate secondary dispersal by dung beetles. *Biotropica*, *54*(1), 215-225.
- Pereira, J., Schlindwein, C., Antonini, Y., Maia, A.C.D., Dötterl, S., Martins, C., Navarro, D.M., & Oliveira, R. (2014).

 Philodendron adamantinum (Araceae) lures its single cyclocephaline scarab pollinator with specific dominant floral scent volatiles. Biological Journal of the Linnean Society, 111(3), 679-691.
- Peris, D., Delclòs, X., & Jordal, B. (2021). Origin and evolution of fungus farming in wood-boring coleoptera palaeontological perspective. *Biological Reviews*, 96(6), 2476-2488.
- Piccini, I. (2018). Dung beetles as drivers of ecosystem multifunctionality.
- Pokhrel, M. R., Cairns, S. C., Hemmings, Z., Floate, K. D., & Andrew, N. R. (2021). A review of dung beetle introductions in the Antipodes and North America: Status, opportunities, and challenges. *Environmental Entomology*, 50(4), 762-780.
- Pokhrel, R. P., Gordon, J., Fiddler, M. N., & Bililign, S. (2021). Determination of emission factors of pollutants from biomass burning of African fuels in laboratory measurements. *Journal of Geophysical Research:*Atmospheres, 126(20), e2021JD034731.
- Priya, S., Dhandapani, A., Kumar, R. N., & Iqbal, J. (2024). Integrated Approach (MCD19A2 and PM10 Datasets) for Spatiotemporal Assessment of Aerosol and Revealing Approachable Predictive Model Across the Mega-Mining Region (Jharkhand), India Along with its Accuracy Measures. *Journal of the Indian Society of* Remote Sensing, 1-18.
- Rabitsch, W., & Zulka, K. P. (2024). The insect decline syndrome. In *Biological Invasions and Global Insect Decline* (pp. 47-89). Academic Press.
- Raderschall, C. A., Lundin, O., Aguilera, G., Lindström, S. A., & Bommarco, R. (2022). Legacy of landscape crop diversity enhances carabid beetle species richness and promotes granivores. *Agriculture, Ecosystems & Environment*, 340, 108191.
- 826 Rathoure, A. K. (Ed.). (2024). Impact of Societal Development and Infrastructure on Biodiversity Decline. IGI Global.
- Renahan, T., & Sommer, R. J. (2021). Nematode interactions on beetle hosts indicate a role of mouth-form plasticity in resource competition. *Frontiers in Ecology and Evolution*, *9*, 752695.

- Riddick, E. W. (2020). Volatile and non-volatile organic compounds stimulate oviposition by aphidophagous predators. *Insects*, *11*(10), 683.
- Rivera, J. D., de Los Monteros, A. E., Saldana-Vazquez, R. A., & Favila, M. E. (2023). Beyond species loss: How anthropogenic disturbances drive functional and phylogenetic homogenization of Neotropical dung beetles. *Science of the Total Environment*, 869, 161663.
- Rodrigues, J. G. C., Cardoso, F. V., Santos, C. C. D., Matias, R. R., Machado, N. T., Duvoisin Junior, S., & Albuquerque, P. M. (2023). Biocatalyzed Transesterification of Waste Cooking Oil for Biodiesel Production Using Lipase from the Amazonian Fungus *Endomelanconiopsis endophytica*. *Energies*, *16*(19), 6937.
- Romiti, F., Pietrangeli, E., Battisti, C., & Carpaneto, G. M. (2021). Quantifying the entrapment effect of anthropogenic beach litter on sand-dwelling beetles according to the EU Marine Strategy Framework Directive. *Journal of Insect Conservation*, 25, 441-452.
- Rondoni, G., Borges, I., Collatz, J., Conti, E., Costamagna, A.C., Dumont, F., Evans, E.W., Grez, A.A., Howe, A.G.,
 Lucas, E. & Maisonhaute, J.É. (2021). Exotic ladybirds for biological control of herbivorous insects—a
 review. *Entomologia Experimentalis et Applicata*, 169(1), 6-27.
- Rondoni, G., Collatz, J., Jonsson, M., Rubbmark, O. R., Riddick, E., Schmidt, J., & Brodeur, J. (2024). Recent advances in characterizing trophic connections in biological control. *Biological Control*, 105656.
- Rondoni, G., Onofri, A., & Ricci, C. (2012). Laboratory studies on intraguild predation and cannibalism among coccinellid larvae (Coleoptera: Coccinellidae). *European Journal of Entomology*, *109*(3).
- Roth, Z., Komsky-Elbaz, A., & Kalo, D. (2020). Effect of environmental contamination on female and male gametes— A lesson from bovines. *Animal Reproduction*, *17*(3), e20200041.
- Sabino, W., Costa, L., Andrade, T., Teixeira, J., Araújo, G., Acosta, A.L., Carvalheiro, L. and Giannini, T.C. (2022).
 Status and trends of pollination services in Amazon agroforestry systems. *Agriculture, Ecosystems & Environment*, 335, 108012.
- Sabu, T. K., & Nithya, S. (2016). Comparison of the arboreal dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of the wet and dry forests of the western Ghats, India. *The Coleopterists Bulletin*, 70(1), 144-148.
- Salazar-Rivera, G.I., Pereira-Santana, A., Hernández-Velázquez, I.M., Olivares-Miranda, M., Ibarra-Laclette, E.,
 Gschaedler Mathis, A.C., Enríquez-Vara, J.N. & Zamora-Briseño, J.A. (2024). Disentangling the gut bacterial
 communities of the agave weevil, *Scyphophorus acupunctatus* (Coleoptera:
 Curculionidae). *Symbiosis*, *92*(3), 381-392.
- Salem, H., & Kaltenpoth, M. (2022). Beetle–bacterial symbioses: endless forms most functional. *Annual Review of Entomology*, 67(1), 201-219.
- Sánchez-Bayo, F., & Wyckhuys, K. A. (2021). Further evidence for a global decline of the entomofauna. *Austral Entomology*, 60(1), 9-26.
- Sayers, T. D., Steinbauer, M. J., & Miller, R. E. (2019). Visitor or vector? The extent of rove beetle (Coleoptera: Staphylinidae) pollination and floral interactions. *Arthropod-Plant Interactions*, *13*, 685-701.
- Schmidt, J. H., Hallmann, J., & Finckh, M. R. (2020). Bacterivorous nematodes correlate with soil fertility and improved crop production in an organic minimum tillage system. *Sustainability*, *12*(17), 6730.
- Scholtz, C. H., Davis, A. L. V., & Kryger, U. (2009). *Evolutionary biology and conservation of dung beetles* (pp. 1-567). Sofia-Moscow: Pensoft.

- Schowalter, T. D. (2012). Insect responses to major landscape-level disturbance. *Annual review of entomology*, *57*(1), 1-20.
- 870 Scudder, G. G. (2017). The importance of insects. *Insect biodiversity: science and society*, 9-43.
- 871 Segura, D. F., Cingolani, M. F., Wajnberg, E., & Beukeboom, L. W. (2024). Entomophagous insects.
- 872 Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R. & Bae, S. (2021). The contribution of insects to global forest deadwood
- decomposition. *Nature*, *597*(7874), 77-81.
- 875 Servín-Pastor, M., Salomão, R.P., Caselín-Cuevas, F., Córdoba-Aguilar, A., Favila, M.E., Jácome-Hernández, A., Ravila, M.E., Jácome-Hernández, A., Lozano-Sánchez, D. & González-Tokman, D. (2021). Malnutrition and parasitism shape ecosystem services provided by dung beetles. *Ecological Indicators*, 121, 107205.
- 878 Seymour, R. S., White, C. R., & Gibernau, M. (2009). Endothermy of dynastine scarab beetles (*Cyclocephala colasi*)
 879 associated with pollination biology of a thermogenic arum lily (*Philodendron solimoesense*). *Journal of*880 *Experimental Biology*, 212(18), 2960-2968.
- Shah, N. A., & Shah, N. (2022). Ecological benefits of scarab beetles (Coleoptera: Scarabaeidae) on nutrient cycles: a review article. *Advances in Biochemistry and Biotechnology*, 7(1), 1-6.
- 883 Shi, G., Chen, C., Cao, Q., Zhang, J., Xu, J., Chen, Y., Wang, Y. & Liu, J. (2024). Spatiotemporal Dynamics and 884 Prediction of Habitat Quality Based on Land Use and Cover Change in Jiangsu, China. *Remote* 885 Sensing, 16(22).
- Similä, M., Kouki, J., & Martikainen, P. (2003). Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management*, 174(1-3), 365-381.
- 888 Smith, R., Hauck, R., Macklin, K., Price, S., Dormitorio, T., & Wang, C. (2022). A review of the lesser mealworm 889 beetle (*Alphitobius diaperinus*) as a reservoir for poultry bacterial pathogens and antimicrobial 890 resistance. *World's Poultry Science Journal*, 78(1), 197-214.
- Smith, C. M., Gedling, C. R., Wiebe, K. F., & Cassone, B. J. (2017). A sweet story: Bean pod mottle virus transmission dynamics by Mexican bean beetles (*Epilachna varivestis*). *Genome Biology and Evolution*, *9*(3), 714-725.
- 893 Smith, R. I., Dick, J. M., & Scott, E. M. (2011). The role of statistics in the analysis of ecosystem services. *Environmetrics*, 22(5), 608-617.
- 895 Soares, A. O., Honěk, A., Martinkova, Z., Brown, P. M., & Borges, I. (2018). Can native geographical range, dispersal 896 ability and development rates predict the successful establishment of alien ladybird (Coleoptera: 897 Coccinellidae) species in Europe?. *Frontiers in Ecology and Evolution*, 6, 57.
- Sota, T., Takami, Y., Ikeda, H., Liang, H., Karagyan, G., Scholtz, C., & Hori, M. (2022). Global dispersal and diversification in ground beetles of the subfamily Carabinae. *Molecular phylogenetics and evolution*, *167*, 900 107355.
- Sousa-Lopes, B. D., Alves-da-Silva, N., Ribeiro-Costa, C. S., & Del-Claro, K. (2019). Temporal distribution, seed
 damage and notes on the natural history of *Acanthoscelides quadridentatus* and *Acanthoscelides winderi* (Coleoptera: Chrysomelidae: Bruchinae) on their host plant, *Mimosa setosa var. paludosa* (Fabaceae:
 Mimosoideae), in the Brazilian Cerrado. *Journal of Natural History*, 53(9-10), 611-623.
- 905 Stals, R., & Prinsloo, G. (2007). Discovery of an alien invasive, predatory insect in South Africa: the multicoloured 906 Asian ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae): research in action. *South* 907 *African Journal of Science*, 103(3), 123-126.

- 908 Stanbrook-Buyer, R., Bhat, M., & King, J. R. (2024). Economic value of dung removal by dung beetles in US sub-4 tropical pastures. *Basic and Applied Ecology*, 79, 123-130.
- 910 Stone, R. L., Bonat, S., Newsome, T. M., & Barton, P. S. (2023). Responses of necrophilous beetles to animal mass mortality in the Australian Alps. *Journal of Insect Conservation*, *27*(6), 865-877.
- 912 Stork, N. E., McBroom, J., Gely, C., & Hamilton, A. J. (2015). New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences*, 112(24), 7519-7523.
- 915 Sun, W., Tang, W., Wu, Y., He, S., & Wu, X. (2023). The Influences of Rainfall Intensity and Timing on the Assemblage of Dung Beetles and the Rate of Dung Removal in an Alpine Meadow. *Biology*, *12*(12), 1496.
- 917 Tarhan, L. G. (2018). The early Paleozoic development of bioturbation-evolutionary and geobiological consequences. *Earth-Science Reviews*, 178, 177-207.
- 919 Thien, L.B., Bernhardt, P., Devall, M.S., Chen, Z.D., Luo, Y.B., Fan, J.H., Yuan, L.C. & Williams, J.H. (2009). 920 Pollination biology of basal angiosperms (ANITA grade). *American Journal of Botany*, 96(1), 166-182.
- Tigreros, N., Kozhoridze, G., Davidowitz, G., & Ziv, Y. (2023). Influence of the direct and indirect effects of habitat fragmentation, via microclimate change, on animal locomotion. *Landscape Ecology*, *38*(3), 847-859.
- Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual review of ecology,* evolution, and systematics, 45(1), 471-493.
- 925 Traylor, C. R., Ulyshen, M. D., & McHugh, J. V. (2023). Forest age drives saproxylic beetle biodiversity in the southeastern United States. *Biological Conservation*, 285, 110238.
- 927 Trumbo, S. T., & Sikes, D. S. (2021). Resource concealment and the evolution of parental care in burying 928 beetles. *Journal of Zoology*, 315(3), 175-182.
- Tseng, M., Kaur, K.M., Pari, S.S., Sarai, K., Chan, D., Yao, C.H., Porto, P., Toor, A., Toor, H.S. & Fograscher, K. (2021). Data from: Decreases in beetle body size linked to climate change and warming temperatures.
- Tseng, M., Kaur, K.M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C.H., Porto, P., Toor, A., Toor, H.S. & Fograscher,
 K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, 87(3), 647-659.
- Tully, K., & Ryals, R. (2017). Nutrient cycling in agroecosystems: Balancing food and environmental objectives.

 Agroecology and Sustainable Food Systems, 41(7), 761-798.
- Ulyshen, M. D. (2018). Saproxylic diptera. In *Saproxylic insects: diversity, ecology and conservation* (pp. 167-192).
 Cham: Springer International Publishing.
- Ulyshen, M. D. (2016). Wood decomposition as influenced by invertebrates. *Biological Reviews*, 91(1), 70-85.
- van Lenteren, J. C., Loomans, A. J., Babendreier, D., & Bigler, F. (2008). Harmonia axyridis: an environmental risk
 assessment for Northwest Europe. From Biological Control to Invasion: the Ladybird Harmonia axyridis as
 a Model Species, 37-54.
- Vaz, S., Manes, S., Khattar, G., Mendes, M., Silveira, L., Mendes, E., de Morais Rodrigues, E., Gama-Maia, D., Lorini,
 M.L., Macedo, M. & Paiva, P.C. (2023). Global meta-analysis of urbanization stressors on insect abundance,
 richness, and traits. *Science of the Total Environment*, 165967.

- Verma, R.C., Waseem, M.A., Sharma, N., Bharathi, K., Singh, S., Anto Rashwin, A., Pandey, S.K. & Singh, B.V.
 (2023). The role of insects in ecosystems, an in-depth review of entomological research. *International Journal of Environment and Climate Change*, 13(10), 4340-4348.
- 948 Vieira, M. D. C. (2024). The economic value of ecosystem services provided by dung beetles (Coleoptera: Scarabaeinae) to Australia.
- Vitali, F., Habel, J. C., Ulrich, W., & Schmitt, T. (2023). Global change drives phenological and spatial shifts in Central
 European longhorn beetles (Coleoptera, Cerambycidae) during the past 150 years. *Oecologia*, 202(3), 577 587.
- 953 Vulinec, K. (2002). Dung Beetle Communities and Seed Dispersal in Primary Forest and Disturbed Land in Amazonia1. *Biotropica*, 34(2), 297-309.
- Vulinec, K., Mellow, D. J., & da Fonseca, C. R. V. (2007). Arboreal foraging height in a common neotropical dung beetle, *Canthon subhyalinus* Harold (Coleoptera: Scarabaeidae). *The Coleopterists' Bulletin*, 75-81.
- Wang, Y., Yang, J.B., Wang, J.F., Li, L.L., Wang, M., Yang, L.J., Tao, L.Y., Chu, J. & Hou, Y.D. (2017). Development
 of the forensically important beetle *Creophilus maxillosus* (Coleoptera: Staphylinidae) at constant
 temperatures. Journal of medical entomology, 54(2), 281-289.
- Weedon, J. T., Cornwell, W. K., Cornelissen, J. H., Zanne, A. E., Wirth, C., & Coomes, D. A. (2009). Global meta-analysis of wood decomposition rates: a role for trait variation among tree species?. *Ecology Letters*, 12(1), 45-56.
- Wetherbee, R., Birkemoe, T., Burner, R. C., & Sverdrup-Thygeson, A. (2021). Veteran trees have divergent effects on beetle diversity and wood decomposition. *PloS one*, *16*(3), e0248756.
- Wijas, B. J., Cornwell, W. K., Oberle, B., Powell, J. R., & Zanne, A. E. (2024). Faster than expected: release of nitrogen
 and phosphorus from decomposing woody litter. *New Phytologist*.
- Willsey, T., Chatterton, S., & Cárcamo, H. (2017). Interactions of root-feeding insects with fungal and oomycete plant
 pathogens. Frontiers in Plant Science, 8, 1764.
- Wislocki, J. (2021). Burrowing Techniques, Behaviors, and Trace Morphologies of Extant Larval to Adult
 Beetles (Master's thesis, Ohio University).
- Wu, C., Ulyshen, M. D., Shu, C., Zhang, Z., Zhang, Y., Liu, Y., & Wang, G. G. (2021). Stronger effects of termites
 than microbes on wood decomposition in a subtropical forest. Forest Ecology and Management, 493,
 119263.
- Wu, Y., Wang, Q., Yang, W., Zhang, S., Mao, C.X., He, N., Zhou, S., Zhou, C. & Liu, W. (2024). The cluster digging
 behavior of larvae confers trophic benefits to fitness in insects. *Insect Science*, 31(3), 870-884.
- 976 Yang, L. H., & Gratton, C. (2014). Insects as drivers of ecosystem processes. *Current Opinion in Insect Science*, 2, 977 26-32.
- Young, O. P. (2015). Predation on dung beetles (Coleoptera: Scarabaeidae): a literature review. *Transactions of the American Entomological Society*, 141(1), 111-155.
- Zajicek, P., Welti, E. A., Baker, N. J., Januschke, K., Brauner, O., & Haase, P. (2021). Long-term data reveal unimodal
 responses of ground beetle abundance to precipitation and land use but no changes in taxonomic and
 functional diversity. *Scientific Reports*, 11(1), 17468.

983	Zhao, T., Kandasamy, D., Krokene, P., Chen, J., Gershenzon, J., & Hammerbacher, A. (2019). Fungal associates of
984	the tree-killing bark beetle, Ips typographus, vary in virulence, ability to degrade conifer phenolics and
985	influence bark beetle tunneling behavior. Fungal ecology, 38, 71-79.

- Zhou, Y., Zhang, H., Liu, D., Khashaveh, A., Li, Q., Wyckhuys, K. A., & Wu, K. (2023). Long-term insect censuses
 capture progressive loss of ecosystem functioning in East Asia. *Science Advances*, 9(5), eade9341.
- Zumr, V., Nakládal, O., Gallo, J., & Remeš, J. (2024). Deadwood position matters: Diversity and biomass of saproxylic
 beetles in a temperate beech forest. *Forest Ecosystems*, 11, 100174.