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Opinion

The underappreciated roles of aboveground vertebrates on belowground communities

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In recent decades, evidence of interactions between aboveground and belowground (i.e., soil) subsystems has accumulated. The effects of aboveground vertebrates on belowground communities have traditionally focused on plant-mediated pathways, but we show that aboveground vertebrates impact belowground communities and ecological functions without plant-mediated pathways via both consumptive and non-consumptive processes. We then show that mobile, aboveground vertebrates have significant but often unrealized potential to structure soil communities from local to macroecological scales by linking aboveground and belowground food webs across habitats and ecosystems. Collectively, this synthesis of aboveground vertebrate effects on belowground communities integrates multiple ecological disciplines to advance a more comprehensive understanding of aboveground–belowground linkages across space and time.

Highlights

Aboveground vertebrates have traditionally been thought to impact belowground communities through plant-mediated interactions. However, aboveground vertebrates can alter belowground communities in ways that do not involve plant-mediated pathways.

Appreciating the overlooked roles of vertebrate consumers on belowground communities through both consumptive and non-consumptive processes may add new insights into the conventional framework of aboveground and belowground biological interactions.

By incorporating the spatial scale effects of aboveground vertebrates on belowground communities, we can develop a mechanistic understanding of the biogeochemical roles of wildlife on processes such as carbon and nutrient cycling that are mediated by belowground communities.

The overlooked pathway in aboveground and belowground linkages

Terrestrial ecosystems are composed of aboveground and belowground (ground being soil) subsystems, and there is accumulating evidence that aboveground and belowground biota are linked across ecological scales [1–3]. Classical approaches have focused on plants and soil microbes linking these communities, but the roles of **aboveground vertebrates** (see Glossary) – including herptiles, birds, and mammals – are less developed and are thought to impact **belowground communities** via plant-mediated trophic interactions [1]. For example, herbivores can influence belowground communities by controlling the quantity and quality of plant materials (e.g., leaf litter) that fuel detrital food webs [1], while predators can trigger trophic cascades through changes in herbivore behavior or density that alter the flow of energy from plants to belowground communities [4,5]. However, recent studies have revealed that aboveground vertebrates also impact belowground communities and soil ecosystem processes (such as **nutrient cycling** and decomposition) independently of plant-mediated pathways [6–12] (Figure 1). Nevertheless, research on soil community ecology and aboveground–belowground linkages has historically underappreciated spatial dynamics among soil organisms [13], because the typical actors – that is, plants, soil invertebrates, and microbes – are generally less mobile than aboveground vertebrates. Aboveground vertebrates, though, can link local soil communities through various mechanisms (such as dispersal and migration) that enable foraging across habitats, ecosystems, and sometimes continents [14,15]. Given the increasing recognition that aboveground–belowground linkages influence population, community, and ecosystem processes, an exploration of vertebrate effects is necessary to extend both the spatial scale of aboveground–belowground linkages and our understanding of the spatial structure of soil biodiversity and its emergent ecosystem functions.

In this opinion article we re-examine the ecological impacts of aboveground vertebrates on communities and their related functions. Specifically, we focus on the **consumptive effects** and

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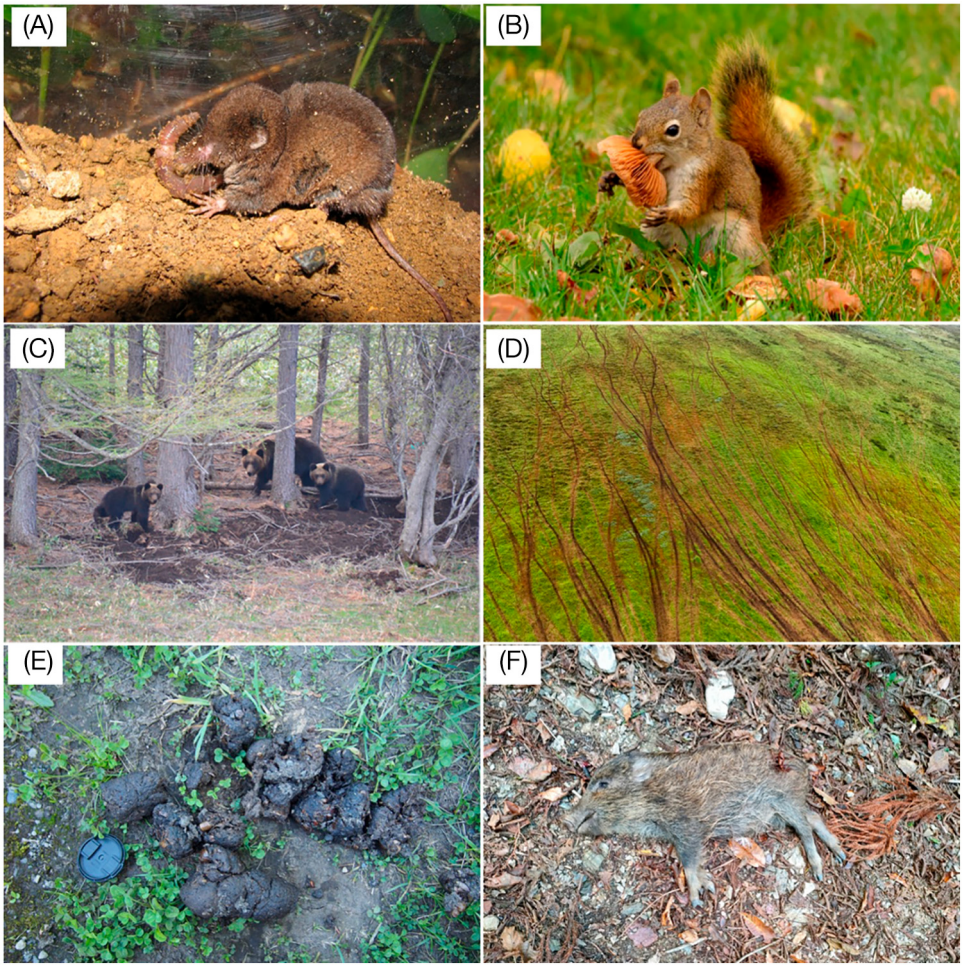

Figure 1. Photos representing consumptive (A,B) and non-consumptive (C–F) effects of aboveground vertebrates on belowground communities. (A) a shrew (*Sorex unguiculatus*) feeding on a belowground earthworm, and (B) an arctic ground squirrel (*Urocitellus parryii*) consuming a mushroom. Aboveground vertebrates often feed on belowground animals and microbes, resulting in consumptive effects on belowground communities. Predation on soil organisms by aboveground predators may alter community composition and ecosystem functioning (e.g., decomposition), while mushroom consumption by mammals can assist spore dispersal and alter the spatial heterogeneity of fungal communities. (C) Brown bears (*Ursus arctos*) digging for cicada nymphs. Large mammals affect belowground communities by modifying soil physical structure through digging and trampling activities, and this physical disturbance has strong impacts on belowground communities that indirectly alter ecosystem functions. (D) Caribou (*Rangifer tarandus*) trail on tundra. (E) A scat of brown bear, and (F) a carcass of wild boar (*Sus scrofa*). Excrement and carrion from animals supply nutrients to soil ecosystems, and animal-mediated fertilization can trigger bottom-up cascades in belowground food webs. Photo credit: (A) Tomoyuki Namba, (B,D) US Fish and Wildlife Service, (C,E,F) Kanji M. Tomita.

non-consumptive effects of mobile, vertebrate consumers (i.e., herptiles, birds, and mammals) which have significant potential to impact belowground communities and ecosystem functions at multiple spatial scales. We first summarize consumptive and non-consumptive effects of aboveground vertebrates on belowground communities as non-plant mediated pathways linking both subsystems (Figure 2), and we then outline the predicted spatial effects of aboveground vertebrates on belowground communities. Collectively, this approach summarizes the ecological roles of aboveground vertebrates across spatial scales to inform the conservation of wildlife and their ecological functions [16].

Glossary

Aboveground vertebrates: vertebrates that primarily inhabit terrestrial environments above the ground, including the soil surface. Aboveground vertebrates also refer to ground-dwelling vertebrates which forage and nest in soil, but not subterranean vertebrates such as pocket gophers and moles. The reason why we especially focused on ground-dwelling vertebrate consumers, such as mammals, birds, and herptiles, is that they have distinct ecological characteristics such as larger body size, longer movement distance, and higher energetic requirement than invertebrates.

Belowground communities: species or groups of organisms in the soil subsystem that depend mainly on soil resources and habitats for at least part of their life cycle, including soil microbes and invertebrates, but not subterranean vertebrates (e.g., burrowing mammals). Plants and algae are not included in belowground communities.

C:N ratio: the ratio of the mass of carbon to the mass of nitrogen in organic matters. Organic materials with a lower C:N ratio are higher quality for soil organisms because N is often a limiting nutrient.

Consumptive effects: animal effects that are exerted through consumption, here outlined as direct predation (i.e., trophic effects), energy transfer via tissue assimilation, and secondary dispersal via endozoochory.

Detritus: any form of nonliving organic matter, including dead plant tissue (e.g., leaf litter and dead wood), animal carcasses, urine, and feces. Most aboveground biomass is not consumed and ultimately enters detrital food webs.

Food web coupling: linkages between food web compartments (e.g., aboveground versus belowground), trophic levels, or resource channels (e.g., 'green' versus 'brown') due to animal foraging and the movement of energy between populations, communities, or ecosystem boundaries.

Multichannel feeding: foraging on resources from multiple energy channels, such as 'green' plant-based food webs and 'brown' detrital food webs.

Non-consumptive effects: animal effects that are exerted in the absence of consumption, including physical

Consumptive effects of aboveground vertebrates on belowground communities

Trophic effects

Aboveground vertebrates can affect belowground communities through the consumption of flora and fauna that structures ecosystem properties via multiple mechanisms (Figure 2A). Most directly, predation by aboveground vertebrates can regulate the demography, movement, and foraging of belowground prey, leading to trophic cascades that impact community dynamics and ecosystem processes [7,17]. For example, numerous aboveground vertebrates (e.g., small mammals, birds, amphibians) consume soil-dwelling invertebrates, thereby structuring the density, abundance, and diversity of belowground faunal communities [7,18,19]. In turn, predator-induced changes in soil invertebrate communities have been linked to trophic cascades that alter decomposition, carbon storage, and nutrient cycling [7,18,20]. For instance, woodland salamanders (*Ensatina eschscholtzii*) slowed litter decomposition and facilitated soil carbon storage by suppressing decomposer densities [20], while the exclusion of birds and mammals released soil invertebrates from predation [17], thereby altering nutrient cycling. Given the broad home ranges and large body size that can be achieved by many terrestrial vertebrates, they can have widespread effects on belowground communities and ecosystem processes that span significantly larger spatial scales than belowground consumers alone [7].

Nutrient transport

Aboveground vertebrates can also impact belowground communities through the transportation of energy and nutrients between terrestrial subsystems. **Multichannel feeding** by aboveground vertebrates is increasingly recognized as a critical link between aboveground and belowground systems that can structure food webs, nutrient cycling, and ecosystem stability [21,22]. For example, small mammals (e.g., shrews of the Soricidae, voles of the Cricetidae) often feed at the interface of aboveground–belowground subsystems and rely heavily on belowground energy channels through the direct consumption of fungi and detritivorous invertebrates [7,23], with consequences for trophic position and food chain length [24,25]. The consumption and assimilation of belowground energy by aboveground mammalian consumers can also transfer significant quantities of carbon between trophic compartments, the strength of which may dictate terrestrial carbon storage [6]. Larger consumers, including mammalian carnivores, can similarly structure energy flow between aboveground and belowground systems by provisioning nutrients from prey carcasses to soil communities, with cascading effects on belowground microbes, invertebrates, and biogeochemistry [9,26] (see later).

Endozoochory

Aboveground vertebrates also structure belowground communities through the consumption and transport of propagules such as fungal spores [27,28]. For example, small mammals can facilitate the establishment and recovery of mycorrhizal symbionts following disturbance by transporting fungal inocula [29], thereby promoting forest establishment and succession [30]. Interestingly, some studies found that invertebrate eggs can tolerate passing though the gut of birds and mammals [31,32], suggesting that soil arthropods, like fungal spores, can also be dispersed through endozoochory by aboveground vertebrates. Directional spore dispersal may also influence the roles of aboveground vertebrates in ecosystem processes such as wood decomposition and forest regeneration through spore transportation. For example, small mammals both facilitate seedling establishment and forest regeneration by transporting mycorrhizal fungi spores in their feces, but may also enhance wood decomposition by depositing scats containing saprotrophic fungal spores in shelters such as coarse woody debris [33].

Non-consumptive effects of aboveground vertebrates on belowground communities

Detritus supply

Aboveground vertebrates are an important source of **detritus** – the primary input from aboveground to belowground subsystems – by providing excrement and carrion to belowground

disturbance by digging and trampling, detritus supply through the production of carcasses and excrement, and propagule dispersal through phoresy. This term has been conventionally used for representing risk effects of predators on prey. However, our definition of 'non-consumptive effects' includes a broader meaning of ecological effects of animals.

Nutrient cycling: the movement and transformation of nutrients (such as nitrogen, phosphorus, sulfur) that are essential for the growth and functioning of organisms, driven by biotic and abiotic components of ecosystems.

Phoresy: a commensal relationship in which one organism is transported by a different species by attaching to its surface.

Zoogeochemistry: the effects of animals on the spatial distribution and cycling of nutrients.

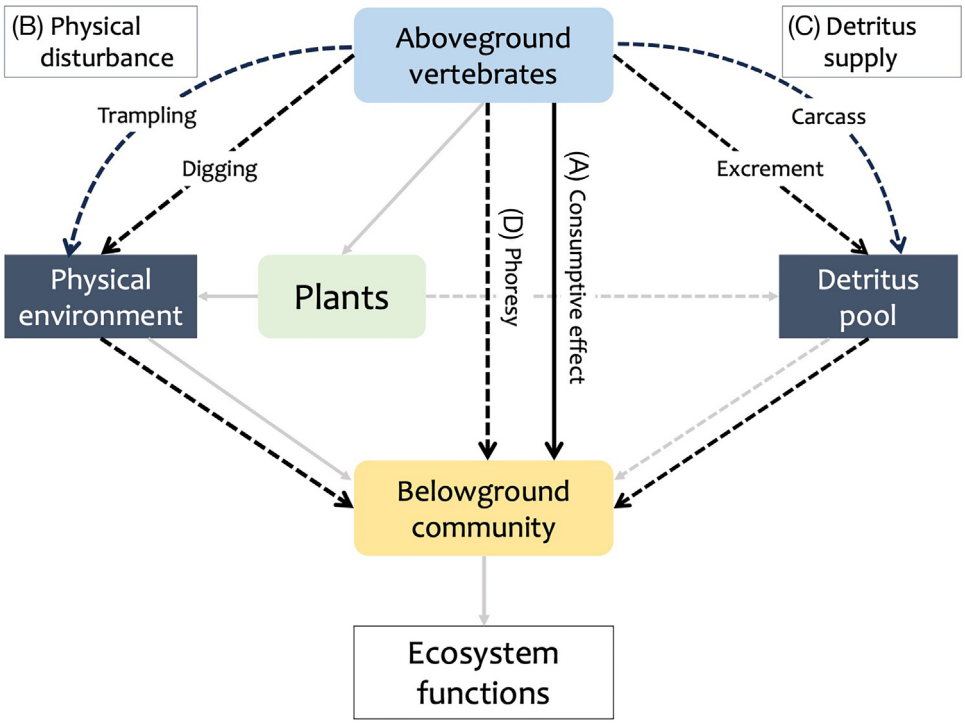

Figure 2. A diagram showing pathways from aboveground vertebrates to belowground communities. Aboveground vertebrates affect belowground communities via (1) trophic cascades that alter the quantity and quality of nutrients flowing from predators to herbivores, plants, and detritus derived from plants (gray dashed arrows), or (2) modification of soil physical environment by decreasing plant cover (gray solid arrow). Aboveground vertebrates also affect belowground organisms without plant-mediated pathways via both consumptive (black solid arrow) and non-consumptive (black dashed arrow) pathways. Aboveground vertebrates prey upon soil organisms or assist their movement through endozoochory of fungal spores, and thereby alter composition and spatial structure of belowground communities: (A) consumptive effects. Non-consumptive pathways are divided into three pathways: (B) physical disturbance: aboveground vertebrates modify the soil environment through physical disturbances such as digging and trampling, or (C) detritus supply: aboveground vertebrates change the availability of detritus by providing carcass and excrement into detrital pools, or (D) phoresy: aboveground vertebrates contribute to forming spatial structure of belowground communities and expanding their distribution through transporting soil fauna by attaching to their surface. These pathways have been historically underappreciated when describing aboveground–belowground linkages despite the diversity and ubiquity of such interactions (examples shown in Figure 1).

communities [34]. The origin of detritus can include animal tissues (e.g., carrion) and excrement (e.g., feces and urine), and plant tissues (e.g., leaf and root litter) [34]. Animal-derived detritus plays a disproportionate role in nutrient cycling and community dynamics due to richer nutrients (e.g., high N) that are more labile and bioavailable than plant litter, even though non-living plant material dominates the detritus pool in terms of quantity [35,36]. Animal-derived detritus can therefore generate biogeochemical hotspots that enhance the spatial heterogeneity of soil nutrients and alter belowground community dynamics [37,38].

The influence of animal detritus on belowground communities is primarily regulated by the quality of the nutrients. Animal detritus such as carcasses generally contain lower **C:N ratios** than plant detritus, and consist of non-structural carbohydrates, thereby providing a higher quality resource for soil organisms [35]. Consequently, carrion inputs directly alter soil nutrient pools, thereby altering soil microbial and arthropod communities, and plants [9,35]. However, the stoichiometry and decomposability of animal-borne detritus differs among body tissues, including muscle, bone,

and viscera [39]. For example, deposition of ungulate parturition (e.g., placenta) alters soil ecosystem processes on sites dominated by ectomycorrhizal plants but not ericoid mycorrhizal plants, indicating that animal detritus effects on soil processes also vary with belowground community composition (e.g., fungal diversity) [39]. Like carrion, the C:N ratio of feces and urine is generally lower than that of plant detritus (but higher than that of carrion), thus generating a high-quality resource for belowground communities [35]. The quality of excrement, however, can also vary depending on animal diet, digestive system, body size, and predation risk [40,41]. Ultimately, animal detritus and associated **zoogeochemistry** is a substantial pathway by which animals alter belowground communities (Figure 2C), but more information is needed to understand the context in which these effects are expected to be most pronounced.

Phoresy

Phoresy is a widespread interaction across terrestrial and aquatic ecosystems and is important for animals with low mobility to disperse to new habitats [42]. Soil animals are likely to disperse to new habitats through phoresy with aboveground vertebrates (Figure 2D) [43,44]. For example, oribatid mites may disperse by attaching to the surface of aboveground vertebrates, as seen among small rodents in restored heathlands, suggesting that phoresy is also important for ecosystem restoration by aiding in the recovery of soil ecosystem processes [43]. Collectively, the transport of propagules (e.g., seeds, spores) and soil fauna by aboveground vertebrates can have widespread effects on ecosystem functions via changes in belowground community.

Physical disturbance

Physical disturbance such as digging, burrowing, and trampling can affect belowground communities through damage-induced mortality of belowground organisms and changes in soil properties (e.g., compaction, biochemistry) (Figure 2B) [8,45–47]. Physical disturbances can also have contrasting effects on belowground communities. For instance, digging enhances soil water infiltration and porosity by reducing soil density, while trampling induces soil compaction that reduces water infiltration and porosity [8]. Both processes have the potential to alter belowground communities. Trampling by domestic cattle, for example, was found to reduce the body size of soil nematodes by limiting soil pore space [48], while digging promotes larger body size in belowground communities by increasing the degree of soil porosity [49]. Such body size changes in belowground communities would consequently alter their ecosystem functions such as carbon cycling [50].

The effects of physical disturbance on belowground community composition and ecosystem processes depends on the behavioral and morphological traits of target species [51,52]. For example, a global meta-analysis has suggested that the negative effects of trampling (e.g., soil compaction) by mammalian herbivores on soil fauna abundance increases with animal body mass [51], indicating that body size is an important trait for determining the strength of trampling effects by aboveground vertebrates on belowground communities. Digging behaviors such as nesting and foraging similarly determine the distribution, frequency, and interval of disturbance regimes. Indeed, nesting and foraging burrows have different impacts on belowground communities depending on excavation depth, spatial distribution, and frequency of use [52], but these impacts have not been clearly distinguished [45]. For instance, nest burrows are disturbed repeatedly and can provide large cavities with stable microclimates and humidity for soil fauna [53,54]. Conversely, digging for food occurs less frequently, is shallower, and is more widely distributed, thus forming a patchier disturbance gradient than nest burrows. Belowground community composition in nest burrows is also likely to differ between active and inactive nests because soil organisms can more easily invade active nests by attaching to the body surfaces of nesting

mammals [43], thereby creating an interactive effect of physical modification and phoretic dispersal on belowground community composition.

Spatial effects of aboveground vertebrates on belowground community

Aboveground vertebrates also affect belowground communities across horizontal space [15,26]. The spatial scale at which aboveground vertebrates play these roles, however, depends on their activity type, home range size, and life history. For example, the spatial effects of foraging, defecating, burrowing, and daily movement likely operate within the home range of a given species, while long-distance transport of detritus (e.g., via excrement) is a function of migration or dispersal distance and contingent upon gut retention times [55]. On macroecological or even continental scales, migratory animals can affect the spatial distribution of soil fauna and belowground community composition by assisting range expansions via phoresy. Thus, the spatial scale at which animals link soil food webs is determined by both foraging and movement patterns. We outline four possible spatial effects of aboveground vertebrates on belowground communities associated with the consumptive and non-consumptive effects summarized earlier (Figure 3), recognizing that there is no current consensus on what effects dominate at a given spatial scale (see Outstanding questions).

Spatial coupling of local soil food webs via predation

Local food webs are inherently linked to others by mobile consumers [56], and this spatial **food web coupling** can affect food web stability [56]. Theory suggests that food webs can be stabilized by mobile consumers that increase foraging in habitats with abundant resources and decrease foraging in habitats with less abundant resources [57]. In belowground food webs, top predators have historically been assumed to be soil organisms with low mobility, such as spiders, pseudoscorpions, mesostigmatid mites, or centipedes [58]. Trophic links facilitated by animal movement has not traditionally been considered in soil ecology, but incorporating aboveground vertebrates as mobile consumers in soil food webs will further our understanding of the effects of vertebrates above the ground on soil food web stability across spatial scales [Figure 3(1)].

Increasing spatial heterogeneity of detritus availability and soil properties

Consumptive and non-consumptive activities that influence belowground communities – such as latrines, burrows, trails, and nutrient transport – are spatially heterogeneous [38,59–62]. Through these activities, aboveground vertebrates enhance the spatial heterogeneity of detritus availability and associated soil properties that influence belowground community composition [Figure 3(2)] [37]. For example, seasonal aggregation of large ungulates can create nutrient hotspots via excrement deposition [63], and severe winters can result in high ungulate mortality [64], both of which increase the input of animal-derived nutrients to wintering habitats and alter the spatial heterogeneity of soil nutrients. Nest sites such as fox dens also generate biogeochemical hotspots by increasing detritus availability (e.g., prey carcasses, excrement) and altering the soil physical environment (e.g., via digging) relative to adjacent sites [38,65], thereby increasing the spatial heterogeneity of soil nutrients and associated belowground fauna.

Cross-ecosystem detritus transport

Large mammals which move beyond ecosystem boundaries can influence belowground communities by transporting detritus (excrements and killed carcasses) derived from allochthonous resources [Figure 3(3)] [15]. For instance, ungulates that use several ecosystems and habitats with low and high forage availability on a daily basis may play important roles in less productive systems by linking soil food webs in both locales. In the Andes, predator-driven movement of vicuñas (*Vicugna vicugna*) between nutrient-rich meadow habitat and nutrient-poor plains habitat structures the biogeochemistry of latrines and subsidizes soil nutrients between habitats [59].

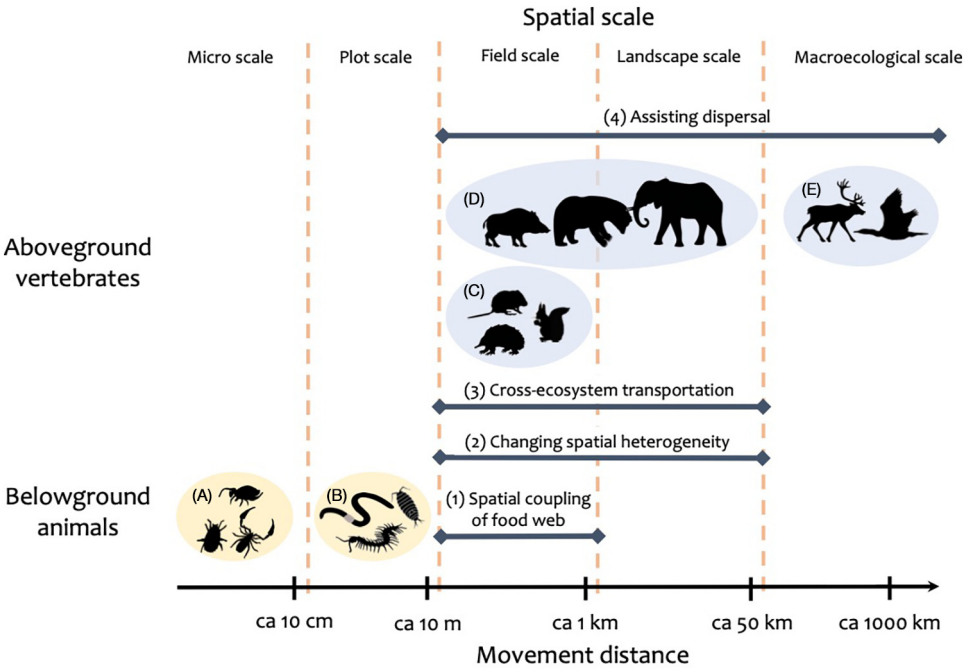

Figure 3. Heuristic diagram illustrating how aboveground vertebrates can structure belowground communities across spatial scales. Aboveground vertebrates (blue circles) (C–E) generally move or migrate further than belowground animals (yellow circles), (A) soil microinvertebrates, (B) soil macroinvertebrates: small mammals move a few dozen meters to one kilometer (C); large vertebrates can move dozens of kilometers across ecosystems (D); and migratory animals can move over 1000 km (E). Aboveground vertebrates may have spatial effects on belowground communities through both consumptive and non-consumptive pathways (dark blue bars), including: (1) coupling local soil food webs via foraging (consumptive); (2) increasing spatial heterogeneity of detritus availability and soil properties (consumptive and non-consumptive); (3) transporting detritus between ecosystems (non-consumptive); (4) assisting dispersal through endozoochory (consumptive) and phoresy (non-consumptive). The spatial scale of each effect depends on the behaviors (e. g., foraging, defecation, and migration), movement, and home range size of focal species.

Given that aboveground vertebrates such as ungulates and seabirds often forage in habitats with higher primary productivity than resting habitats, their daily movement is likely to contribute to the directional input of detritus (e.g., feces, carcass) from highly to poorly productive ecosystems [47,59,66].

Dispersal and range expansion of soil organisms by endozoochory and phoresy

Long-distance transport of propagules such as spores or soil arthropods via both consumptive and non-consumptive effects can impact belowground communities across scales [Figure 3(4)]. For example, mycophagy by aboveground mammals (Figure 1B) can alter the distance and direction of fungal spore dispersal at the field scale [67], but dispersal distance via endozoochory is limited by the gut retention time of the vector species. Aboveground vertebrates can also be a dispersal vector for soil animals and may contribute to ecological processes such as community assembly at large spatial scales [42]. Through phoretic association, aboveground vertebrates may enable the invasion of novel habitats and govern the spatial patterns of soil animals by assisting their passive dispersal [42]. Phoretic associations among soil fauna and small mammals likely contribute to the spatial structure of belowground communities at field scales [42,43], while phoresy on migratory birds and mammals could enable range expansions or long-distance dispersal of soil fauna at macroecological scales

[44]. More research is needed to understand these phoretic interactions, possibly by searching for soil animals on migratory animals [44], examining the attachment of animals to transportation surfaces, and identifying the phylogenetic patterns of soil organisms along migration routes [68].

Toward understanding the roles of aboveground vertebrates on biogeochemical models

Animal-mediated impacts on carbon and nutrient cycling have recently been suggested as natural solutions to mitigate global climate change while simultaneously facilitating the conservation and management of large-bodied vertebrates [69]. Documented zoogeochemical effects of vertebrates focus largely on aboveground trophic cascades that influence plant communities and the flow of energy and nutrients between trophic compartments [69,70]. However, belowground community composition and species interactions are among the most important drivers affecting ecosystem processes such as decomposition and carbon sequestration [71]. The consumptive and non-consumptive effects of aboveground vertebrates on belowground communities should therefore also be considered when characterizing zoogeochemical effects of animals on ecosystem processes across space (Figures 2 and 3). Recent emphases on zoogeochemistry and ecosystem functions have yet to fully consider the direct effects of aboveground vertebrates on belowground communities outlined herein [12,72]. Our proposed mechanisms by which vertebrates impact belowground communities may also contribute to a more comprehensive understanding of the aboveground vertebrate effects on biogeochemical processes. Future research should consider whether aboveground–belowground interactions dampen or amplify ecosystem effects in order to develop more realistic zoogeochemical models.

Concluding remarks

Herein we outline the importance of aboveground vertebrates on belowground communities and call for continued research on aboveground–belowground linkages. Novel methods such as stable isotope analysis, DNA metabarcoding, and biologging have recently enabled ecologists to rethink ecological networks by empirically quantifying consumptive and non-consumptive interactions across habitat boundaries and cryptic species interactions [7,73] (see Outstanding questions). However, research on aboveground–belowground linkages has not yet matched recent calls for rethinking ecosystem networks, and a comprehensive understanding of interactions between aboveground and belowground communities and their ecosystem consequences requires further empirical research. Nevertheless, increasingly available animal trait data – including body mass, diet [74], movement [75], occurrence (Snapshot Global: https://snapshot-global.org/) [76], and carrion provisioning [77] – will enable future exploration of aboveground–belowground interactions and the cascading effects of aboveground vertebrates on soil ecosystem process across spatial scales (see Box 1).

Outstanding questions

How much energy do aboveground vertebrates consume from belowground biota, and what are the consequences? Emerging tools like compound-specific stable isotope analysis and DNA metabarcoding now enable researchers to quantify trophic linkages between aboveground and belowground taxa, but the consequences for aboveground vertebrates (e.g., fitness) and belowground communities (e.g., species diversity and composition) remain uncertain.

How do both consumptive and non-consumptive impacts of aboveground vertebrates on belowground communities influence zoogeochemical effects on ecosystem processes such as carbon cycling?

How do vertebrate effects vary across spatial scales? At what spatial scale(s) do aboveground vertebrate effects control belowground community composition and emergent ecosystem functions? Ultimately, at what spatial scales do which effects dominate?

How do climate-induced or anthropogenically assisted range expansions of aboveground vertebrates impact the dispersal of soil organisms by phoretic association? Testing tolerance to staying on animal surfaces across life stage (i.e., eggs, dormant stages, adults) is needed to understand these associations.

Author contributions

K.M.T., P.J.M., and K.M. conceived the idea for this study. K.M.T led the writing of the manuscript with assistance from P.J.M. All authors commented on and agreed with the submitted version of this manuscript. S.F., F.H., T.M., and T.T. contributed equally to this paper (author order is arranged alphabetically).

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Box 1. Will aboveground vertebrate effects on belowground communities strengthen or dampen as global change progresses?

Rapid ecological changes such as climate warming and land-use change have threatened biodiversity and ecosystems in recent decades. Global change is predicted to dramatically alter the nature of aboveground–belowground linkages because these stressors differently influence aboveground and belowground communities [78]. Consequently, the behavioral- and population-level responses of aboveground vertebrates to global change are likely to alter their effects on belowground communities. In Taiga and tundra systems, belowground energy channels (e.g., fungi) increasingly support aboveground vertebrates like small mammals due to climate warming, and the decomposition of permafrost soils by climate warming, thereby strengthening trophic linkages between aboveground and belowground systems and altering nutrient cycles [6]. Winter climate changes such as warming, snow reduction, and rain-on-snow events also impact the mortality and habitat selection of overwintering ungulates that could alter the amount and spatial distribution of detritus originating from ungulate feces and carcasses [79]. At the same time, conservation efforts and recent land-use change can also increase the abundance of mobile consumers such as geese, whose overwintering regions in the Arctic tundra have been adversely affected by increased soil disturbances from foraging behaviors [80].

Global change also has significant potential to alter the zoogeochemical effects of aboveground vertebrates on belowground systems. For example, the rate of detritus decomposition is important for determining the amount of detrital pool inputs that regulate biogeochemical processes, but the decomposition rates of animal-borne detritus (e.g., carcasses, feces) may be accelerated at higher temperatures and levels of precipitation [81]. Rising temperatures also facilitate microbial activities that can alter the detection of carcasses and feces by aboveground vertebrates [81]. Thus, climate warming and land-use change could influence carcass consumption rates by aboveground scavengers [81], thereby altering the timing and availability of carcass inputs to detrital pools. Hence, global change can impact inputs of animal detritus not only through consumption, but also through non-consumptive effects mediated by the aboveground vertebrates.

Climate-induced range expansions are leading to novel communities in many northern habitats, with likely impacts on belowground food webs and ecosystem functions [14,78]. Given that aboveground vertebrates generally have high mobility, they also have a higher likelihood of invading northern habitats than belowground animals, and these climate-mediated invaders may also facilitate the establishment of belowground consumers to novel ranges through phoresy [44]. Indeed, Lebedeva and Krivolutsky [44] found 180 species of living oribatid mites on 150 species of Arctic birds, suggesting a mobile bird species likely plays critical roles in the range expansions of soil fauna. Overall, considering the roles of aboveground vertebrates on aboveground–belowground linkages will be increasingly important for predicting the ecosystem consequences of changes in species composition and interactions due to global change.

Declaration of interests

The authors declare no competing interests.

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