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ÉCOLE DOCTORALE ***Santé, Sciences Biologiques et Chimie du Vivant (SSBCV)***
UNITÉ de RECHERCHE INRAE Écosystèmes Forestiers, UR1455 (EFNO)

THÈSE présentée par :
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pour obtenir le grade de : **Docteur de l'Université d'Orléans**
Discipline/Spécialité : **Biologie**

A comprehensive investigation into the diet of the brown bear (*Ursus arctos*) in the Pyrénées and its role in the dispersal of plants and fungi.

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“To reconnect with nature is key if we want to save the planet”*

Dr. Jane Goodall

***** *Se reconnecter avec la nature est la clé si nous voulons sauver la planète.*

Remerciements / Acknowledgment

Bah voilà c'est fini, trois années qui n'ont ressemblé à aucune autre et qui ont été une source incroyable de bonheur. Du bonheur car j'ai pu étudier une espèce unique en son genre et particulièrement mythique : l'ours brun. Du bonheur aussi car j'ai eu la chance d'être encadré par une équipe de choc incroyable : Christophe Baltzinger, Tanguy Daufresne, Cécile Vanpé et Mélanie Roy. Vous m'avez apporté tellement de choses sur le plan scientifique mais aussi humain. Votre bienveillance et expertise sans faille m'ont permis d'avancer sereinement dans cette thèse et je vous en remercie sincièrement. Vous êtes une source d'inspiration pour la suite. Vous êtes géniaux.

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List of content

Avant-propos

Ce travail de thèse de doctorat est le fruit d'une collaboration entre l'INRAE (Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement) et l'OFB (Office français de la biodiversité) via la convention N°OFB-22-1125 et s'inscrit dans le programme de recherche ECOSYBEAR du Service d'espèces à enjeux de l'OFB qui s'intéresse au Rôle de l'Ours brun dans le fonctionnement des écosystèmes pyrénéens. Plus précisément, cette thèse s'inscrit dans deux projets du programme : ECOSYBEAR 1 et ECOSYBEAR 2.

ECOSYBEAR 1 vise à evaluer le rôle de l'ours en tant qu'espèce de liaison mobile dans les flux biotiques et abiotiques à travers le paysage (dispersion de graines, spores, symbioses mycorhiziennes, parasites et nutriments).

ECOSYBEAR 2 cherche à caractériser les interactions trophiques et non trophiques (compétition, prédation, facilitation…) de l'ours avec d'autres espèces de la faune (sanglier, grand tétra, cerf, chevreuil, petits et moyens carnivores, rapaces…).

Ce travail de thèse a été aussi le fruit de deux collaborations entre l'OFB et le CNRS notamment pour les Chapitre III, IV et VI, dans le cadre de deux conventions (N°OFB.22.0773 et N°OFB-23-0498)

L'essentiel et la quasi-totalité du temps consacré à ce travail de thèse à été réalisé à l'UR EFNO (Nogent-sur-Vernisson, France). Différentes missions ont eu lieu avec le reste de mon encadrement pour réaliser du terrain ou des expérimentations dans les Pyrénées avec l'OFB (Villeneuve de Rivière, France) ou à l'UMR Eco&Sols et l'UMR CEFE (Montpellier, France).

Lors de cette thèse j'ai pu encadrer un stagiaire de Master 1, Yannis Clavier (Master Biodiversité Ecologie Evolution, Université de Poitiers) sur le projet ECOSYBEAR 1 dont le travail est en cours de valorisation et est présenté dans ce manuscrit. Également j'ai pu encadrer un stagiaire de Master 2, Samuel Delorme (Master 2 Génomique Environnementale, Université Claude Bernard de Lyon) sur le projet ECOSYBEAR 2 dont le travail n'est pas présenté dans cette thèse mais qui est en cours de valorisation.

Publication d'articles scientifiques / Scientific article publication

- **Pauly, G.**, Vanpé, C., Roy, M., Quenette, P. Y., Sentilles, J., Dumas, Y., Chevalier A., Chevalier R., Daufresne, T. & Baltzinger, C. (2025). Endozoochorous plant dispersal by the brown bear (*Ursus arctos*) in the Pyrénées: angiosperms but also ferns and mosses and the importance of disaggregation agents. Botany Letters, 172(1), 119-131 - *Publié / Published*

- **Pauly, G.**, Vanpé, C., Roy, M., Sentilles, J., Chapelin-Viscardi, J. D., Daufresne, T., & Baltzinger, C. (2025). - Dung beetles, but not rodents, contribute to brown bear feces removal, disaggregation, and secondary seed dispersal. Ecosphere, 16(8), e70382.- *Publié / Published*

- **Pauly, G.**, Roy, M., Vanpé, C., Sentilles, J., Quenette, P. Y., Benoiston, A. S., , Moreau L., Iribar-Pelozuelo A., Daufresne T. & Baltzinger, C.- Do Sex, Age or Ecological Needs Shape an Endangered brown bear Population Diet? New Insights from Faecal Metabarcoding. New Insights from Faecal Metabarcoding. Biological Conservation - Accepté à la publication / *Accepted for publication*

- **Pauly, G.**, Vanpé, C., Roy, M, Clavier Y., Chevalier A., Sentilles J., Daufresne T., Baltzinger, C. (2025) - Assessing endozoochorous seed dispersal from consumption to germination using brown bear faeces. - En révision majeure / *In major revision* - Ecology and Evolution

- **Pauly, G.**, Vanpé, C., Roy, M., Quenette, P. Y., Daufresne, T., & Baltzinger, C. (2025). - Can omnivores be considered keystone species? Bears as a study case. - Soumis / *Submitted* - Ecosphere

- **Pauly, G.**, Vanpé, C., Roy, M, Daufresne T., Baltzinger, C. - The role of brown bear in the potential co-dispersal of mycorrhiza, endophytes and pathogens together with their hosting plants - En prépartion / *In prepartion*

Communication des travaux de thèse / Scientific communication

Colloque / Scientific congress

- **Pauly G.**, Vanpé C., Roy M., Sentilles J., Quenette P. Y., Iribar-Pelozuelo A., Daufresne T., and Baltzinger C. - **L'ours disperse-t-il toutes les plantes qu'il consomme ?** - *35th "Biotechnocentre" Congress*, Nouan-Le-Fuzelier (France) - 19-20 October 2023. ~ Poster

- **Pauly, G.**, Vanpé, C., Roy, M., Quenette, P. Y., Sentilles, J., Dumas, Y., Chevalier A., Chevalier R., Daufresne, T. & Baltzinger, C. - **Not only fleshy fruits: endozoochorous dispersal by European brown bears !** - *8th Symposium of Frugivory and Seed Dispersal*, Ilheus (Brazil) - 04 to 08 August 2024. ~ Oral presentation

- Vanpé, C., **Pauly, G.**, Daufresne, T. & Baltzinger, C., Sentilles, J., Quenette, P. Y., Roy, M., - **FACING THE CHALLENGES OF STUDYING ENDOZOOCHOROUS SEED DISPERSAL EFFECTIVENESS Lessons from the brown bear** - *8th Symposium of Frugivory and Seed Dispersal*, Ilheus (Brazil) - 04 to 08 August 2024. ~ Oral presentation

- **Pauly G.**, Vanpé C., Roy M., Chevalier A., Chevalier R., Dumas Y., Clavier Y., Quenette P. Y., Sentilles J., Delorme S., Iribar-Pelozuelo A., Benoiston A. S., Moreau L., Daufresne T., and Baltzinger C.- **From consumption to germination: analysis of the whole seed dispersal process by Eurasian brown bear in Pyrénées mountains** - *International Congress of the French Society of Ecology and Evolution (SFE²)*, Lyon (France) - 21 to 25 October 2024. ~ Oral presentation

- **Pauly, G.**, Roy, M., Vanpé, C., Sentilles, J., Quenette, P. Y., Benoiston, A. S., Moreau L., Iribar-Pelozuelo A., Daufresne T. & Baltzinger, C. - **Do Sex, Age or Ecological Needs Shape an**

Endangered brown bear Population Diet? New Insights from Faecal Metabarcoding. New Insights from Faecal Metabarcoding. - *International Wildlife Congress*, Lillehammer (Norway) - 1 to 4 September 2025. ~ Poster

Workshop

- **Pauly, G.**, Vanpé, C., Roy, M., Sentilles J., Quenette P. Y., Iribar-Pelozuelo A., Daufresne T. & Baltzinger C. - **Brown bear diet and dispersal of seeds and mycorrhizal spores across pyrenean landscapes** - *Research network on brown bear in the Pyrenees workshop*, Villeneuve-de-Rivière (France) - 09 October 2023

Formation / Training course

- **Pauly, G.**, Roy, M., Vanpé, C., Sentilles, J., Quenette, P. Y., Benoiston, A. S., Moreau L., Iribar-Pelozuelo A., Daufresne T. & Baltzinger, C. - **Sex, age or biological needs: What shape the brown bear - New insights from faecal metabarcoding in an endangered population from South-Western Europe.** - *METAMAZONE,* Video conference - 12 June 2025

J'ai pu communiquer mes travaux de thèse de manière plus informelle à plusieurs reprises avec des présentations à l'O.F.B, l'U.R EFNO, l'U.M.R CEFE, au GSTOP (Groupe de Suivi Transfrontalier de l'Ours Pyrénées), au consortium CONNECT (sur la dispersion des graines par les non frugivores)

Formations suivies / Professional training courses completed

- "**Réseau Ours Brun (ROB)**" par l'OFB à Villeneuve-De-Rivi-re (France) -13/14 Avril 2023 | "**Brown Bear Network (ROB)**" provided by the OFB at Villeneuve-De-Rivière (France) - 13-14 April 2023

- "**Rédaction vulgarisée**" par Centre Sciences à Orléans (France) – 28 Août 2023 | **"Writing for the general public**" provided by the Centre Sciences at Orléans (France) - 28 August 2023

- "**Ecole chercheurs Revues systématiques de la littérature et Méta analyses**" par l'INRAE à Rennes (France) – 09 au 13 Octobre 2023 | "**Research School on Systematic literature reviews and meta-analysis**" provided by the INRAE at Rennes (France) – 09 to 13 October 2023

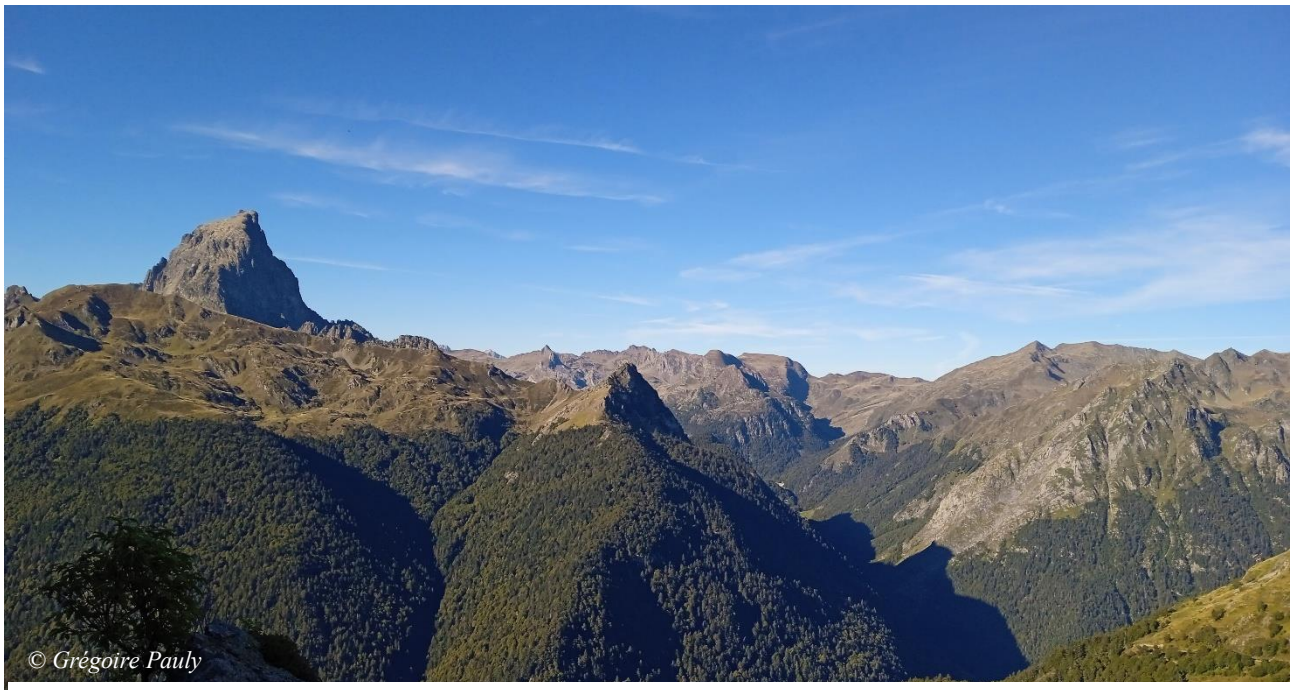
- "**Formation à l'utilisation de l'ADN environnemental**" par l'UMR Dynafor et l'UMR CRBE et l'Ecole d'ingénieur de Purpan à Toulouse (France) – 27 au 30 Novembre 2024 | **"Training in the use of environmental DNA**" provided by the UMR Dynafor, UMR CRBE, Engineering School of Purpan at Toulouse (France) - 27 to 30 November 2024

- "**Analyzing networks of ecological data**" par le CESAB à Montpellier (France) – 22 au 26 Avril | "**Analyzing networks of ecological data**" provided by the CESAB at Montpellier (France) – 22 to 26 Avril 2024

- "**Cours d'anglais**" par l'UR EFNO à Nogent-Sur-Vernisson (France) – 2023 à 2025 | "**English lessons**" provided by the UR EFNO at Nogent-Sur-Vernisson (France) – 2023 to 2025

- “**Recherche reproductible : principes méthodologiques pour une science transparente**” par l’INRIA au format MOOC - 2024 | **“Reproducible research: methodological principles for transparent science”** provided by the INRIA in MOOC format - 2024

Part 1 - General introduction



Pyrenean landscape with the 'Pic du Midi d'Ossau'.

Chapter I - The importance of external vectors in the plant life

I.1 Résumé

Les plantes sont des organismes immobiles devant utiliser des vecteurs extérieurs (biotiques ou abiotiques) pour se reproduire (pollinisation) et assurer la survie de leur descendance (dispersion des diaspores). La dispersion des diaspores permet aux plantes de coloniser de nouveaux sites ou de fuir des contraintes locales (e.g. compétition, agents pathogènes). Dans le contexte des changements globaux, la dispersion des plantes, et notamment celle qui permet des déplacements sur de longues distances apparaît comme cruciale. En effet elle permet aux plantes de pouvoir suivre les déplacements de niche écologique lié à ces changements globaux, qui est d'autant plus marqué dans les écosystèmes montagneux. Si les vecteurs abiotiques sont nombreux (e.g. vent, eau, gravité), ce sont les vecteurs biotiques, notamment la mégafaune ou la faune migratrice, qui sont particulièrement importants dans la dispersion longue distance des diaspores. Ces animaux peuvent transporter des diaspores de manière externe (i.e. épizoochorie) dans le pelage ou sur les pattes, ou de manière interne (i.e. endozoochorie) à l'issue de la consommation de graines ou de fruits. L'endozoochorie est historiquement associé à la consommation de fruits charnus, attirant l'animal qui ingère le fruit et disperse par la même occcasion les diaspores qu'il contient. Pourtant de récentes recherches ont montré que les plantes à fruits non charnus sont aussi consommées et dispersées par les animaux. De plus, d'autres organismes comme les mousses, fougères ou champignons peuvent être consommés et dispersés par endozoochorie. Ainsi, les omnivores qui se nourrissent volontiers de fruits, de parties

végétatives et de champignons peuvent ingérer et disperser un cortège important et diversifié d'organismes. L'Ours brun, étant un omnivore typique, consommant tout type de nourriture, peut représenter un agent crucial dans ce mécanisme.

I.2 The need for plants of external vectors to mate, move and establish

In ecosystems, organisms can be categorised in a very simple way as being immobile or mobile. **Mobile organisms** can travel across the landscape to feed, such as migratory birds, which travel thousands of kilometres to find a suitable feeding area and escape harsh periods. The mobility and dispersal is also crucial for mating opportunities and promotes gene flow (Saastamoinen et al., 2017). Once bred and given birth, animals can move in safer places than usual to raise young while minimizing mortality risk, as illustrated by fallow deer (*Dama dama,* L. 1758), which can use richer (Kjellander et al., 2012) or safer habitat (Ciuti et al., 2006).

However, for **immobile organisms**, including plants, the story is not the same: for mating or to optimize the survival of offspring through dispersal and establishment, those organisms rely on external vectors. For **reproduction**, plant exhibit various organisation of pollen-bearing anther (male organ) and ovule-connected stigma (female organ), which can be extremely diverse from monoecy at flower level (e.g. *Veronica persica*, Poir. 1808) to dioecy at individual level (e.g. *Ilex aquifolium*, L. 1753), and both can also occur at inflorescence levels or organised in partial dioecy (e.g. gynodioecy, androdioecy, trioecy). In addition, in monoecious species, a highly diverse flowering pattern also exists from synchrone flowering to duodichogamy, the rarest form of flowering (Pauly et al., 2023). All of those strategies are a trade-off between the limitation of inbreeding and the optimization of gene flow and the reproductive success mediated by external vectors to guarantee offspring (Lloyd, 1982; Lloyd and Webb, 1986). To be pollinated (**Fig. I.1**), plants need vectors either abiotic or biotic, even if some species can achieve auto-pollination (e.g. *Decodon verticillatus,* L. 1753, Eckert, 2000). Among abiotic vectors, pollen can be dispersed by the wind, especially at high latitude or in arid environments (Regal, 1982) but also in some cases by water (Cox, 1988). However, abiotic pollination remains less important than biotic vectors, which allow the pollination of 87.5% of plants (Ollerton et al., 2011). Biotic vectors are typically insects including bees, but also flies, butterflies or

beetles and also vertebrates including birds, bats (Faegri and Van Der Pijl, 2013), lizards (Olesen and Valido, 2004) and even canids (Lai et al., 2014).

Once pollinated, the plants produce **propagules** (e.g. seeds) that are dispersed more or less far from the mother plant also by abiotic or biotic vectors (**Fig. I.1**). This **dispersal** phase is crucial in plant dynamics, as it is the only phase at the species level allowing displacement (see section I.3 The importance of seed dispersal).

Once dispersed, the plants need to meet relevant edaphic and climatic conditions to establish, but also the presence of symbiotic mycorrhiza. Indeed, 85% of plants are associated with mycorrhizal fungi (Brundrett and Tedersoo, 2018) one of the hypotheses explaining seedling **establishment** success is the presence of mycorrhizae (**Fig. I.1**), which improves the plant access to water and nutrients (Simard and Durall, 2004). Association to mycorrhizae can be a matter of life or death, particularly in hostile environments such as those exposed to drought or located at high altitudes and many studies have demonstrated the benefits of mycorrhizae on seedling survival or growth (reviewed in Simard and Durall, 2004).

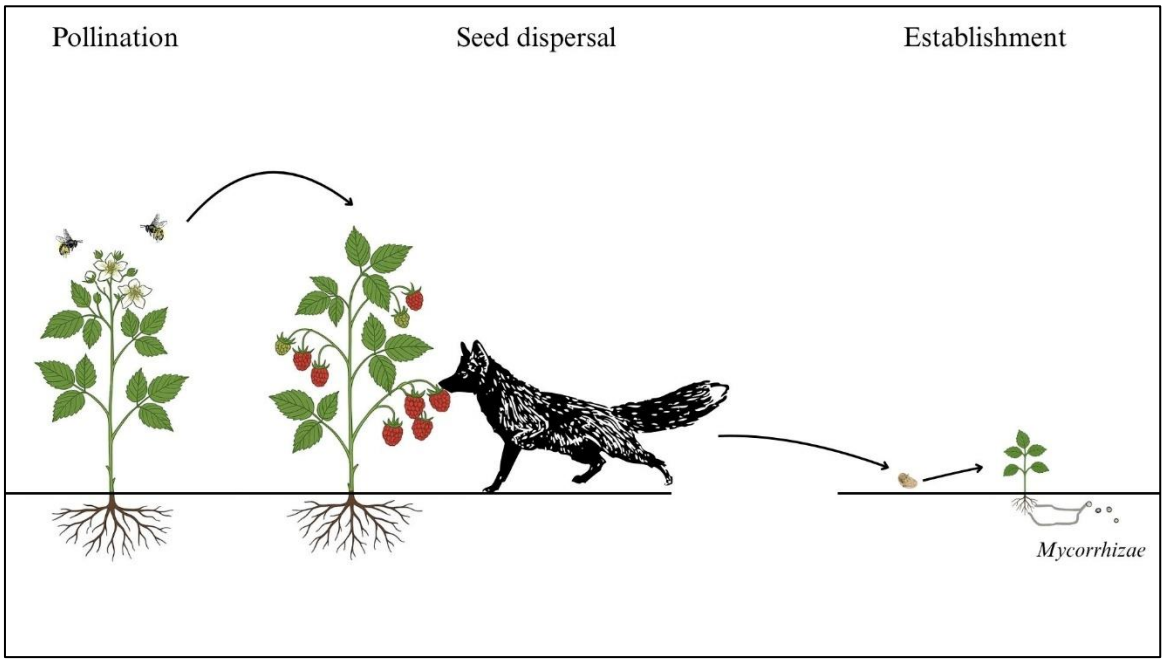


Figure I.1: Raspberry bush being pollinated by insects, then seed dispersed by mammals eating fleshy fruits with seed germinating and establishing thanks to mycorrhizal fungi. © Grégoire Pauly. Illustrations obtained freely on Canva.com

I.3 The importance of seed dispersal

An effective seed dispersal is primordial, because it represents the sole phase allowing plant species to move over the landscape (Beckman and Sullivan, 2023).

I.3.1 The evolutionary interests of seed dispersal

The advantages and evolutionary interests of seed dispersal have been the subject of historical and well-known hypotheses. According to the seminal paper of Howe and Smallwood (1982), there are three important hypotheses, which are not exclusive for plant species but can differ in importance.

(i) **The *Colonization hypothesis*** is based on the fact that habitat change in time due to disturbance such as treefall, landslide or fire and wide seed dispersal allows access to such disturbed sites potentially leading to plant establishment.

(ii) **The *Directed dispersal hypothesis*** is more related to plants with specific requirements and that dispersal (mostly mediated by animals) is non-random and oriented towards specific sites that may induce germination and establishment. For instance, there is evidence of such dispersal compiled by (Wenny, 2001) with directed dispersal of mistletoes by passerine birds in particularly favorable habitats.

(iii) **The *Escape hypothesis or Janzen-Connell hypothesis***, first proposed by Janzen (1970) and Connell (1971), is based on the fact that near the parent plant, the survival may be reduced due to unfavorable abiotic (nutrient or water) or biotic (intraspecific competition, pathogen, or seed predation) conditions. This hypothesis is now one of the most widely captured and discussed (Howe and Miriti, 2000). For instance, some evidence rapidly argued in favor of this hypothesis, such as a study on Graceful Platypodium (*Platypodium Elegans*, Vogel 1837) seedlings that showed higher survival as distance from mother plants increased, related to the absence of pathogen fungi (Augspurger, 1983). In fact, according to Howe and Miriti (2000), the comprehensive study by Harms et al. (2000) on more than 380 000 seeds and thousands of seedlings highlighted the high negative density-dependent effect on seedlings near the parent tree surrounded by propagules from the same species. This somewhat closed the debate around this hypothesis.

I.3.2 The importance of long-distance seed dispersal

According to these three hypotheses, the **long-distance dispersal** (hereafter LDD) of plants is particularly important. While most seed dispersal events do not exceed a few tens of meters (Howe and Smallwood, 1982), LDD events represent a small proportion of dispersal events and generally exceed 1 km (Nathan et al., 2008). LDD processes operate at levels crossing landscape, regional and even biogeographical scales, with significant implications for gene flow, colonization, escape from

harsh environment and assemblage of new local communities, especially in fragmented landscapes (Nathan et al., 2008). In their review, Nathan et al. (2008) highlighted that LDD generally occurs in open terrestrial areas and implies abiotic and biotic vectors such as large animals, extreme meteorological events, ocean currents or human transportation.

In the context of the recent acceleration of human-induced **global changes,** LDD became even more important, allowing plants to follow niche shifts either in latitude or altitude (Chen et al., 2011; Nuñez et al., 2023; Parmesan and Yohe, 2003). Among the numerous ecosystems threatened by climate changes, mountain ecosystems are the most vulnerable with fast climatic shifts (Knight, 2022). In their well-conducted paper, Mendes et al. (2025), investigating plant-seed dispersal vector interactions within and between five altitudinal zonations in Tenerife Island (Spain). They highlighted the dispersal of several plants at a higher altitude by medium- and large-sized birds in ways that enable them to keep pace with ecological niche shifts. Such uphill seed dispersal was also demonstrated for other vectors such as the brown bear (*Ursus arctos* L. 1758) in Japan (Naoe et al., 2016) or mesocarnivores in Spain (González-Varo et al., 2017). However, the contrary also occurred with downhill seed dispersal, especially for the fall-winter plant populations, with animals tending to descend to lower altitude (González-Varo et al., 2017; Naoe et al., 2019). Such downhill seed dispersal can be an important threat for plants that need to escape climate changes (Naoe et al., 2019). Nevertheless, LDD appears as a key mechanism under global change.

I.4 The different types of seed dispersal vectors

While seeds can be transported by either abiotic or biotic vectors, each dispersal mechanism varies in frequency according to biome, climate and availability of dispersers (Beckman and Sullivan, 2023).

I.4.1 The abiotic dispersal vectors of seeds

Among abiotic seed dispersal mechanisms, **anemochory** (i.e. seed dispersal by wind) can be quite frequent in windy and dry areas as early pinpointed by Howe and Smallwood (1982) and congruent with recent findings in Amazonia (Correa et al., 2023). This mechanism of dispersal is usually associated with seed appendages, which favor release and limit seeds' falling speed, such as the wing of maple (*Acer* sp. L., 1753) seeds inducing an autorotation or the pappus on the lighter seeds of dandelion (*Taraxacum* sp. Weber ex F.H.Wigg., 1780, **Fig**. **I.2**) favoring the flight of the seeds (Seale and Nakayama, 2020, and see figure 1 inside for mechanical details). Dandelion species can be transported over long distance (LDD) when updraft occurred (Tackenberg et al., 2003), a phenomenon already described in tree species (Nathan et al., 2002). Other seeds displayed a balloon form (e.g. *Cardiospermum* spp. L. 1753) or are so light that they can be dispersed with the dust (Van der Pijl, 1982). Some plants (e.g. *Oxalis* L. 1753) show adaptation to release seeds through a passive or active ballistic mechanism (i.e. **autochory**) (Seale and Nakayama, 2020, and see figure 1 inside for mechanical details) and appear as the rarest form of dispersal.

Figure I.2: Taraxacum sp. seed with pappus photographed with camera microscope Keyence VHX 6000 by Grégoire Pauly.

Hydrochory (i.e. seed dispersal by water) also occurs especially in wetlands and riparian areas and is a key mode of dispersal in riparian plant communities (Nilsson et al., 2010). Seed dispersed by water display specific characteristics including buoyancy and falling velocity in water (Beckman and Sullivan, 2023). There is also other more specific adaptation permitting a dispersal at the surface of the water (i.e. nautochory), on the bottom of the stream (i.e. bythisochory) or by the action of rain (i.e. ombrochory) that may trigger a ballistic release (Parolin, 2006). Finally hydrochory over oceans (i.e. thalassochory), favored by low density and protective tissues is a key mechanism of LDD (Nathan et al., 2008) and has been recognised as a significant vector in the colonization of isolated Azores Islands (Heleno and Vargas, 2015).

I.4.2 The biotic dispersal vectors of seeds

Actually, most plants appear to rely on animal vectors to disperse their seeds (**zoochory**) far more than on abiotic vectors, whether in tropical regions (Correa et al., 2023) or at global scale (Rogers et al., 2021) and especially tree species (Howe and Smallwood, 1982). Such mechanisms triggered by animals represent a form of **transport engineering** (Wilby et al., 2001).

Probably the most documented mode is **endozoochory**, meaning the dispersal of seeds after consumption and release through defecation (**Fig. I.3**) or regurgitation by animals, including mammals (e.g. ungulates, Baltzinger, 2016), birds (Wenny et al., 2016), reptiles (Valido and Olesen, 2019) and even fish (Horn et al., 2011). Basically, it follows the consumption of a fleshy fruit, a rich and attractive fruit rewarding the consumer, which co-evolves with targeted seed dispersers to match odor, color and size preferences (Beckman and Sullivan, 2023; Valenta and Nevo, 2020). However, many unattractive fruits or seeds of herbaceous plants are also internally dispersed especially by herbivores, because the seed-plants display attractive and palatable vegetative parts for the mammals, which consume the foliage along the seed (i.e. *foliage is a fruit* hypothesis, Janzen, 1984).

Nevertheless, once consumed, the seeds may resist mastication or be broken into pieces, drawing the limits between seed consumer and seed predator (Janzen, 1984). Thereafter, seeds pass through the animal's gut, which can favor germination by removing inhibitors contained in pulp or through scarification, but can also be detrimental for the seeds (Traveset et al., 2007). The ingested seeds can be released after regurgitation, a process described as partial endozoochory (Baltzinger, 2016), or after defecation within faeces. Faeces can represent a fertile environment for the dispersed seeds, which can enhance seed germination and seedling survival and growth, even if the reverse has also been observed due to potential toxic compounds (Traveset et al., 2007), representing a potential filter or booster of germination and growth.

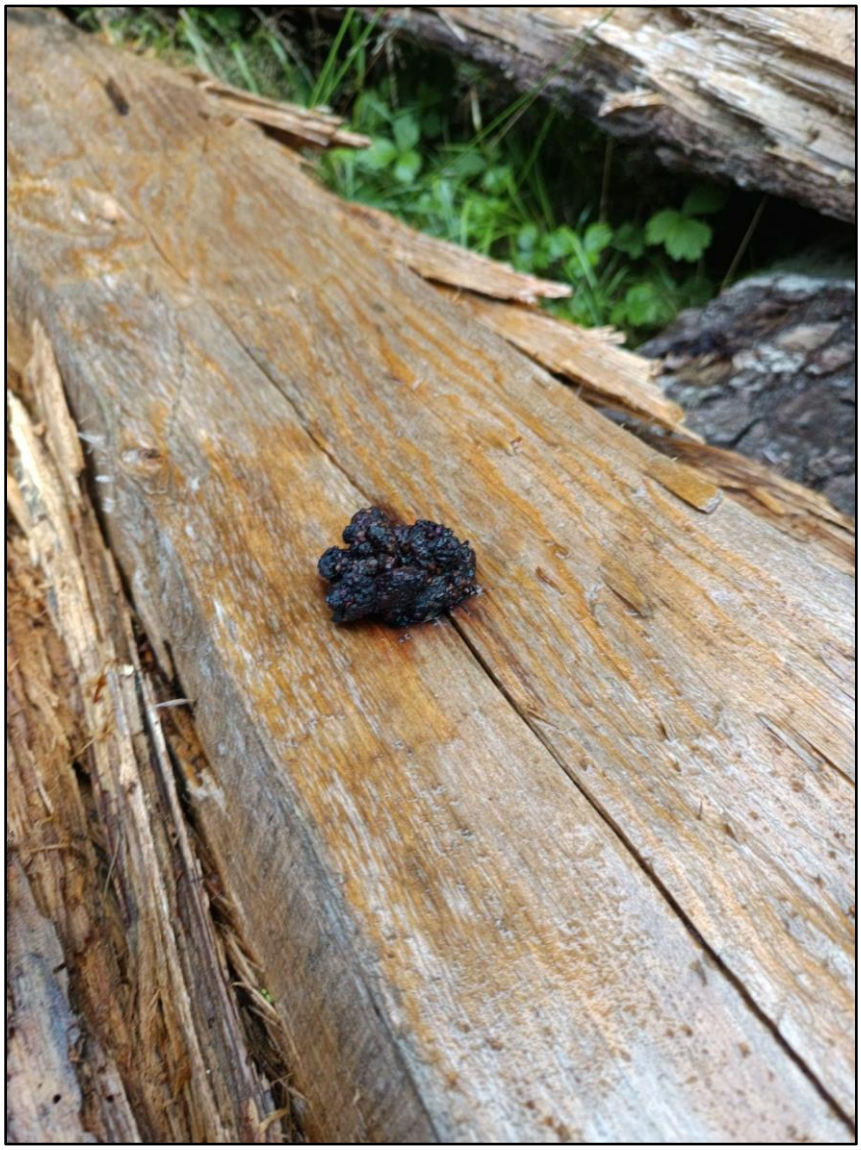


Figure I.3: Mustelid faeces composed of *Rubus* sp. seeds found in Pyrénées at Saint-Béat-Lez (Haute-Garonne, France). Photo by Grégoire Pauly.

Contrasting with herbivores or frugivores, the guild of granivores are directly attracted by the seeds as a reward and not secondary attributes (foliage or fruits) (Maria Gomez et al., 2019). Part of the seeds are consumed directly, and the rest can be hoarded at different places, transported in the mouth or beak to be consumed at a later time (i.e. **synzoochory**). However, numerous seeds are never consumed, espcially when the consumer stores superfluous seeds, forgets them or if it dies (Van der Pijl, 1982). Seed dispersal by synzoochory mainly involves Corvids or Rodents, but also marsupials, land crabs or insects (Maria Gomez et al., 2019). Insects can indeed transport seeds and some plants

are even specialized in such dispersal by associated protein- or lipid-rich structures in the form of elaiosomes to attract ants (**myrmecochory**) or hornets (**vespicochory**) (Beckman and Sullivan 2023)

Numerous plants are also transported externally (**epizoochory**) by sticking to mammal fur (Albert et al., 2015), bird-feathers (Vivian-Smith and Stiles, 1994), hooves (Albert et al., 2015) or talons. The presence of hooks or spines (Van der Pijl, 1982) and an elongated shape favors epizoochory in the fur, while a rounded shape favors dispersal within the hooves (Albert et al., 2015).

I.4.3 The unreliability of seed dispersal syndromes in the zoochorous processes

As mentioned in the previous section, each mechanism of dispersal is related to seeds with typical appendages or adaptations favoring wind or water transport, or the attraction of specific animals. Those adaptations constitute the typical **dispersal syndromes** integrated by Van der Pijl (1982). Based on this, most studies that investigated anemochory, endozoochory or epizoochory used those syndromes. However, Green et al. (2022) highlighted that most of the syndromes can be too restricted, such as the endozoochory syndrome (i.e. fleshy fruits), which is limited to frugivory, overlooking a whole range of plants with dry fruits dispersed by endozoochorous agents such as herbivores or waterbirds. They showed that dispersal syndromes were unreliable as most of the seeds dispersed by endozoochory by ducks and ungulates do not match the endozoochory syndrome but rather anemochory, hydrochory or epizoochory syndromes (**Fig. I.4**). This paper stigmatises studies solely focusing on syndromes, especially those dealing with LDD, because they probably missed a significant part of the vegetation dispersed. Nathan et al. (2008) also suggested that Dandelion (anemochory syndrome) can be dispersed over long distances mostly by hydrochory or epizoochory rather than by anemochory due to high half-time buoyancy and potential high time long-term retention. And we could pinpoint many more examples. Consequently, the dispersal of non-fleshy fruited plants by mammals may have been overlooked.

Figure I.4: Gramineae (non-endozoochorous syndrome) seedling sprouting from roe deer faeces. Photo taken by Christophe Baltzinger in 2010 as part of the DIPLO project (on plant dispersal by wild ungulates).

I.5 Diplochory and its importance in seed dispersal processes

The journey of seeds does not end after a dispersal event and may be transported by another vector resulting in two successive dispersal events (a **primary seed dispersal** and a **secondary seed dispersal)**, so called **diplochory** (Vander Wall and Longland, 2004).

Diplochory may imply both abiotic and biotic vectors. For instance, some pine species such as Jeffrey pine (*Pinus jeffreyi* Balf. 1853) display wings for wind dispersal but also large seeds, which interest scatter-hoarding animals (Vander Wall and Longland, 2004). Some plant species, using ballistic dispersal, can be subsequently dispersed by ants (Vander Wall and Longland, 2004), such as the Great-spur Violet (*Viola selkirkii* Pursh ex Goldie, 1822) (Ohkawara and Higashi, 1994).

Diplochory also occurs through two biotic vectors. For instance, **diplosynzoochory** involve two synzoochorous agents, with likely a corvid or squirrel as primary disperser and a ground-dwelling rodent as secondary disperser (Maria Gomez et al., 2019). In other cases, following primary endozoochorous dispersal, seeds can be freely available in the faeces to scatter-hoarding rodents (e.g. *Guarea glabra* Vahl 1807 dispersed by birds and then by agoutis, Wenny, 1999) or ants (e.g. *Commiphora guillaumini* H.Perr dispersed by Lesser Vasa parrots and then ants, Böhning-Gaese et al., 1999).

The above-mentioned diplochory examples occurred by a consumer targeting the seeds, but other events occur without the seeds being targeted. Following an endozoochorous primary event, the vector can be predated by another animal, which thus ingest the seeds previously consumed (**diploendozoochory**). Numerous examples are reported including predation of lizards (*Gallotia* spp. Boulenger, 1916) by cats (*Felis silvestris catus* L. 1758) in Canary Islands (Nogales et al., 2015) or the predation of Deer Mice (*Peromyscus maniculatus* Wagner, 1845) by Great Horned Owls (*Bubo virginianus* Gmelin, 1788) in Montana (Pearson and Ortega, 2001). In their review, Hämäläinen et al. (2017) highlight the positive effect of diploendozoochory through effect on germination, in LDD and alternative deposition sites.

Furthermore, endozoochorous agents releasing the seeds within faeces may interest numerous **coprophagous animals**, including dung beetles (**Fig. I.5**), known for accidental secondary seed

dispersal, as seed is a contaminant on a dung beetle's perspective (Andresen and Urrea-Galeano, 2022). Dung Beetles are a group world-dispersed of recognized importance in the translocation and removal of vertebrate faeces, with implication in nutrient cycling, bioturbation, pest and parasites suppression, pollination and seed dispersal (Milotić et al., 2019; Scholtz et al., 2009). The role of dung beetles in secondary seed dispersal has been well documented in tropical or temperate locations (see table 1 in Andresen and Urrea-Galeano, 2022). The functional group of dung beetles including dwellers (endocoprids use faeces directly), tunnelers (paracoprids bury a faeces portion directly from the faeces) and rollers (telecoprids relocate faeces portions by rolling away fecal balls and then bury the portion) is an important determinant in the destination and fate of the seeds (Andresen and Urrea-Galeano, 2022; Milotić et al., 2019). Finally, faeces characteristics, such as dung type, amount and location or seed density, related to the primary seed disperser agent are also determinant in dung beetle's attractivity(Andresen and Urrea-Galeano, 2022). From the seed's perspective, they can be moved deeply by dung beetles in the soil from few to 40 cm and horizontally from several centimeters to several meters. Vertical seed displacement induced can limit seed predation and may favor germination or survival (Andresen and Urrea-Galeano, 2022). Furthermore, dung beetles may also reduce the negative density-dependent effect within faeces on germination, especially from large mammals (Stricklan et al., 2020). In another way, horizontal seed displacement mediated by dung beetles can favor germination while avoiding the negative effect of burying (Andresen and Urrea-Galeano, 2022).

Figure I.5: Dungbeetles near brown bear faeces observed at Melles in the Pyrénées (France). Photo by Grégoire Pauly.

I.6 Are seeds the only type of propagules dispersed by animals ?

Zoochorous agents appear to be the most important vectors of seeds, particularly in LDD and altitudinal dispersal (Nathan et al., 2008). However, is often referred to as 'seed dispersal', most studies on material dispersal by animals are strongly biased towards seed-bearing plants, in other words, angiosperms and gymnosperms. However, other propagules can be dispersed by animals.

I.6.1 Plant spore dispersal: Ferns, mosses and liverworts

Other plant life-forms, dispersing as spores, including Bryophytes (i.e. mosses), Marchantiophytes (i.e. liverworts) or Pteridiophytes (i.e. ferns) are generally considered to be dispersed abiotically,

particularly by the wind (Glime, 2021; Mehltreter et al., 2010). However, numerous evidence suggests they can be transported by both vertebrates and invertebrates.

For **mosses**, evidence of zoochorous spore dispersal is presented in the well-documented book by Glime (2021). For instance, Glime (2021) suggested that hairy insects and spiders can transport sticky moss spores , as illustrated in an experimentation on the adhesion of asexual moss spores to *Lasius platythorax* (Seifert, 1991) (Rudolphi, 2009) or the dung mosses of the Splachnaceae family specially adapted for coprophilous fly dispersal (Glime 2021). Moss spores can be also transported on bird feet, feathers and animal fur (Barbé et al., 2016; Glime, 2021). Endozoochorous moss dispersal events have also been documented in slugs (Boch et al., 2015), birds (Deregnier et al., 2023; Glime, 2021; Wilkinson et al., 2017) and mammals (Bråthen et al., 2007; Glime, 2021; Parsons et al., 2007). Furthermore, as a form of synzoochory, birds may also transport moss fragments during nest construction (Osorio Zúñiga et al., 2014).

Liverworts, also called hepatics, have been documented in endozoochorous dispersal events by slugs (Boch et al., 2015)) or birds (Proctor, 1972).

Finally, zoochorous agents have also been documented in **fern dispersal** (Brock, 2025). For instance, ferns can be transported in the form of spores, sporangia or sporophytes on fur of red squirrels (*Sciurus vulgaris* L. 1758) (Barbé et al., 2016) or feathers of mallard ducks (*Anas platyrhynchos* L. 1758) (Coughlan et al., 2017) and even on the skin of red-blacked salamanders (*Plethodon cinereus* Green, 1818) (Oralls et al., 2016). Fern dispersal following consumption has also been documented in slugs (Boch et al., 2013), waterbirds (Lovas-Kiss et al., 2018), bats (Brock and Collier, 2020) and ungulates (Bråthen et al., 2007).

The zoochorous dispersal of ferns, mosses or liverworts appears particularly important in LDD events or directed dispersal but remains underexplored (Brock, 2025; Deregnier et al., 2024; Glime, 2021).

I.6.2 Fungi spore dispersal

Fungi are particularly important organisms in ecosystems, with highly variable lifestyles including **pathogens**, **mycorrhizae**, **endophytes** and decomposers. The concept of dispersal of fungi can be different due to their lifestyle, but it is typically described in three stages: release, transport, and colonisation (Chaudhary et al., 2022). In their review, Chaudhary et al. (2022) supported that fungi dispersal can be the result of spore, sporocarpe but also hyphal transport and the most common and likely mode of dispersal is abiotic (by wind or water), while highlighting several zoochorous fungi dispersal. Indeed, fungi can be transported at the surface of invertebrate bodies at small scale (e.g. collembola) or at the kilometre-scale (flying insects) and a recent study also suggested that folivorous insects can transfer endophytes to other plants by ingestion (Hannula et al., 2019).

The dispersal of fungi, by vertebrates has also been documented, promoting LDD (Chaudhary et al., 2022; Elliott et al., 2022; Vašutová et al., 2019), and seems to be mainly associated with **ectomycorrhizal fungi**. For instance, studies showed the presence of mycorrhizal spores in the faeces following fungi consumption in rodents (Stephens et al., 2021; Stephens and Rowe, 2020; Vernes and Dunn, 2009), ungulates (Ashkannejhad and Horton, 2006; Nuñez et al., 2013), birds (Correia et al., 2019) and probably most of the mycophagous animals (Elliott et al., 2022) with implications on local fungi communities (Gehring et al., 2002) with cascading effects on plant communities (Nuñez et al., 2013).

It has also been recently demonstrated that birds can co-disperse arbuscular mycorrhizae and their plant host in one endozoochorous event (Correia et al., 2019). Considering the huge importance of

mycorrhizae in harsh environments and for plant establishment (see I.1), such dispersal or co-dispersal may be crucial in the global changes context. In this regard, other fungi associated with plants (e.g. endophytes, pathogens) may be consumed accidentaly along plant tissues and be transported through endozoochory.

I.6.3 Animal propagules

Animal material can also be transported by other animals, usually their predator. For instance, a recent force-feeding study demonstrated that mallards can transport viable and fertilized eggs of bony fishes (Lovas-Kiss et al., 2024). Invertebrates **propagules** can be also dispersed externally as documented in African Elephant (*Loxodonta africana* Cuvier, 1825, Vanschoenwinkel et al., 2011) or internally following consumption by waterbirds with evidence of viable water invertebrate propagules in the faeces (Barboza et al., 2022; Green et al., 2008; van Leeuwen et al., 2012). Both dispersal types have important ecological implications, especially in isolated aquatic habitats (Lovas-Kiss et al., 2024).

I.7 Endozoochorous agents as a vector of life ?

Animal-mediated dispersal, and in particular endozoochory, therefore is quite important in the dispersal, especially in LDD, of plants, fungi and even animal propagules. However, such dispersal or co-dispersal depend on the biology and ecology of consumers from specific guilds. **Frugivorous birds** have been reported to disperse fleshy-fruits and fungi (Correia et al., 2019), whereas dry-fruit, moss, fern or invertebrate dispersal is more related to other bird guilds (Glime, 2021; Green et al., 2008; Lovas-Kiss et al., 2024, 2018). In contrast, **herbivores**, especially ungulates, have been reported to disperse fleshy fruits but also dry fruits, ferns, mosses and even fungi (Ashkannejhad and Horton, 2006; Bråthen et al., 2007; Green et al., 2022; Nuñez et al., 2013).

Finally, **omnivorous birds** (e.g. mallards) are well-documented in the dispersal of all plant, invertebrate and even fish propagules (Glime, 2021; Green et al., 2008; Lovas-Kiss et al., 2024, 2018). But lesser is known on the role of **large omnivorous mammals** on propagule dispersal. However, the above-mentioned evidence suggests that large omnivores could be good candidates in the dispersal of different plants and other materials, thanks to their long distance displacement and their diet based on many different resource types. Within this guild, omnivorous bears (Ursidae, Fischer von Waldheim, 1817) appear probably as the most typical omnivores, eating aquatic and terrestrial vertebrates, dry-fruited and fleshy-fruited plants, invertebrates and fungi (Reuter et al., 2023). However, their role as seed dispersal agents is still biased towards fleshy-fruited plant dispersal (García-Rodríguez et al., 2021a), even if there are some reports on dry-fruited plant dispersal (Karimi et al., 2020; Lalleroni et al., 2017). Nothing is known on their role on moss or fern dispersal, even if they are known to consume them (García-Rodríguez et al., 2021b; McLaren et al., 2021) and only one report suggests implication of a bear species (*Ursus americanus* Pallas, 1780) in the dispersal of fungi (Cázares and Trappe, 1994) despite opportunistic mycophagous behaviour (Elliott et al., 2022).

Hence, further studies on the role of omnivorous bears as primary dispersers of plants and other materials is expected to improve our knowledge and provide a better understanding of the role of animals as vector of living form dispersal for plant dynamics and ecosystem functioning.

I.8 Objectives of this PhD thesis

In this doctoral thesis, I therefore studied the role of an emblematic omnivorous mammal, the brown bear (*Ursus arctos*), in the dispersal of plants and other propagules. Prior to investigating its role in propagule dispersal (see **Chapter I** for a general introduction of propagule dispersal), I thought it important to understand the role of brown bear but also other omnivorous bears in ecosystem functioning, as omnivores may interact with diverse ecosystem components. To this end, I first

realised a review of the role of world omnivorous bears in ecosystems through their trophic interactions and their role as ecosystem engineers, in order to challenge the often overlooked importance of this guild (see **Chapter II** and **Fig. I.6**). To investigate more thoroughly the role of omnivorous bears in the dispersal of propagules, I focused on the study case of the Pyrenean brown bear population (see I.8 for brown bear history in the Pyrénées). As a first step, I described the Pyrenean brown bear diet based on metabarcoding analyses of faecal eDNA using four markers specific to plants, vertebrates, arthropods and fungi. The aim was to provide an up-to-date description of the Pyrenean endangered brown bear population diet (see section I.9 for brown bear diet in the Pyrénées) according to the time of the year, their sex and age (see **Chapter III**). I then explored the role of brown bears in plant dispersal, starting with the same batch of faeces and using several methods as a first step to investigate plant dispersal, taking into account the various filters of endozoochory (consumption, mastication, gut passage and faecal matrix). Here, I also compared the inference ability and relevance of various methods (see **Chapter IV**). In the next chapter, I explored plant dispersal in more detail with germination experiments and the role of the faecal matrix for seedling emergence and growth (see **Chapter V**). As I have found that brown bears consume fungi (mycorrhizae, endophytes, pathogens), I inferred fungi dispersal and examined the co-consumption of fungi and their host plants to identify potential joint dispersal (see **Chapter VI**). Finally, following a faeces release, diplochory frequently occurs associated with small animals focusing on seeds or dung beetles focusing on fecal material. I thus performed an experiment in the Pyrénées to test the role of dung beetles and rodents on secondary seed dispersal, faecal removal and disaggregation (see **Chapter VII**). Finally, I discuss my combined results, stress the limits and draw future directions for brown bear research.

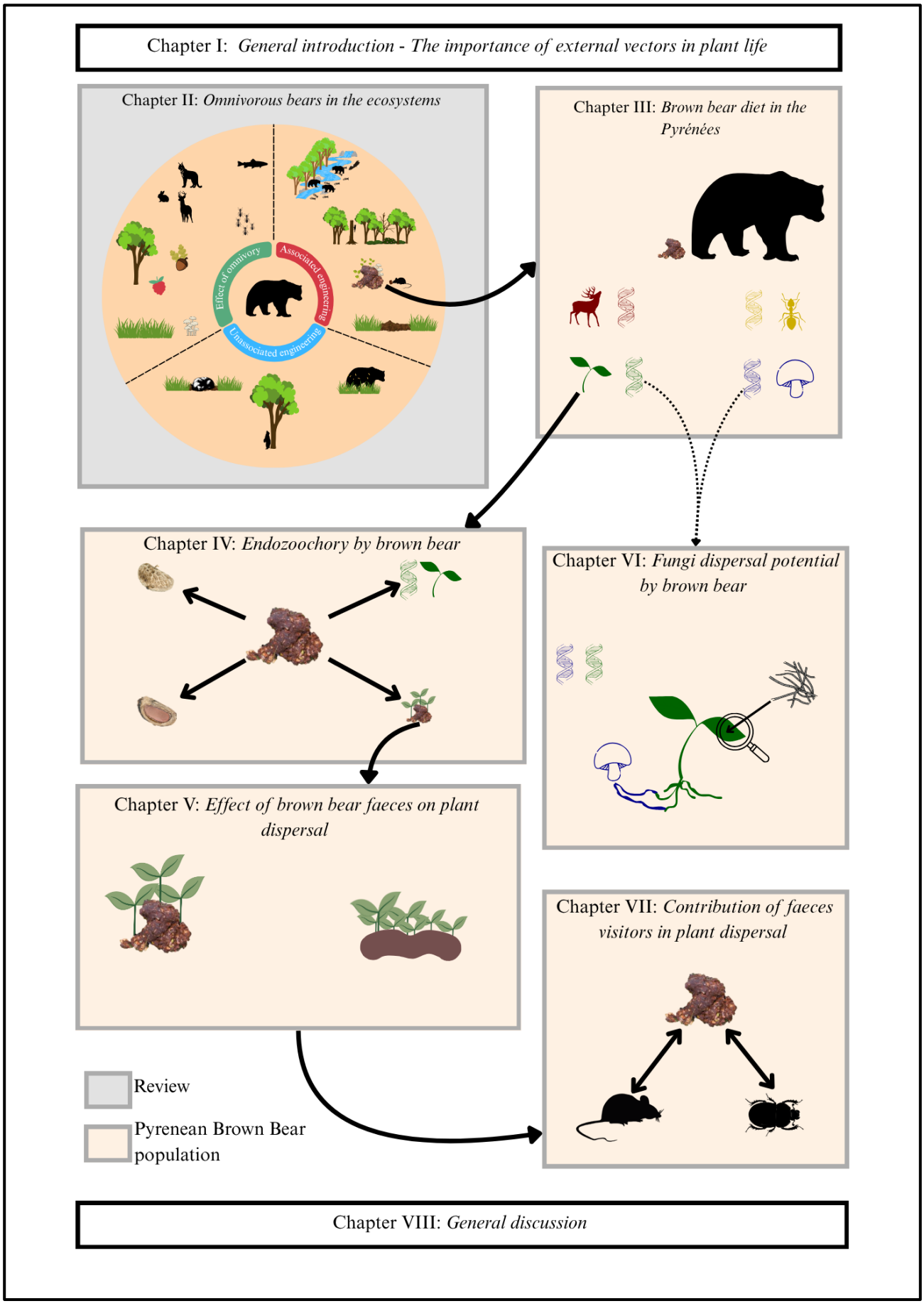


Figure I.6: Thesis structure and chapter organisation. Chapter titles have been deliberately simplified.

I.9 Brown bear in the Pyrénées

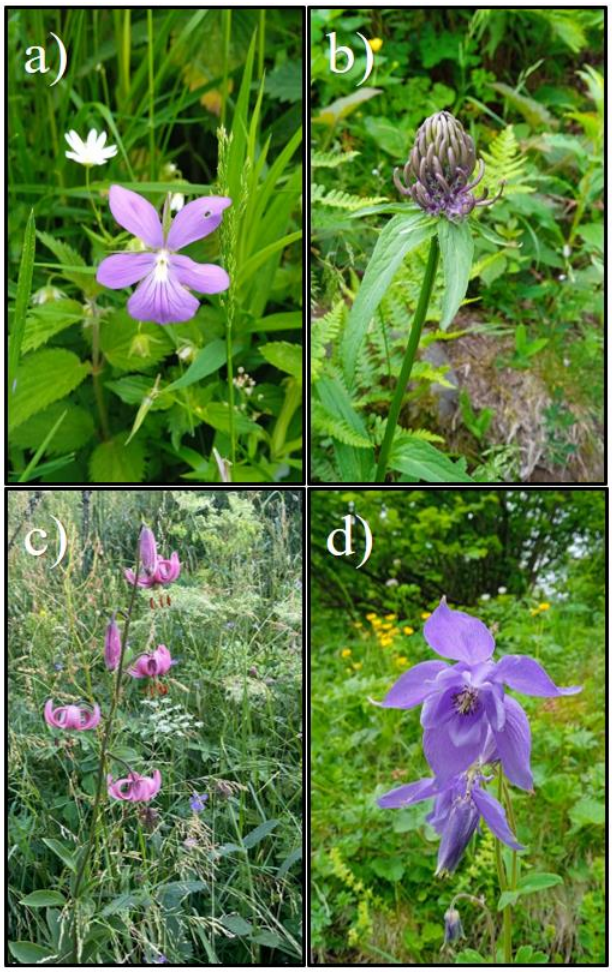


Figure I.7: Plants found in the Pyrénées. a) *Viola cornuta* b) *Phyteuma* sp. c) *Lys martagon* d) *Aquilegia pyrenaica*. Photos by Grégoire Pauly.

The Pyrénées are a major mountain chain in south-western Europe, shared between France (department of Pyrénées-Atlantiques, Hautes-Pyrénées, Haute-Garonne, Ariège and Pyrénées Orientales), Spain (autonomous communities of Navarra, Aragon and Catalunya) and Andorra representing 36,600 km² and peaking at 3,404 meters in altitude at the Aneto peak. The Pyrénées are home to a wide variety of flora (**Fig. I.7**) including 3500 plant species including medio-european, atlantic, mediterranean and boreo-alpine flora in which floral group distribution is mainly driven by altitudinal zonation. The Pyrenean flora displays also a high level of endemism including 258 taxa (Ninot et al., 2017). The Pyrénées mountains are particularly exposed to global changes and the altitudinal zonation may shift in the next few years (Knight, 2022; Ninot et al., 2017). About the animal diversity and zoochorous agents (**Fig. I.3**, **I.8**), the Pyrénées hosts a quite diverse megafauna, including numerous ungulates (chamois, ibex, wild boar, red and roe deer), many mesocarnivores (pine marten, fox, badger,..), brown bear and occasionally Wolf and Iberian Lynx.

The brown bear, a worldwide distributed species, has always been present in the Pyrénées, but experienced a drastic decline in population mainly due to hunting, poaching, poisoning and habitat loss related to forestry activities (Etienne and Lauzet, 2023). The population reached the brink of

extinction in 1995 with only 5 individuals on the occidental side of Pyrénées and it therefore became crucial to reinforce the population since then. Translocations of brown bear from Slovenia occurred four times in the central Pyrénées in 1996-1997 (three bears), 2006 (five bears), 2016 (one bear) and once in the occidental Pyrénées in 2018 (two bears) ("Ours brun (Ursus arctos)," 2020). Thanks to an impressive monitoring of the population based on genetic identification of hair and faeces, the French Office of Biodiversity identified at least 96 individuals in 2024 and estimated the population at 104 individuals, which are all Slovenian descendants from at least mother or father (Sentilles et al. 2025). The population is still fragile, mostly due to inbreeding (Auclair et al., 2025) and habitat loss, and the last IUCN status (2017) classified Pyrenean brown bear in critical danger of extinction, the worst conservation status ("Ours brun (Ursus arctos)," 2020)

Figure I.8: Picture of subadult female brown bear in the Pyrénées by Jérôme Sentilles.

Males and females show an important body size dimorphism : ~1m and 0.85m height at the withers respectively and 150-270kg and 70-130kg respectively. The annual life cycle of Pyrenean brown bear can be decomposed in six phases (**Fig. I.9**): The winter dormancy in which bear hibernate in a den and when females give birth (mid-December to March), post winter dormancy, an erratic feeding and emerging period (March to May), the mating characterised by high displacement rate in search of mate (May to July), the pre-hyperphagia period, a safer time for cub raising and muscle recovery (July to mid September), hyperphagia period, characterised by massive consumption of fat food items (mid-September to mid-November) and finally pre-winter dormancy, characterised by the search of appropriate den (mid-November to mid-December). During the year, the Pyrenean brown bear diet was described as highly seasonal but mostly based on plants (vegetative part or fruits) and includes meat (small mammals, domestic or wild ungulates) and insects (mostly colonial) (Berducou et al., 1982; Couturier, 1954; Lagalisse et al., 2003). However, since the late 1990s and Lagalisse and colleagues work, the diet of this population has never been updated although the population changed demographically and genetically, highlighting the need to re-investigate the diet of this population (see Chapter III).

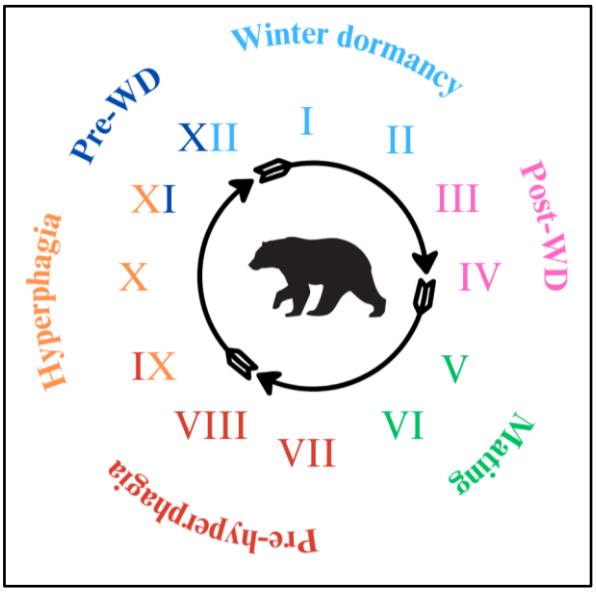


Figure I.9: Annual cycle of the Brown Bear in the Pyrénées from January (I) to December (XII). A month is colored by the color of the Brown Bear ecological period. WD = Winter Dormancy.

I.10 Materials used

For chapters III, IV, V, VI and VII we used Pyrenean brown bear faeces as biological material (**Fig. I.10**, **a)** and **b)**). To facilitate the detection of faeces, we used two scat detection dogs trained and used

by our OFB colleague and co-authored of several chapters Jérôme Sentilles (Sentilles et al., 2021) (**Fig. I.10**, **a)** and **c)**).

Figure I.10: a) brown bear faeces marked by a scat detection dog. b) brown bear faeces containing pyrenean chamois remains. c) The two scat detection dogs Iris and Silva. d) A brown bear winter den. Picture(s) a) taken by Jérôme Sentilles; pictures b), c) d) taken by Grégoire Pauly.

The dogs, called Iris and Silva, are female purebred Belgian malinois and contribute massively to the faeces collection. To detect faeces, often with dogs, systematic and opportunistic methods were carried out. Systematic methods consist of detecting faeces based on known visitation sites or bordering such sites, which covered 4310 km² in 2022. Detection is principally performed along itineraries traveled at least 10 times a year (from May to mid November) and represented by blue lines on **Figure I.11**, or prospection in known feeding sites. Other systematic prospection was performed to detect winter dens (**Fig. I.10**, **c**) or daybeds, where faeces are also searched. The

opportunistic method is mainly performed following the sighting of brown bear by nature users or stakeholders, and depredation events on domestic ungulates or hives (Sentilles et al., 2023).

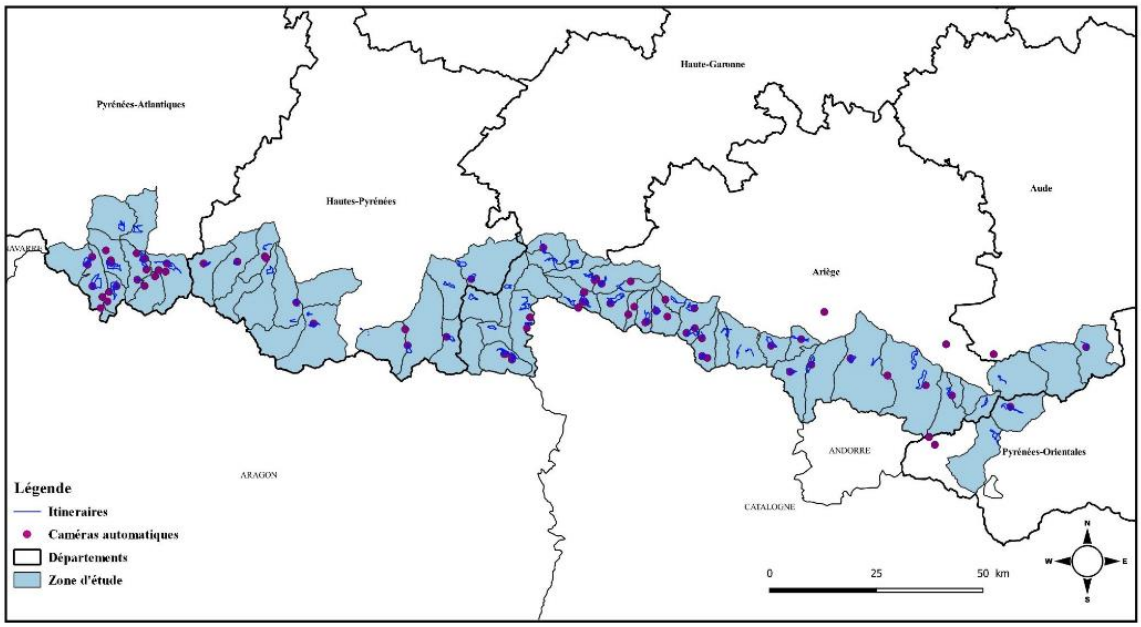


Figure I.11: Distribution of itineraries (blue lines) followed in the French Pyrenees in 2022 extracted from "Rapport annuel du Réseau Ours Brun" published by Sentilles and collegues in 2023.

Based on faeces retrieved prior and during the PhD thesis we built a collection of 176 unique faeces from 2017 to 2024 (**Fig. I.12, I.13**). Each faeces has been genotyped to identify the sex and the individual using two distinct molecular tools, and the age is deduced thanks to the intense monitoring of this population (Sentilles et al., 2025). Brown bear ages are categorised in cubs until one year, subadults between one and three years for females and one and five years for males, after they are adults. The collection was thus composed of 89 females faeces (71 adult faeces, 4 subadults, 9 cubs and 4 undetermined), 57 male faeces (28 adults, 18 subadults, 7 cubs and 4 undetermined) and 30 undetermined.

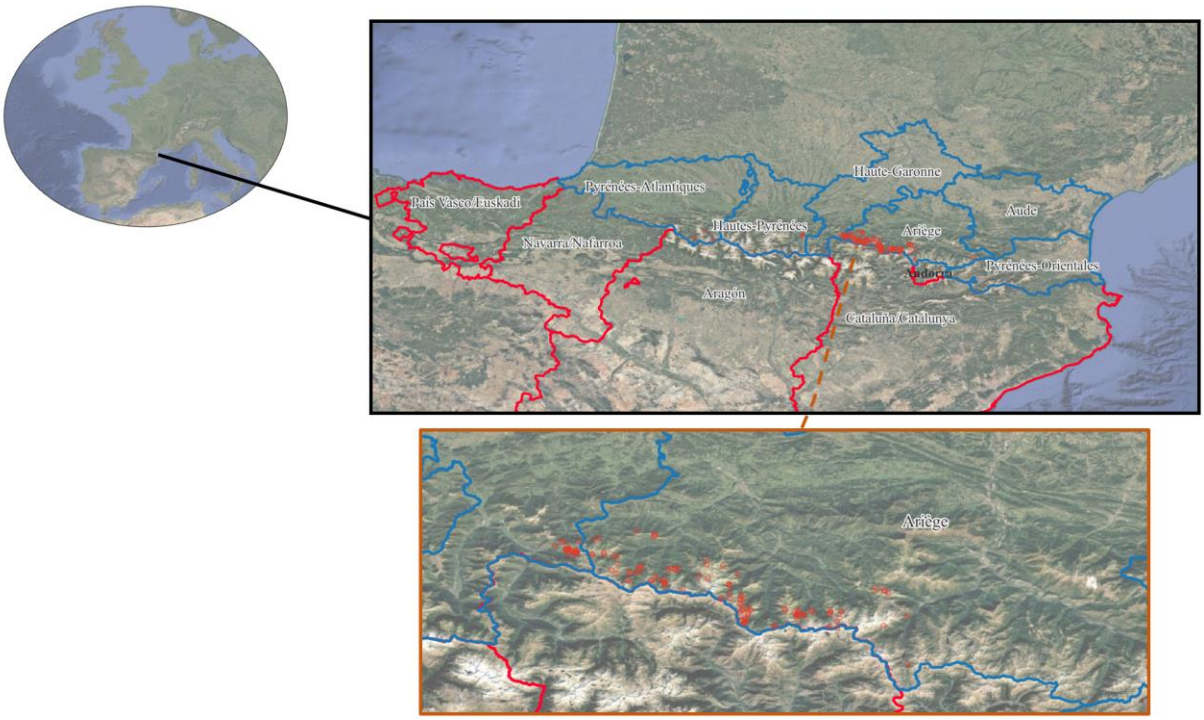


Figure I.12: Distribution of 176 brown bear faeces (brown dot) collected in the Pyrenees for this thesis

Those faeces were used for metabarcoding of faecal eDNA (see **Chapter III, IV and VI**), seed extraction (see **Chapter IV**), germination experiment (see **Chapter IV, V**) and secondary seed dispersal experiment (see **Chapter VII**). Most of those faeces were used in at least two chapters reinforcing the connectivity of our results (**Fig. I.13**).

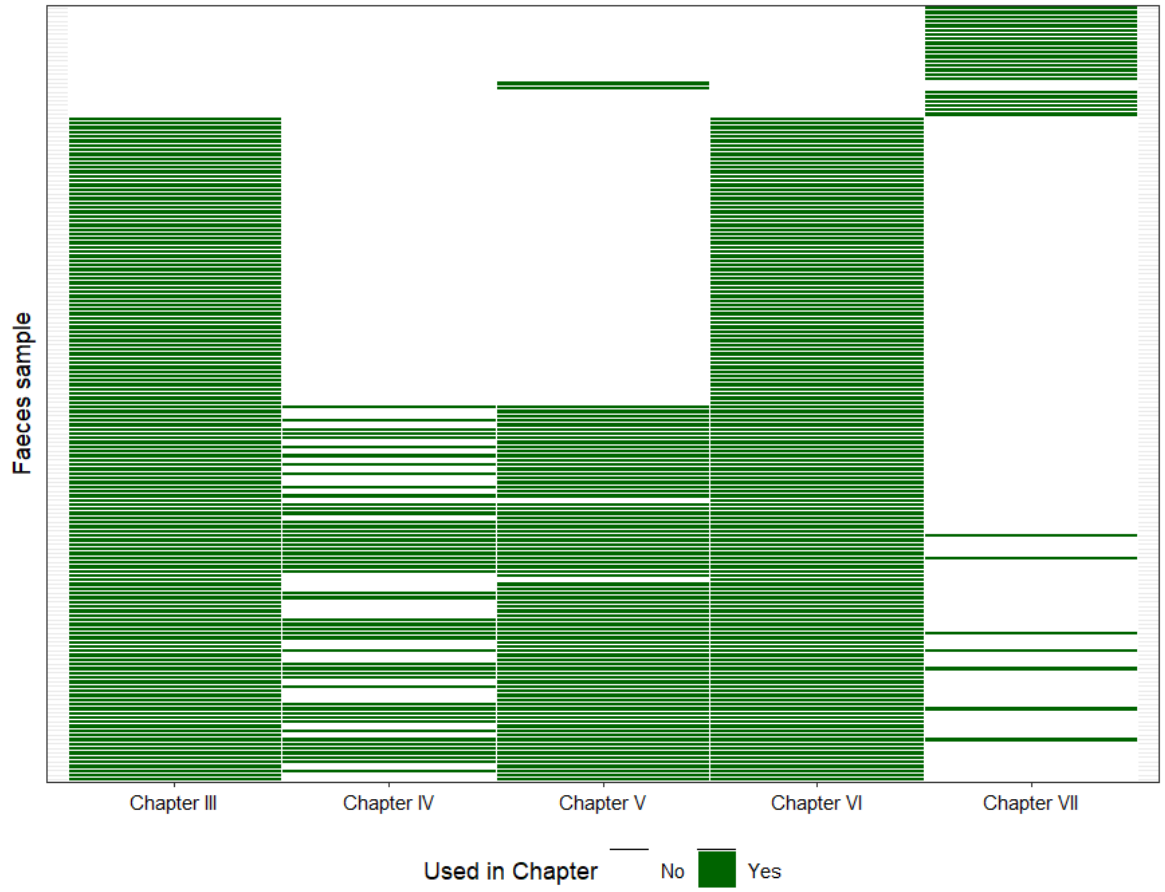


Figure I.13: Representation of faeces samples used (y axis) per chapters (x axis).

Chapter II - Omnivorous bears in the ecosystems: their trophic interactions and role as ecosystem engineers

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II.1 Résumé

Contexte : Le rôle fonctionnel des herbivores et des carnivores dans les écosystèmes est bien étudié, ils sont connus pour exercer des effets directs sur ce qu'ils consomment, mais aussi des effets cascades modifiant le fonctionnement de l'écosystème. Les omnivores résident à l'interface entre ces deux guildes et parce qu'ils mangent un peu de tout, leur rôle dans les écosystèmes semble avoir été négligé. Cependant nous pensons que pour ces mêmes raisons ils jouent un rôle crucial dans les écosystèmes via une diversité d'interactions trophiques et non trophiques avec de nombreux compartiments de l'écosystème. Les interactions non trophiques (i.e. ingénierie de l'écosystème) peuvent induire des modifications structurelles ou le transport de matériel induisant des effets importants sur l'écosystème. Pour mieux comprendre le rôle des omnivores, nous avons réalisé une revue de la littérature sur chaque type d'interaction déclenchée par des omnivores terrestres, en utilisant les Ours (Ursidae) comme étude de cas.

Méthodes : Nous avons réalisé des équations de recherche en anglais sur *Web of Science* pour chaque type d'interaction (trophique ou non trophique) et chaque espèce d'ours omnivore (*Ursus arctos*; *Ursus americanus*; *Ursus thibetanus*; *Helarctos malayanus*; *Tremarctos ornatus*; *Melursus ursinus*). Nous avons utilisé 411 références qui pour la plupart portent sur *U. arctos* et *U. americanus* et dans une moindre mesure *U. thibetanus*. A l'inverse, pour *H. malayanus*, *T. ornatus* et *M. ursinus* nous avons retrouvé que peu de littérature scientifique anglophone.

Résultats : À partir de ce corpus d'articles nous avons mis en avant une forte diversité d'interactions avec de nombreux compartiments de l'écosystème impliquant les ours omnivores. Par exemple, l'ours brun montre une forte variabilité dans son régime alimentaire pouvant être principalement herbivore ou bien carnivore, en incluant des niveaux variables d'entomophagie. Cela induit des effets variables sur les espèces consommées (recrutement des plantes et des proies animales, paysage de la peur pour

les proies animales), les co-consommateurs (paysage de la peur, kleptoparasitisme) et sur l'ingénierie associée (dispersion de graines, perturbation du sol, altération de l'ingénierie des ongulés prédatés). On retrouve aussi ce type d'interaction chez *U. americanus* ou *thibetanus* mais aussi d'autres spécificités documentés chez chaque espèce, comme la confection de nid dans les arbres par *U. thibetans*.

Conclusions : Notre revue montre que les ours omnivores interagissent avec de nombreux compartiments de l'écosystème (plantes, insectes, vertébrés aquatiques, vertébrés terrestres) via différentes intéractions, trophiques ou non-trophiques. Nous pensons, que même si une analyse plus poussée de ces interactions peut être nécessaire, les ours omnivores peuvent être considérés comme des espèces clés de voûte non pas du fait de quelques fortes interactions mais plutôt par une multitude d'interactions d'intensité variable avec divers compartiments de l'écosystème.

Mots clés : Ursidae, Ingénieur de l'écosystème, Intéractions trophiques, Intéractions non-trophiques, Omnivores

II.2 Abstract

The functional roles of herbivores and carnivores in ecosystems are well studied, they exert top-down direct and indirect control and can modify ecosystems through engineering. Omnivores lie at the interface between these two guilds, and because they may consume a little of everything, their role in ecosystems has been somewhat overlooked. However, for these reasons we believe that omnivores may play a pivotal role in ecosystems through trophic and non-trophic interactions with other guilds, from primary producers to apex consumers. To gain a better understanding, we performed a literature review for both interactions triggered by a group of terrestrial omnivores: Bears. We submitted equation searches on the Web of Science for each type of interaction and omnivore bear species. We kept 411 references highlighting a wide range of trophic and non-trophic interactions in various ecosystems. Our review shows the large number, diversity and significance of interactions in the ecosystem trigerred by omnivorous bears, but also a huge global variability in interactions from bear to bear species and among sites. This involved interactions with woody and non-woody plants, insects, terrestrial and aquatic vertebrates, soil community and even fungi. We argue, even if further research is required, that omnivores may constitute keystone species, not solely due to few strong interactions but rather to multiple interactions of varying strength with various ecosystem components, turning them into potential targets for ecosystem conservation.

Keywords: Ursids, Ecosystem engineers, Trophic interactions, Non-trophic interactions, Omnivores

II.3 Introduction

Within ecosystems, species interact with each other in trophic and non-trophic interactions. Direct trophic interactions lead to detrimental effects on the species consumed with cascading effects along the food chain (Paine, 1980). For instance, large predators exert direct top-down control on herbivores and mesopredators through predation and indirectly through fear, with cascading consequences on herbivory and prey (Ripple et al., 2014a). Similarly, herbivores exert a top-down modulation on plant species diversity, abundance and traits according to soil nutrients, plant life forms and herbivores involved (Bernes et al., 2018). These interactions can be pervasive when triggered by apex consumers (Hairston et al., 1960) and lead to significant effects at the landscape scale on ecosystem functions and associated biodiversity (Ripple et al., 2014a).

Non-trophic interactions of some species, also directly or indirectly modulate resource availability via changes in physical states or transport of biotic or abiotic materials, which turn those species into ecosystem engineers (as first defined by Jones et al., 1994). Ecosystem engineering is now widely accepted and known to trigger many interactions (Jones et al., 1994), with effects at spatial and temporal scales, e.g. beaver dams or bioturbation by earthworms (Hastings et al., 2007).

Both non- and trophic interactions appear crucial in ecosystem functioning. Wilby et al. (2001) first proposed a framework for herbivores encompassing both interactions to understand their impacts on an ecosystem. Since then, several modelling studies (Sanders et al., 2014) and empirical works (Kéfi et al., 2015) have highlighted the importance of both types of interactions in structuring ecosystems. A recent review showed that many guilds with various animal sizes are described as keystone species through their trophic or non trophic interactions. However, omnivores compared to other guilds remain poorly documented (Shukla et al., 2023). Yet true omnivores (i.e. consume both plant and animal materials, Coll and Guershon, 2002) can interact with potentially different ecosystem

compartments via trophic interactions. In fact, they have been the subject of numerous theoretical and empirical studies on their trophic role in the food web, with frequent contrasting results (Wootton, 2017). Interestingly, in a recent study based on empirical food webs, true omnivores are identified as organisms that can stabilise communities (McLeod and Leroux, 2021). Furthermore, the authors argue that the multiple interactions of true omnivores may turn them into keystone modules when the whole food web is considered, and properly understanding such species could lead to better adapted conservation strategies (McLeod and Leroux, 2021).

Although not considered in the above-mentioned studies, true omnivores may also trigger numerous non-trophic interactions. Several studies have stressed the complex role of omnivores in aquatic ecosystems, with trophic and non trophic interactions on different organisms (Usio and Townsend, 2002). In terrestrial ecosystems, Li et al. (2024) showed the importance of omnivorous invertebrates interacting with plant and soil dynamics. As well as large omnivores, like the European Badger (*Meles meles* L. 1758) which controls mesopredators by predation (Trewby et al., 2014) and has engineering effects on ecosystems (Kurek et al., 2022). By consuming fruits or seeds, omnivorous vertebrates are also effective long-distance seed dispersers (Tochigi et al., 2022). Targeting organisms triggering non-trophic interactions that can induce engineering processes can also be effective ecosystem conservation strategies (Boogert et al., 2006; Crain and Bertness, 2006).

In this context, a clear understanding of both types of interactions by omnivores would be a first step towards a better assessment of their importance in the ecosystem. However within omnivores, few studies have encompassed both trophic and non-trophic interactions of terrestrial vertebrate omnivores on ecosystems, making their overall effect rather cryptic (see Massei and Genov, 2004 for Wild Boar (*Sus scrofa* L. 1758), and Levi et al., 2020 for Ursidae in salmon ecosystems). This lack of studies encompassing both trophic and non-trophic interactions by omnivores and the somewhat diverging results of theoretical studies based on trophic interactions illustrate the complexity of their

effects on ecosystems (Terradas and Peñuelas, 2011) and probably the difficulty in understanding their potential role as engineers or keystone organisms.

We argue that to properly understand omnivores and possibly consider them as targets in ecosystem conservation strategies, we need to investigate all their interactions with all the compartments of the ecosystems with which they may interact. To evaluate how far terrestrial vertebrate omnivores may influence their ecosystems, we carried out a literature review to compile both interactions triggered by a well-studied group of terrestrial true omnivores. We aimed to apply a comprehensive approach to their functional role in ecosystems, reflecting the diversity and complexity of their interactions. So, we chose omnivore bears (Ursidae) as they are apex consumers with a flexible diet including five main food types: fibrous, non-fibrous plants, invertebrates, vertebrates and fungi (Reuter et al., 2023). Bears are also widely distributed (Luna-Aranguré and Vázquez-Domínguez, 2024), except Antarctica (literally, opposed to bears) and Africa, where they became extinct in the late 19th century (Hamdine et al., 1998).

II.4 Methods

II.4.1 Study species and adopted framework

Literature search focused on the six true omnivorous bear species: brown bear (*Ursus arctos* L. 1758), american black bear (*Ursus americanus* Pallas 1780), asian black bear (*Ursus thibetanus* Cuvier 1823), sun bear (*Helarctos malayanus* Raffles 1821), sloth bear **(***Melursus ursinus* Shaw 1798) and spectacled bear (*Tremarctos ornatus* Cuvier 1825). Among which, only *Ursus arctos* and *Ursus americanus* are not in danger of extinction, while the other bears are classified as vulnerable by the IUCN. We thus excluded polar bear (*Ursus maritimus* Phipps 1774) and giant panda (*Ailuropoda*

melanoleuca David 1829), respectively carnivorous with rare plant consumption (Willson, 1993) and herbivorous with rare animal (Long et al., 2004) consumption (**Table II.1**).

Table II.1: Main ecological and conservation features of the Ursidae.

Ursidae species	Diet[1]	Habitat[10]	Range[10]	IUCN status (last assessed) [10]	Main threats[10]
Ailuropoda melanoleuca	H[2]	**Forest**	China	VU (2016)	RC, EM, T, BU , HID, NSM, P, GE, CC
Helarctos malayanus	O[3]	Forest, shrubland, Artificial	South-East Asia	VU (2016)	AA, EM, T, BU, NSM
Melursus ursinus	O[4]	**Forest, Savanna, Shrubland,** Grassland, Artificial	India, Sri Lanka, Bhutan and Nepal	VU (2016)	RC, AA, EM, T, BU, HID, CC
Ursus americanus	O[5]	Forest, Shrubland, **Grasslands**, Wetlands, Desert, Artificial	North America	LC (2016)	RC, AA, T, BU
Ursus arctos	O[6]	**Forest**, **Shrubland**, Grasslands, Wetlands, Desert, Artificial	**North America**, **Europe** and Asia	LC (2016)	RC, AA,EM, T, BU, HID, NSM, P, CC
Ursus maritimus	C[7]	Forest, Shrubland, **Grasslands, Marine oceanic, Marine intertidal**, Marine coastal/supratidal, **Other**	Arctic area	VU (2015)	AA, EM, T, BU, HID, NSM, ISD, P, CC
Ursus thibetanus	O[8]	**Forest**, Shrubland, Grasslands, Wetlands, Artificial	Eastern Asia	VU (2016)	AA,T,BU,NSM
Tremarctos ornatus	O[9]	**Forest, Shrubland, Grasslands**	South America	VU (2016)	AA, EM, T, BU, CC

[1] O = Omnivory, H = Herbivory, C = Carnivory; [2] Wei et al. 2017; [3] Sethy & Chauhan 2018; [4] Mewada & Dharaiya 2010; [5] Bull et al. 2001; [6] Mowat & Heard 2006 ; [7] Galicia et al. 2021;[8] Koike 2010; [9] Figueroa 2013
[10] Information from the IUCN red list website (https://www.iucnredlist.org/), main features **in bold**.
[11] AA = Agriculture and Aquaculture, BU = Biological resource use, CC = Climate change, EM = Energy production and mining, GE = Geological event, HID = Human intrusions and disturbance, ISD = Invasive species and disease, NSM = Natural system modification, P = Pollution, RC = Residential and commercial development, T = Transportation and service corridors

To assess the pivotal role of bears in ecosystems through trophic and non-trophic interactions with other guilds, we adopted and transposed the Wilby et al. (2001) framework for herbivores to omnivores. This allows interactions with abiotic and biotic environments to be classified on a gradient from 'pure trophic' (e.g. predation) to 'pure engineer' (e.g. ground daybed). Some interactions are between the two, caused by omnivory but resulting in engineering (e.g. endozoochory) (**Table II.2**). These interactions are identified as "Intrinsic omnivory", "Unassociated engineering" and

"Associated engineering" respectively. Non-trophic interactions, which can be a form of engineering, are also presented in one of the two engineering sections.

Table II.2: Interaction category, definition, type and effects for omnivore species based on Wilby et al. (2001).

Interaction category	Definition	Interaction type	Interaction effects
Intrinsic effects of omnivory	Removal of plant tissue, animal production and animal predation	Direct trophic	Reduce plant fitness, animal fitness or induce mortality (e.g. predation)
		Indirect trophic	Reduce competitive ability, insect colony structure or population recruitment (e.g. fruit predation)
Associated ecosystem engineering effects	*Intimately connected but not part of* the omnivory process	Physical engineering	Alter substrate structure or plant organisms during foraging (e.g. debarking)
		Transport engineering	Disperse materials or propagules after feeding (e.g. endozoochory)
Unassociated ecosystem engineering effects	*Not directly connected* to the omnivory process	Physical engineering	Alter substrate structure or plant organisms during non-foraging sequence (e.g. daybed)
		Transport engineering	Disperse materials or propagules during non-foraging sequence (e.g. epizoochory)

II.4.2 Literature analysis

II.4.2.1 Eligibility criteria

We searched the "Web of Science -WOS- core collection" (Feb.1st, 2023) for all potential references (articles, books, reports including literature reviews, meta-analyses and case studies) in English, using key-words related to the framework interactions (see **Table II.3** for equation research results). We excluded predation on livestock. References obtained from equations in unfamiliar languages (e.g. Croatian) have been translated using DeepL.com, inducing potential minor bias in the understanding. We kept reports that describe interactions quantitatively (e.g. prey mortality percentage through predation) because we considered them as more informative than qualitative reports (e.g. bears predate ungulates). However, some well-described qualitative reports were included in the review

when few evidence existed and if the interaction was of interest at the ecosystem scale (e.g. soil excavation following small mammal predation).

Table II.3: Research equation used to collect articles on omnivorous Ursids.

Interaction category[1]	Topic	Research equation[2]	#of articles
Intrinsic effects of omnivory	Scavenging	(carcass* OR scaveng* OR flies OR decomposer* OR detrivior*)	246
	Kleptoparasitism	("Kleptoparasitism*")	11
	Predation	("Calv*" OR "Calf" OR "Ungulate" OR "Fawn*" OR "Deer" OR "Muskoxen" OR "Reindeer" OR "Moose" OR "Cervid*" OR "Predat*" OR "Mammal*") NOT ("Human*" OR "Livestock*")	1670
	Interactions between/among bears and other carnivores	(Interspecific OR intraspecific) AND ("Carnivor*" OR "Predator*")	84
	Mycophagy	("myco*" OR "Fung*" OR "Mushroom*")	46
	Herbivory	("herbivor*" OR “frugivor*”)	71
	Insectivory	("Ants" OR “Ant” OR "Bee" OR “Bees” OR "Hymeno*" OR "Insect*") AND ("Feed*" OR "eat*" OR “consump*”)	42
Associated ecosystem engineering effects	Insectivory	("Ants" OR “Ant” OR "Bee" OR “Bees” OR "Hymeno*" OR "Insect*") AND ("Feed*" OR "eat*" OR “consump*”)	417
	Herbivory	("herbivor*" OR “frugivor*”)	58
	Seed and mycorrhizal dispersal	("Seed dispersal" OR "dispersal" OR “Endozooch*”)	71
	Damage to trees	(tree OR shrub) AND (damage* OR enginner* OR wound*)	46
Non-associated ecosystem engineering effects	Seed and mycorrhizal dispersal	("Seed dispersal" OR "dispersal" OR “Ectozooch*” OR “Epizooch*”)	417
	Damage to trees	(tree OR shrub) AND (damage* OR enginner* OR wound*)	58

[1] Each topic refers *a priori* to one or more types of interaction described in Wilby et al (2001)

[2] In each research equation, we added: [TOPIC research equation] AND ("Ursus americanus" OR "Ursus arctos" OR "Ursus thibetanus" OR "Ursus spelaeus" OR "Helarctos" OR "Tremarctos" OR "Black bear*" OR "Asiatic black bear*" OR "Brown bear*" OR "Sun bear*" OR "Spectacled bear*" OR "Andean bear" OR "Ursid*" OR "Sloth bear*" OR "Melursus") NOT "Ailuropoda" NOT "Ursus maritimus"

II.4.2.2 Data collection

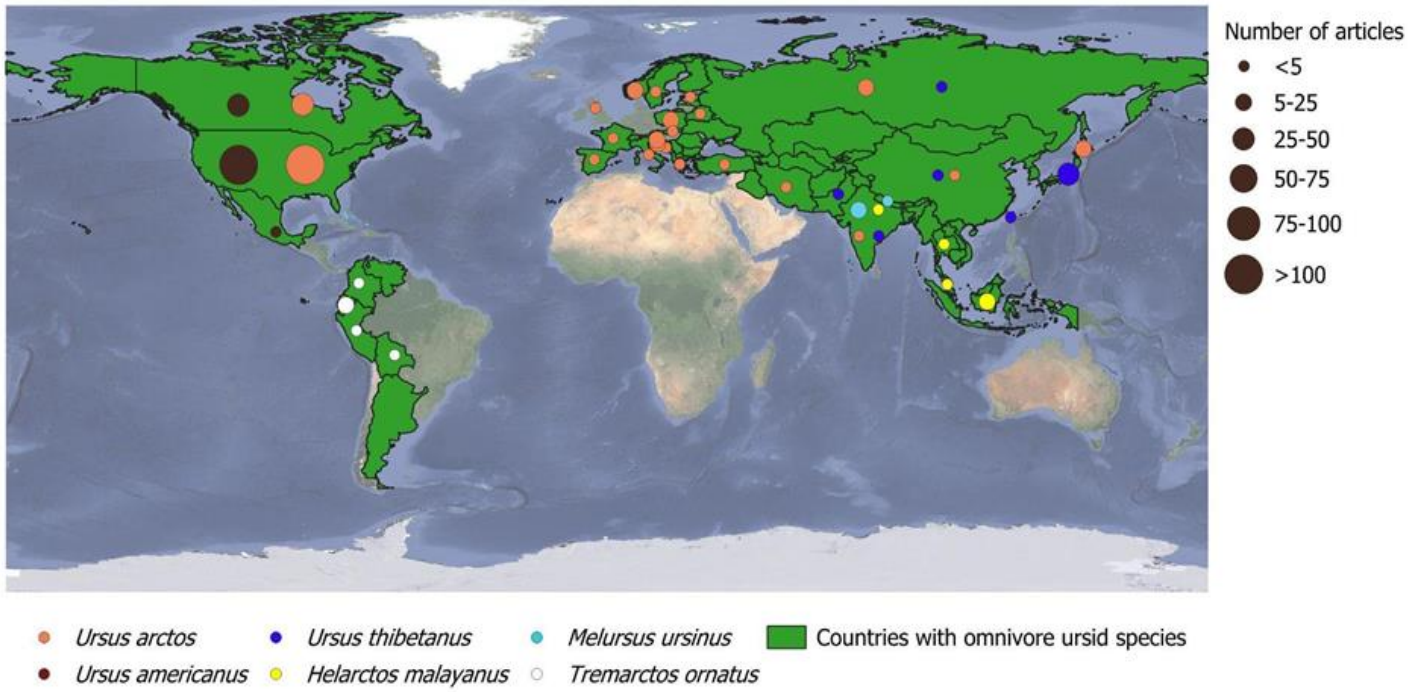

Figure II.1: Global distribution of literature collected on omnivorous ursids. In green the countries with omnivore ursid based on IUCN. The number of studies (according to the dot size) by country are reported for *Ursus arctos* (orange); *Ursus americanus* (black); *Ursus thibetanus* (blue); *Helarctos malayanus* (yellow); *Melursus ursinus* (sky blue) and *Tremarctos ornatus* (white).

We extracted 3,237 references from research equations representing 2,420 after removing duplicates. Based on title and abstract analysis, we excluded 1,766 articles irrelevant to our subject and at least 244 more after full reading. We also included relevant articles that were not initially retrieved from our WOS search (in our database). For each reference selected, we recorded bear species, type of interaction and country of the study. We ended up with 411 relevant references (Flow chart in Appendix II.S1), including 211 unique references for *Ursus arctos (Uar)*, 156 *Ursus americanus (Uam)*, 47 *Ursus thibetanus (Uth)*, 11 *Helarctos malayanus (Hma)*, 9 *Melursus ursinus (Mur)* and 13 *Tremarctos ornatus (Tor)* (**Fig. II.1** for studies repartition and **Fig. II.2** for the number of references per species and interactions, see Appendix II.S2 for study location per species). We focused our review on three bear species with >30 references in our database (*Uar*, *Uam* and *Uth*) providing a

credible insight into possible interactions. Interactions from other bear species (*Hma, Mur, Tor*) are also discussed.

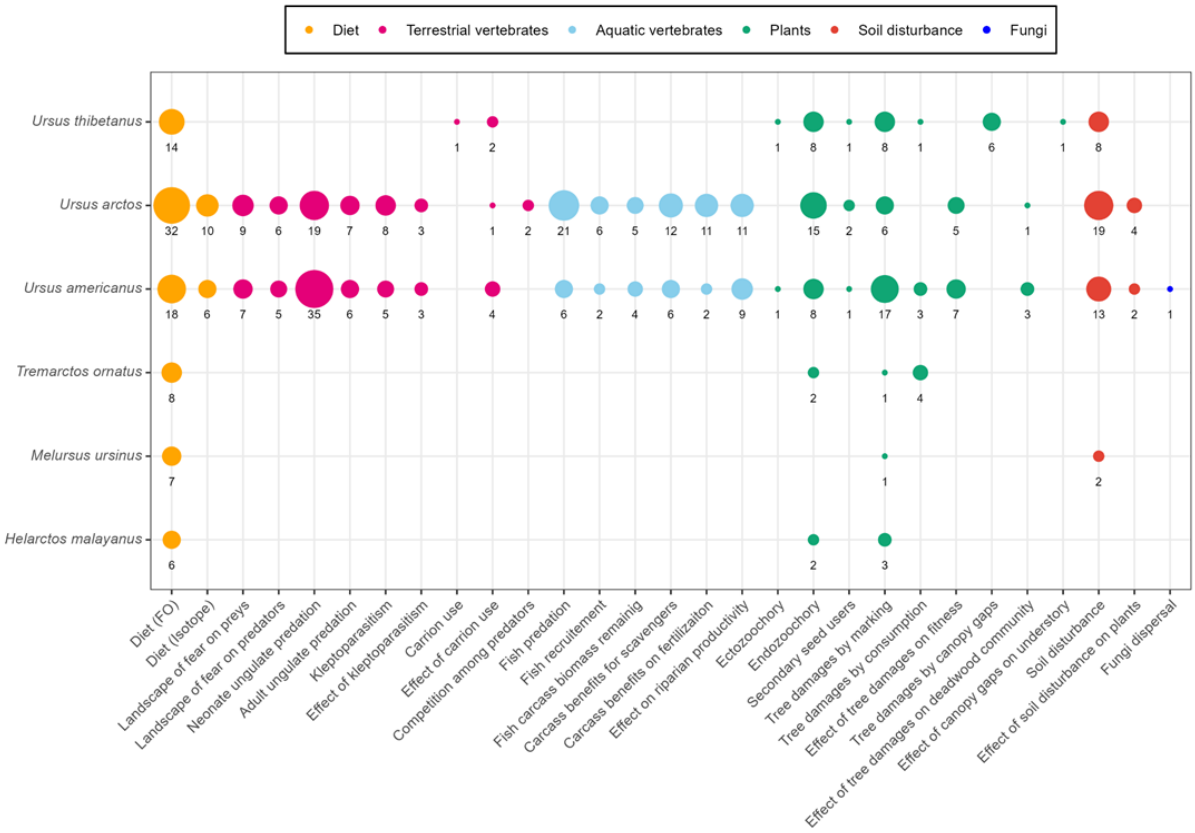

Figure II.2: Matrix diagram of the number of references treating an interaction (x axis) per bear species (y axis), whether it is a trophic interaction (Diet) or an engineer associated with an ecosystem compartment (Aquatic or terrestrial vertebrates, plants, fungi or soil). The diet is documented using FO (frequency of occurrence) or isotope based studies.

II.4.2.3 Interaction map design

For focused bears, we designed a concept map of interactions (**Fig. II.3**,.**5**,.**8**) based on the type of interaction from our adapted Wilby et al. (2001) framework. Each type of interaction was compartmentalised by food types: plants, invertebrates, aquatic vertebrates, terrestrial vertebrates, fungi. Interaction category was colour-coded according to our framework (**Table II.4**) and associated with a range of numeric values of a relevant metric. For interactions reported with different metrics or insufficiently represented, we only cited a relevant pool of articles without further details in the

map. Interactions not quantified were considered undetermined. The interaction map provides a synthetic overview of the main interactions that the focused omnivore species has with other organisms, while facilitating comparison among omnivore species. We did not perform bias analysis but we supposed in particular the presence of reporting bias on these emblematic species. A meta-analysis was not performed due to the multiple interaction and metrics heterogeneity.

Table II.4: Interaction category, definition, type and effects according to Wilby et al. (2001).

Interaction category	Definition	Interaction type	Interaction effects
Intrinsic effects of omnivory	Removal of plant tissue, animal production and animal predation	Direct trophic	Reduce plant fitness, animal fitness or induce mortality (e.g. predation)
		Indirect trophic	Reduce competitive ability, insect colony structure or population recruitment (e.g. fruit predation)
Associated ecosystem engineering effects	*Intimately connected but not part of* the omnivory process	Physical engineering	Alter substrate structure or plant organisms during foraging (e.g. debarking)
		Transport engineering	Disperse materials or propagules after feeding (e.g. endozoochory)
Unassociated ecosystem engineering effects	*Not directly connected* to the omnivory process	Physical engineering	Alter substrate structure or plant organisms during non-foraging sequence (e.g. daybed)
		Transport engineering	Disperse materials or propagules during non-foraging sequence (e.g. epizoochory)

II.5 Results

II.5.1 Ursus thibetanus

Based on the *Uth* references, we were able to highlight an important variety of interactions of varying intensities collected from different sites and studies, compiled in a concept map (**Fig. II.3**, see Appendix II.S3 for details) and detailed below.

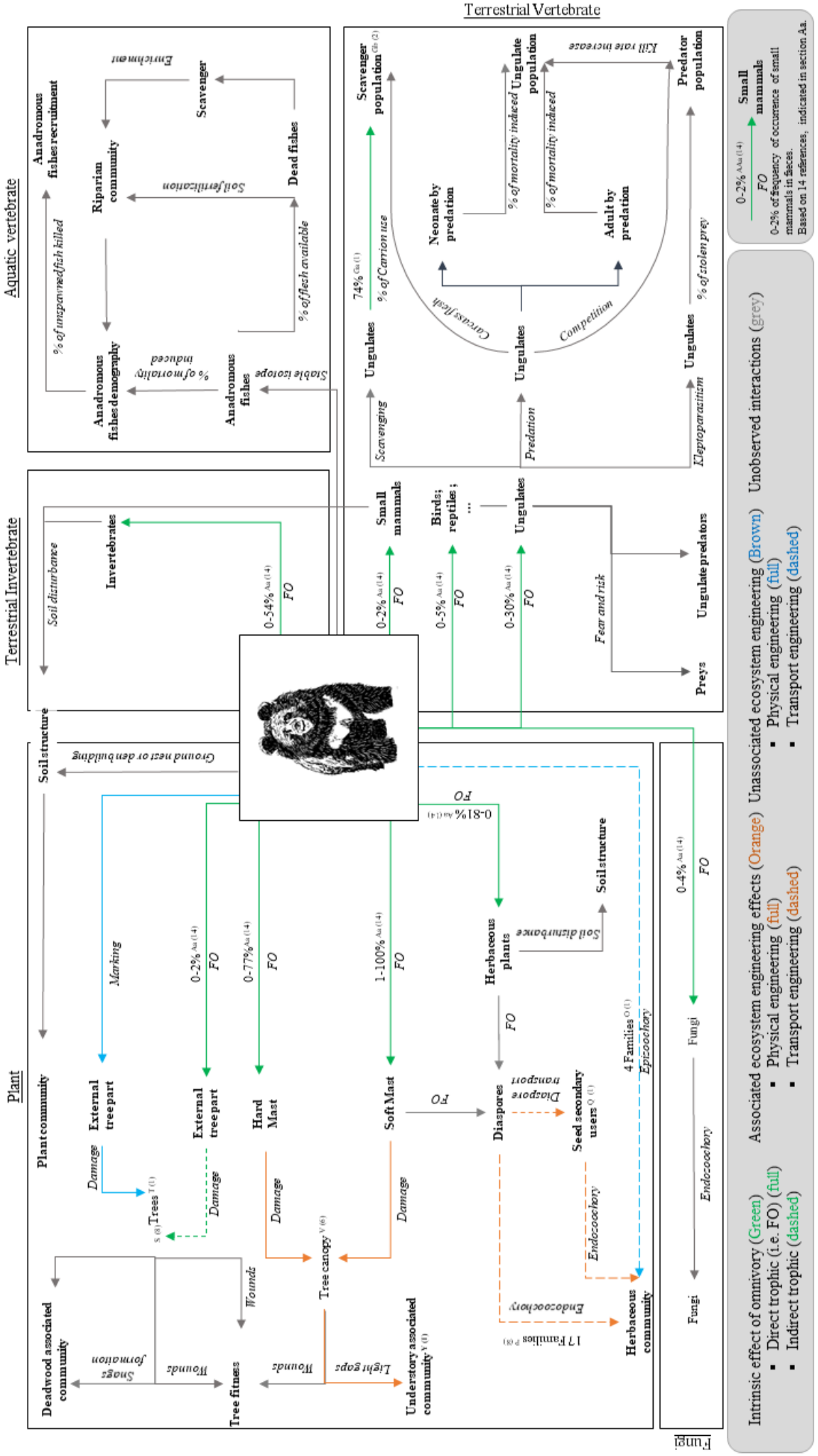
Aquatic vertebrate
Terrestrial Vertebrate
Terrestrial Invertebrate
Plant
Fungi
Anadromous fishes recruitment
Scavenger
Enrichment
Riparian community
Soil fertilization
Dead fishes
% of unspawned fish killed
% of flesh available
Anadromous fishes demography
% of mortality induced
Anadromous fishes
Stable isotope
Scavenger population
74% Ca (1)
% of Carrion use
Ungulates
Scavenging
Carcass flesh
Neonate by predation
% of mortality induced
Ungulate population
Kill rate increase
Predator population
Competition
Adult by predation
% of mortality induced
% of stolen prey
Kleptoparasitism
Ungulates
Predation
Small mammals
Birds; reptiles; ...
Ungulates
0-2% Aa (14)
FO
0-5% Aa (14)
FO
0-30% Aa (14)
FO
Fear and risk
Ungulate predators
Preys
Soil disturbance
Invertebrates
0-54% Aa (14)
FO
Soil structure
Ground nest or den building
Marking
External tree part
Damage
Trees S (8) T (1)
0-2% Aa (14)
FO
External tree part
Damage
0-77% Aa (14)
FO
Hard Mast
Damage
1-100% Aa (14)
FO
Soft Mast
Damage
0-81% Aa (14)
FO
Herbaceous plants
Soil disturbance
Soil structure
FO
Diaspores
Diaspore transport
Seed secondary users O (1)
Endozoochory
4 Families O (1)
Epizoochory
Endozoochory
17 Families P (8)
Herbaceous community
Plant community
Deadwood associated community
Snags formation
Wounds
Tree fitness
Wounds
Tree canopy V (6)
Wounds
Light gaps
Understory associated community V (1)
0-4% Aa (14)
FO
Fungi
Endozoochory
Fungi
0-2% Aa (14)
FO
Small mammals
0-2% of frequency of occurence of small mammals in faeces.
Based on 14 references, indicated in section Aa.
Intrinsic effect of omnivory (Green)
Direct trophic (i.e. FO) (full)
Indirect trophic (dashed)
Associated ecosystem engineering effects (Orange)
Physical engineering (full)
Transport engineering (dashed)
Unassociated ecosystem engineering (Brown)
Physical engineering (full)
Transport engineering (dashed)
Unobserved interactions (grey)

Figure. II.3: Concept map of trophic and non-trophic interactions triggered by *Ursus thibetanus*. In green the direct (full) and indirect (dashed) intrinsic effect of omnivory. In orange the physical (full) and transport (dashed) engineering associated with omnivory. In blue the physical (full) and transport (dashed) engineering associated with omnivory. On arrows, the value (on top of the arrow) and the metrics (on bottom of the arrow) are reported, with the number of studies by superscript. For some interaction only a pool of studies are reported. See Appendix II.S3 for references of each interactions (symbolised by letters).

II.5.1.1 Intrinsic effects of omnivory

Depending on the season and location, *Uth* has a flexible diet (**Fig. II.4**, see appendix II.S3 for details) dominated by plants, insects or vertebrates, while fungi are rather uncommon and fish not documented in our review. Plants are the most frequent items in the diet with herbs, soft and hard masts, consumed mostly in spring, summer and fall respectively. To obtain masts, *Uth* climbs trees, breaking their branches, with potential effects on tree fitness (Takahashi and Takahashi, 2013). While foraging, *Uth* also drops fruits to the ground, making them available to other consumers (Kolchin, 2017). Similarly, it gleans fruits left by tree langurs (*Semnopithecus schistaceus* Hodgson 1840), a common prey of *Uth* (Nautiyal and Huffman, 2018). *Uth* may consume cambium and xylem, wounding trees.

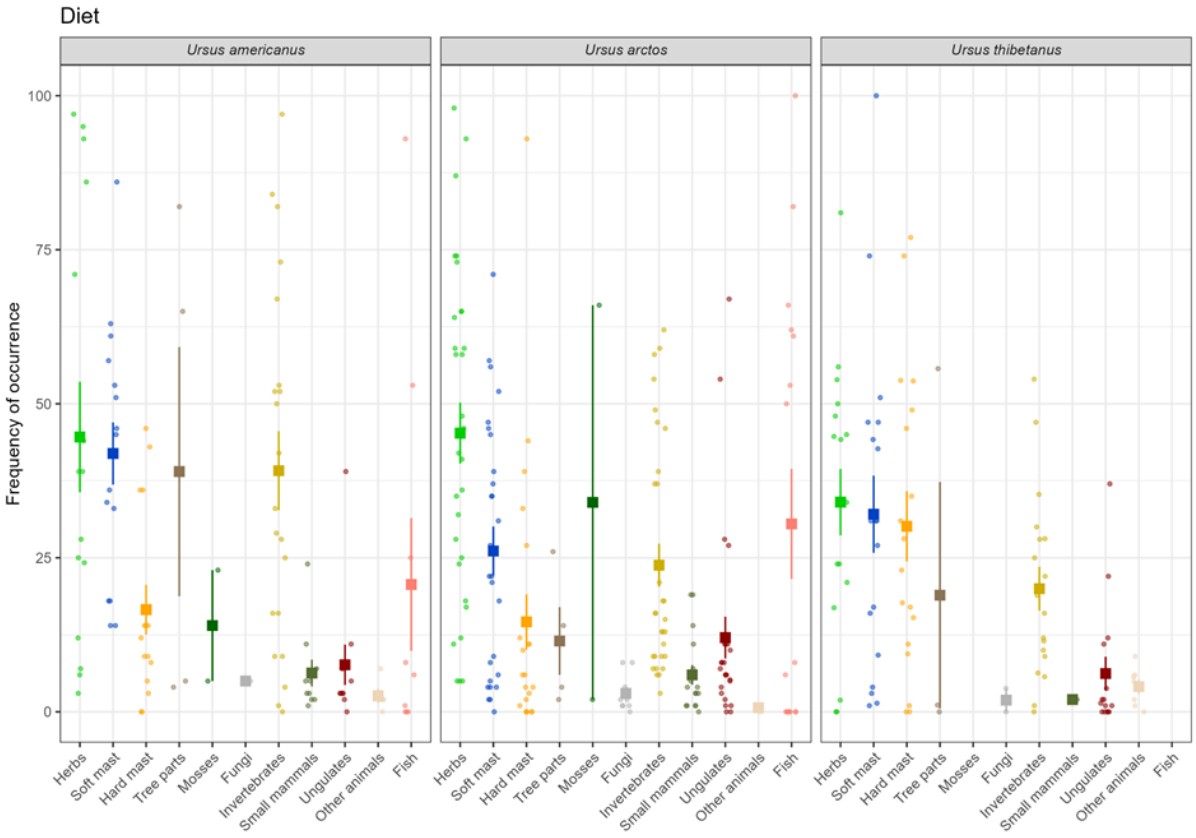

Figure II.4: Annual value of the frequency of occurrence of different groups of food items in the diet of *Ursus thibetanus*, *Ursus arctos*, *Ursus americanus*. The values of Fish are obtained from stable isotope approaches and correspond to the part in percentage of the diet composed of fish. A point corresponds to the minimum or maximum observed per study or site, and the square and the bar correspond to the mean and standard error.

Secondarily, *Uth* feeds upon invertebrates (**Fig. II.4**), particularly on colonial hymenoptera (Fujiwara et al., 2013). *Uth* can spend hours per day feeding on ants(Yamazaki et al., 2012), probably affecting hymenopteran population dynamics.

Terrestrial vertebrates are a rich resource that can be found frequently in faeces (**Fig. II.4**), but little is known on *Uth* effect on prey population dynamics. Conversely, adult ungulates may outcompete *Uth* for plant resources (Koike et al., 2013). As an alternative for vertebrate consumption, *Uth* also scavenges carcasses (**Fig. II.4**). On carcasses, *Uth* is dominant and excludes other scavengers through

interference or fear, while providing similar ecosystem service as usual scavengers (Inagaki et al., 2022, 2020), in some sites may also cache carcasses (Allen et al., 2021b).

II.5.1.2 Associated engineering effects

When foraging in trees, *Uth* creates small canopy gaps by breaking branches. Such engineering allows light to reach understory vegetation, improving fleshy-fruit production and availability to other consumers (Takahashi et al., 2015).

Though mastication destroys hard masts, *Uth* can disperse seeds from many plants, at least 17 families (**Fig. II.3**, see Appendix II.S3) through endozoochory. It is an effective seed disperser thanks to long gut retention time, substantial displacement and a high number of seeds released in adequate sites (Tochigi et al., 2022). However, (Nagamitsu et al., 2019) indicate that a prolonged absence of *Uth* had no effect on the spatial genetic structure of a formerly dispersed tree species, an effect probably mitigated by other factors. *Uth* also disperses plants across altitudinal zonations (Naoe et al., 2019). Furthermore, abundant seeds in faeces can also benefit other seed users (Koike et al., 2012).

Bark feeding causes important damage to conifers and economic losses to forestry (Watanabe, 1980), but may initiate the process of deadwood production. When foraging for colonial insects, *Uth* focuses mostly on accessible nests, and rarely digs (Yamazaki et al., 2012), probably inducing small soil disturbance, even if other study reports excavation activity (Hwang et al., 2002).

II.5.1.3 Unassociated engineering effects

Uth also damages trees by marking (Ogawa et al., 2020), climbing them for shelter (Steinmetz et al., 2011) or building platforms (*Kuma-dama* in Japanese) using broken branches (Takahashi and Takahashi, 2013). Hwang et al. (2002) highlighted the presence of daybeds on the

ground (≤1.3m in diameter) composed of broken branches, crushed and twisted grass. During hibernation, *Uth* prefers natural sites (e.g. tree hollows, pits under tree roots, Yamazaki, 2009) rather than building dens.

Thanks to his fur, it has been reported that *Uth* can transport many seeds, making it an important epizoochorous vector within the community (Kitamura and Terashima, 2020).

II.5.2 Ursus arctos

Based on the *Uar* references, we were able to highlight the widest variety of interactions described within Ursidae, collected from different sites and studies, compiled in a concept map (**Fig. II.5**, see Appendix II.S3 for references and details) and detailed below.

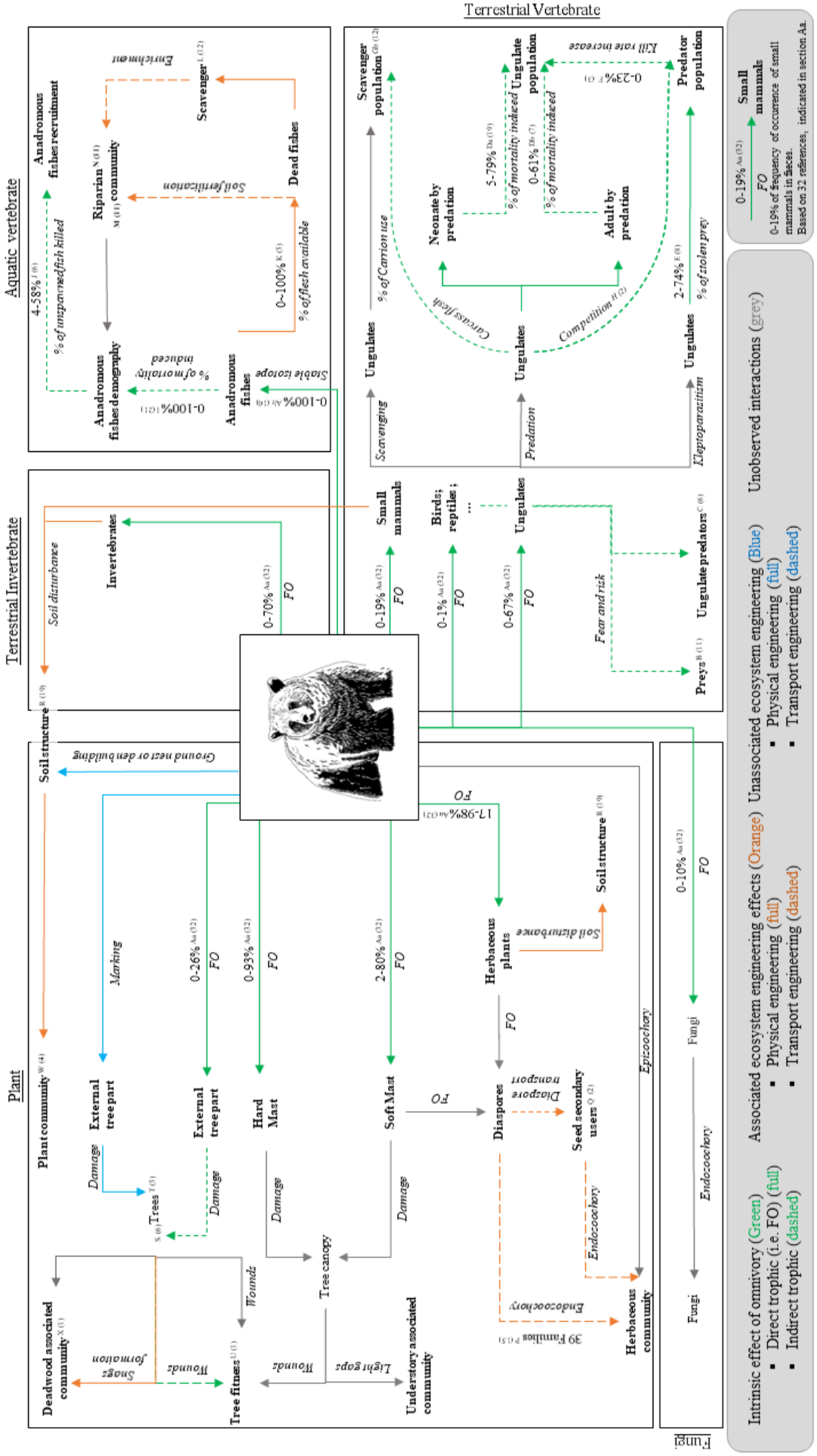
Terrestrial Vertebrate
Aquatic vertebrate
Terrestrial Invertebrate
Plant
Fungi
Scavenger population
Ungulate population
Predator population
Kill rate increase
0-23%
Neonate by predation
Adult by predation
5-79%
% of mortality induced
0-61%
% of mortality induced
% of Carrion use
Carcass flesh
Competition
2-74%
% of stolen prey
Scavenging
Predation
Kleptoparasitism
Ungulates
Anadromous fishes recruitment
Enrichment
Scavenger
Riparian community
Soil fertilization
Dead fishes
4-58%
% of unspawned fish killed
0-100%
% of flesh available
Anadromous fishes demography
% of mortality induced
Anadromous fishes
Stable isotope
0-100%
Small mammals
0-19%
FO
0-19% of frequency of occurrence of small mammals in faeces.
Based on 32 references, indicated in section Aa.
Soil disturbance
Invertebrates
Soil structure
Ground nest or den building
0-70%
FO
Small mammals
Birds; reptiles; ...
Ungulates
0-19%
0-1%
0-67%
Fear and risk
Ungulate predators
Preys
Marking
External tree part
Damage
Trees
External tree part
0-26%
0-93%
Hard Mast
2-80%
Soft Mast
17-98%
FO
Herbaceous plants
Soil disturbance
Soil structure
Diaspores
Diaspore transport
Seed secondary users
Endozoochory
39 Families
Epizoochory
0-10%
Fungi
Endozoochory
Plant community
Deadwood associated community
Tree fitness
Snags formation
Wounds
Tree canopy
Light gaps
Understory associated community
Herbaceous community
Intrinsic effect of omnivory (Green)
Direct trophic (i.e. FO) (full)
Indirect trophic (dashed)
Associated ecosystem engineering effects (Orange)
Physical engineering (full)
Transport engineering (dashed)
Unassociated ecosystem engineering (Blue)
Physical engineering (full)
Transport engineering (dashed)
Unobserved interactions (grey)

Figure II.5: Concept map of trophic and non-trophic interactions triggered by *Ursus arctos*. In green the direct (full) and indirect (dashed) intrinsic effect of omnivory. In orange the physical (full) and transport (dashed) engineering associated with omnivory. In blue the physical (full) and transport (dashed) engineering associated with omnivory. On arrows, the value (on top of the arrow) and the metrics (on bottom of the arrow) are reported, with the number of studies by superscript. For some interaction only a pool of studies are reported. See Appendix II.S3 for references of each interaction (symbolised by letters).

II.5.2.1 Intrinsic effects of omnivory

Uar has been extensively studied throughout its distribution, highlighting its diet variability. Depending on population, the main food type consumed annually can be from plants, terrestrial animals or anadromous fish (**Fig. II.4**, see Appendix II.S3 for references and details). Among the plants, hard mast dominates the diet in temperate regions, soft mast in boreal regions and vegetative parts in tundra (Bojarska and Selva, 2012). Hard and soft masts are key energetic resources during hyperphagia or after hibernation (e.g.MacHutchon and Wellwood, 2003; Naves et al., 2006). In absence of fruits, *Uar* consumes less nutritive forbs and grasses (Rode et al., 2001), cambium and sap that causes damage to trees and exposes them to decomposers (Zyśk-Gorczyńska et al., 2015). Similarly, root (e.g. MacHutchon and Wellwood, 2003) or bulb consumption (Tardiff and Stanford, 1998) may severely affect plants. Occasionally, *Uar* consumes fungi (**Fig. II.4**).

Across its range, the proportion of terrestrial vertebrates in *Uar* faeces varies from 0 to 67% (**Fig. II.4**). Similarly to other bears, the main meat comes from neonate ungulates, though some authors report high predation cases on adult ungulates (**Fig. II.6**). *Uar* is thus an important factor of neonates mortality (Fig 6), outstripping other predators in most cases (e.g. Griffin et al., 2011). It thus limits ungulate recruitment, as confirmed in an exclusion experiment (Senchik et al., 2019). Such predation may also alter prey behaviour in some sites through the landscape of fear (**Fig. II.5**). Overall, *Uar* predation upon ungulates can lead to cascading effects on the ecosystem with potential benefit to many species (Berger et al., 2001).

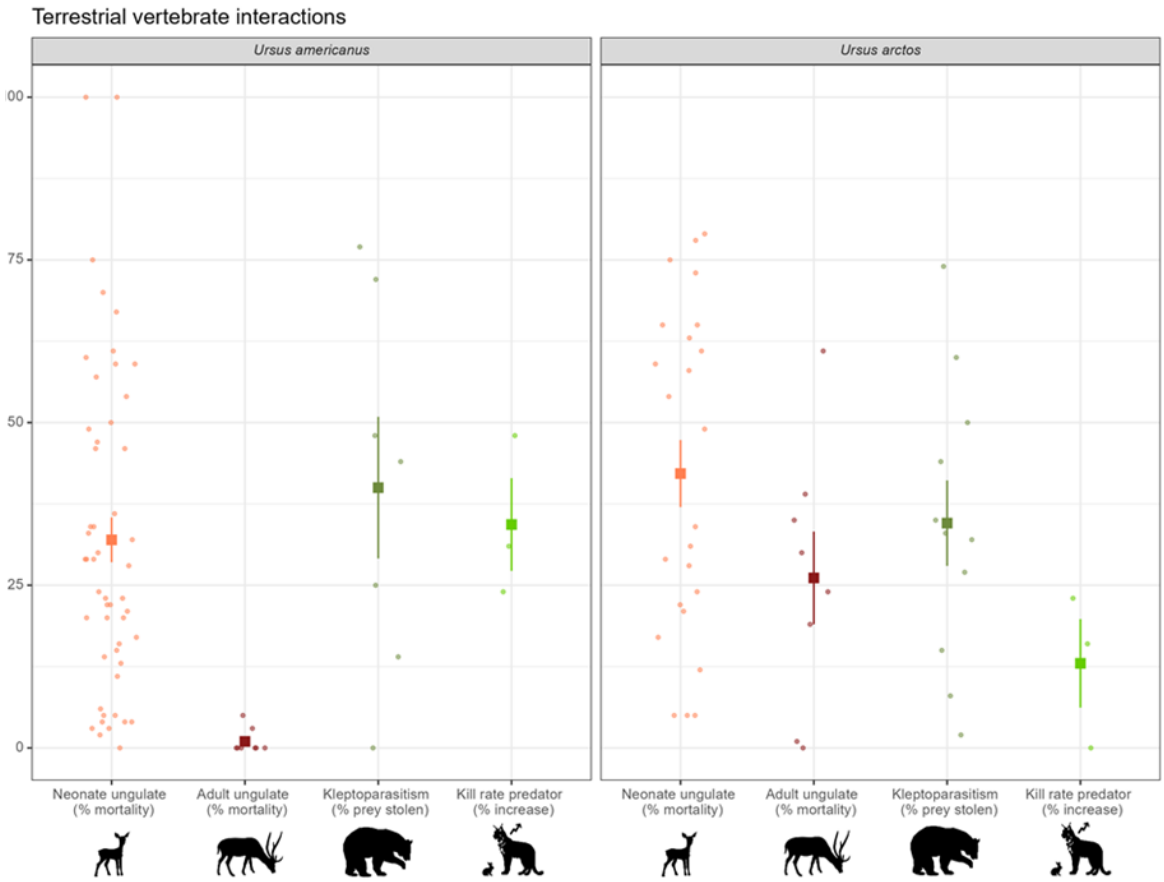

Figure II.6: Predation by *Ursus arctos* and *Ursus americanus* on newborn ungulates (% of mortality induced) and adult ungulates (% of mortality induced). Also shown is the percentage of kleptoparasitism on predators (% of prey stolen by bears) and the increase in predation rates by predators following the theft. A point corresponds to the minimum or maximum observed per study or site, and the square and the bar correspond to the mean and standard error. The silhouettes were obtained freely on Canva.

Among predators consuming ungulates, *Uar* is a dominant competitor. Studies in Scandinavia show that *Uar* induced changes in Grey Wolf (*Canis lupus* L. 1758) habitat use (Sanz-Pérez et al., 2018). *Uar* can steal preys killed by Wolf (Ordiz et al., 2020), Puma (*Puma concolor* L. 1771), (Elbroch and Kusler, 2018) or Lynx (*Lynx lynx* L. 1758) (Krofel et al., 2012), thus reducing the biomass and energy available to them (Krofel et al., 2012). In response predators maye increase their kill rate (**Fig. II.6**), also Lynx may rather focus on rodents (Krofel et al., 2012) whereas Wolf can alter its predation strategy (Tallian et al., 2017). Scavenging in general can thus be an important way of feeding, up to 70% of the terrestrial vertebrates consumed (e.g. Boertje et al., 1988). For instance, *Uar* scavenging

activity may slightly contribute to the carcasses consumption within the ecosystem (Mateo-Tomás et al., 2017) or contribute substantially elsewhere (Krofel et al., 2012). In the latter case, *Uar* excludes subordinate scavengers while leaving little biomass (Krofel et al., 2012). Within its range, studies showed that *Uar* can also cache carcasses to prevent other scavengers from eating it (Allen et al., 2021b).

Uar also predates small terrestrial mammals, especially those living in burrows (MacHutchon and Wellwood, 2003). In its northern range, ground squirrels can be important resources during the pre-dormancy period. *Uar* pursues or excavates the burrow to catch them (Barker et al., 2015). Opportunistically, *Uar* also predates birds or their eggs, disturbing the nests, which may benefit other predators (Barnas et al., 2022).

In North America (Levi et al., 2020), Russia (Seryodkin et al., 2017a) and Japan (Matsubayashi et al., 2015) the massive return of anadromous fish to their spawning grounds represents a major resource pulse for *Uar* (**Fig. II.4**). It is unequivocally the main predator and non-senescent cause of mortality of those fishes (**Fig. II.7**). It can almost capture an entire salmon run, particularly in small, shallow and isolated streams (Quinn et al., 2017). A significant proportion of the salmon killed may not have spawned yet (**Fig. II.7**), affecting salmon recruitment (Quinn et al., 2014) and behaviour (Bentley et al., 2014). Others suggest that the proportion of unspawned salmon predated is negligible compared to other factors that affect recruitment (Van Daele et al., 2013). Furthermore, *Uar* can be a selective force by catching the more catchable larger fish (Quinn et al., 2001), especially in small streams (Andersson and Reynolds, 2017). *Uar* wastes flesh when fish are abundant (Andersson and Reynolds, 2018), leaving important remains (**Fig. II.7**) to aquatic communities when carcasses are released in streams (Hilderbrand et al., 2004). Also, *Uar* occasionally consumes freshwater fish (Sidorovich, 2006) aquatic mammals (Monson et al., 2022) and bivalves (Smith and Partridge, 2004).

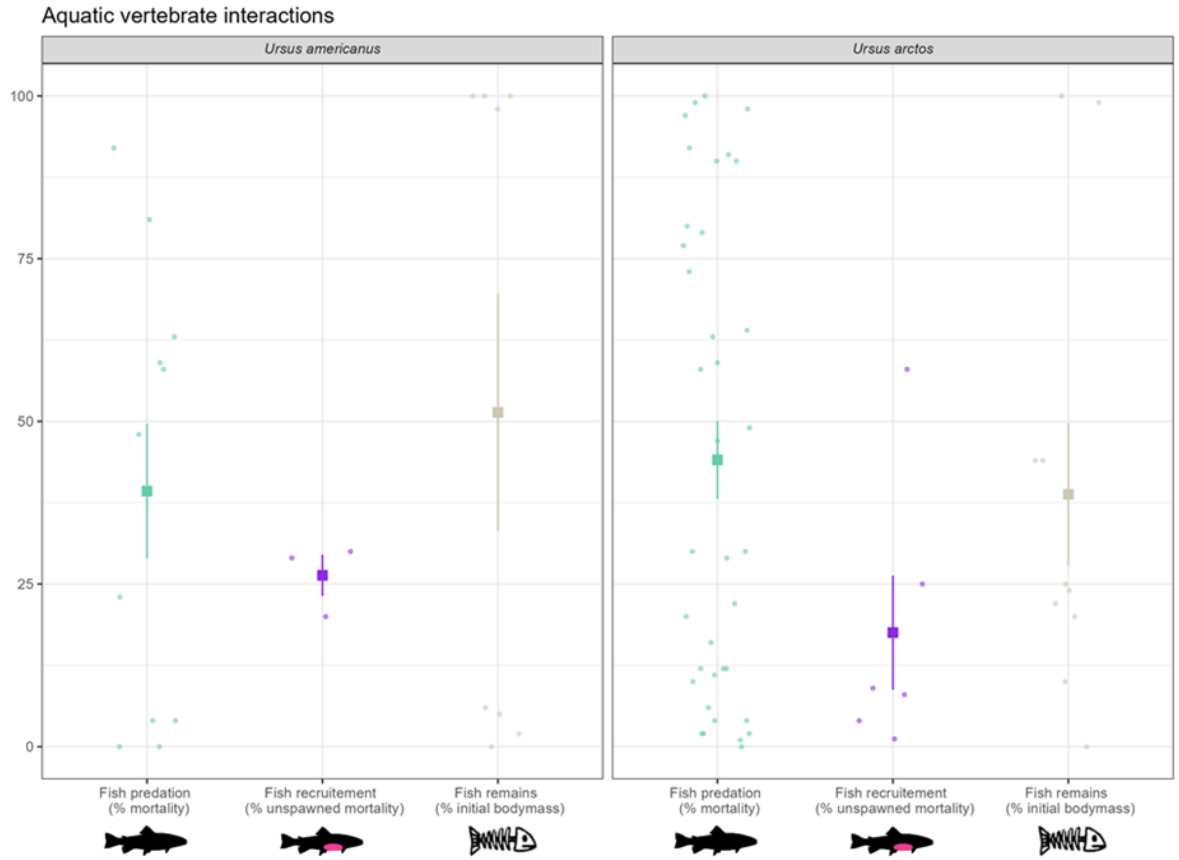

Figure II.7: Predation by *Ursus arctos* and *Ursus americanus* on anadromous salmons (% of mortality induced) and on unspawned salmons (% of unspawned fish killed). At the right, it represents the percentage of body mass left by both bears. A point corresponds to the minimum or maximum observed per study or site, and the square and the bar correspond to the mean and standard error. The silhouettes were obtained freely on Canva.

Invertebrates are an alternative source of proteins (Costello et al., 2016), sometimes constituting a substantial part of the *Uar* diet (**Fig. II.4**). Most of them are colonial hymenoptera such as ants (e.g. Dahle et al., 1998) though other groups can be consumed frequently (García-Rodríguez et al., 2021b). Ant availability relative to other resources and environmental factors probably trigger myrmecophagy and may explain why ants are more important food in Eurasia than America (Bojarska and Selva, 2012; Swenson et al., 1999). *Uar* usually selects nutritive and defenceless ant species and can destroy or disturb many nests (Swenson et al., 1999), which may affect ant population dynamics when most of the mounds are destroyed or disturbed. Other invertebrates are consumed opportunistically: earthworms (Mattson et al., 2002) and midges (Gunther et al., 2018) in Wyoming, army cutworms

(*Euxoa auxiliaris* Grote 1873) in Montana (White et al., 1998) or cicada nymphs (*Lyristes bihamatus* Motschulsky, 1861) in Japan (Tomita and Hiura, 2020).

II.5.2.2 Associated engineering effects

To access roots, bulbs, small mammals or insects, *Uar* excavates soil patches (Butler, 1992). Tardiff and Stanford, (1998) demonstrated that foraging for lily bulbs (*Erythronium grandiflorum* Pursh 1813) in open meadows creates richer nutrient patches than elsewhere. Conversely, in forest, (Tomita and Hiura, 2022) found a negative effect on nutrients and water availability when *Uar* digs for cicada nymphs. *Uar* digs much deeper when foraging for ground squirrels than for plant components (Butler, 1992). In Alaska, Doak and Loso (2003) showed that deeper digging creates microsites more favourable to plants than undisturbed sites. Such evidence suggests that excavation for nut caches (Kendall, 1983), army cutworms, earthworms or ants may induce similar effects.

Uar strips large bark portions for sap and cambium, creating wounds that jeopardise tree survival but initiate wood decay (Seryodkin et al., 2017b), which favor habitat and resources for saproxylophagous organisms (Zyśk-Gorczyńska et al., 2015).

Consumption of fleshy fruits but also dry fruits (intentionally or not) by *Uar* induces dispersal of a significant seed pool through landscapes from at least 39 families (**Fig. II.5**, Appendix II.S3). It is confirmed by both seed count (Lalleroni et al., 2017) and germination experiment (Karimi et al., 2018) studies. Part of the seeds may benefit from the gut passage with earlier (Steyaert et al., 2019) or higher germination (Nowak and Crone, 2012) and also from the fertile deposits (Traveset et al., 2001). The gut passage is quite long allowing long-distance dispersal (Lalleroni et al., 2017). Within the community, *Uar* appears as a unique vector by often moving singular (Karimi et al., 2018) and huge (García-Rodríguez and Selva, 2021) seed pools. This high seed concentration may reduce germination success (García-Rodríguez and Selva, 2021), but faeces visitors (Shakeri et al., 2018) or

precipitation may mitigate this. For rodents, such faeces may represent an energetic banquet with many large seeds available (Shakeri et al., 2018).

In salmon streams, predation by Uar leads to the transfer of large quantities of salmon carcasses from the river to the banks or hundreds of metres away (Quinn et al., 2009). The carcasses leftover can represent over 75% of the initial biomass (**Fig. II.7**). Vertebrates and invertebrates benefit from these carcasses (**Fig. II.5**), with potential cascading effects on other guilds (Christie and Reimchen, 2008) and mutualistic interactions (Lisi and Schindler, 2011) within the ecosystem. Salmons are rich in nitrogen and phosphorus (Gende et al., 2004), and their carcasses contribute to massive soil inputs of marine-derived nutrients (Holtgrieve et al., 2009) along with *Uar* faeces and urine (Hilderbrand et al., 1999). All of this benefits local vegetation, the riparian community and associated dynamics (**Fig. II.5**). Bears appear as the main vectors of salmon nutrient and flesh to terrestrial surroundings in such ecosystems (Levi et al., 2020).

II.5.2.3 Unassociated engineering effects

Uar also damages trees, mainly conifers, through marking (clawing, biting, debarking) reportedly for intraspecific communication (Clapham et al., 2012). Conifers are probably focused for their strong resin odour (Sato et al., 2014 but see González-Bernardo et al., 2021).

Uar rests in daybeds inducing small-scale disturbance in soil and vegetation (Steyaert et al., 2019), which may favour seed germination of dispersed plants (García-Rodríguez and Selva, 2021). For hibernation, *Uar* can use natural cavities or build dens by excavating soil or ant mounds. *Uar* often digs several dens before being satisfied, representing at population level hundreds of m^3/km^2 of soil disturbed prior to hibernating (Butler, 1992).

II.5.3 Ursus americanus

Based on the *Uam* references, this species appears as the second most described Ursidae in terms of ecosystemic interactions. We were able to highlight a wide variety of interactions collected from different sites and studies, compiled in a concept map (**Fig. II.8**, see Appendix II.S3 for references and details) and detailed below.

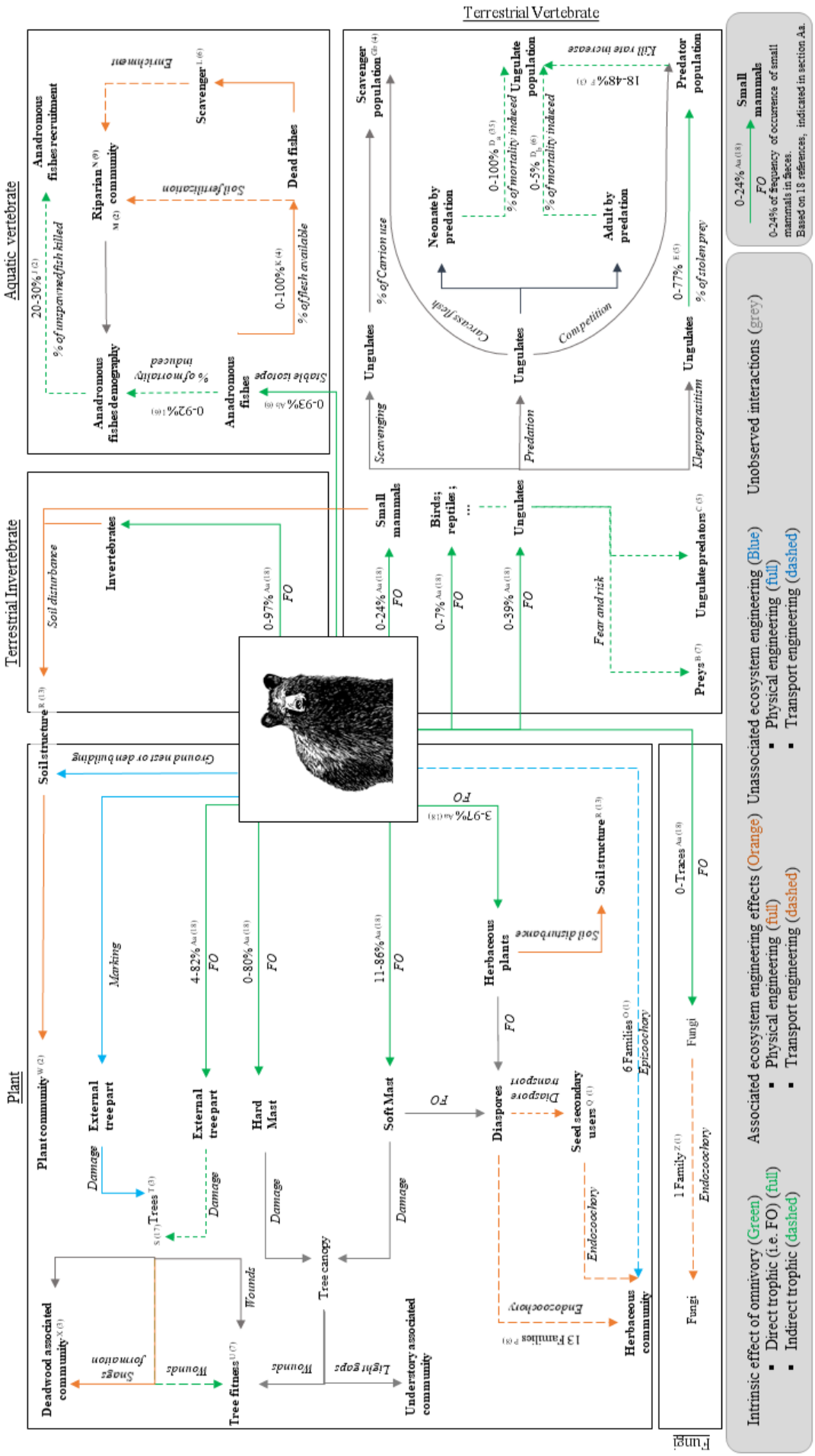
Aquatic vertebrate
Terrestrial Vertebrate
Terrestrial Invertebrate
Plant
Fungi
Anadromous fishes recruitment
Riparian community
Scavenger
Enrichment
Soil fertilization
Dead fishes
20-30%
% of unspawned fish killed
0-100%
% of flesh available
Anadromous fishes demography
0-92%
% of mortality induced
Anadromous fishes
Stable isotope
0-93%
Scavenger population
Predator population
Kill rate increase
18-48%
% of Carrion use
0-100%
% of mortality induced
Ungulate population
0-5%
% of mortality induced
Neonate by predation
Adult by predation
Carcass flesh
Competition
0-77%
% of stolen prey
Ungulates
Scavenging
Predation
Kleptoparasitism
Small mammals
Birds; reptiles; ...
Ungulates
Ungulate predators
Preys
Fear and risk
0-24%
FO
0-7%
FO
0-39%
FO
0-97%
FO
Soil disturbance
Invertebrates
Soil structure
Ground nest or den building
Plant community
External tree part
Damage
Marking
Trees
4-82%
FO
External tree part
Damage
0-80%
FO
Hard Mast
Damage
11-86%
FO
Soft Mast
Damage
3-97%
FO
Herbaceous plants
Soil disturbance
Soil structure
FO
Diaspores
Diaspore transport
Seed secondary users
6 Families
Epizoochory
Endozoochory
13 Families
Endozoochory
Herbaceous community
Tree canopy
Wounds
Deadwood associated community
Snags formation
Wounds
Tree fitness
Wounds
Light gaps
Understory associated community
0-Traces
FO
Fungi
1 Family
Endozoochory
Fungi
0-24%
FO
Small mammals
0-24% of frequency of occurrence of small mammals in faeces.
Based on 18 references, indicated in section Aa.
Intrinsic effect of omnivory (Green)
Direct trophic (i.e. FO) (full)
Indirect trophic (dashed)
Associated ecosystem engineering effects (Orange)
Physical engineering (full)
Transport engineering (dashed)
Unassociated ecosystem engineering (Blue)
Physical engineering (full)
Transport engineering (dashed)
Unobserved interactions (grey)

Figure II.8: Concept map of trophic and non-trophic interactions triggered by *Ursus americanus*. In green the direct (full) and indirect (dashed) intrinsic effect of omnivory. In orange the physical (full) and transport (dashed) engineering associated with omnivory. In blue the physical (full) and transport (dashed) engineering associated with omnivory. On arrows, the value (on top of the arrow) and the metrics (on bottom of the arrow) are reported, with the number of studies by superscript. For some interaction only a pool of studies are reported. See Appendix II.S3 for references of each interaction (symbolised by letters).

II.5.3.1 Intrinsic effects of omnivory

Uam is the most abundant Carnivora species (Ripple et al., 2014b) with a very flexible diet (**Fig. II.4**). Annually, it consumes soft (summer) and hard (fall to early spring) masts (e.g. Benson and Chamberlain, 2006). *Uam* raids rodent caches (Kendall, 1983) or climbs trees for hard mast (Kuhn and Vander Wall, 2007). Herbs are regularly consumed as a sub-optimal but reliable resource when others become scarce (Baldwin and Bender, 2009). During food shortage, *Uam* debarks and damages trees for cambium or sap with tree fitness repercussions (**Fig. II.4**). *Uam* may also ingest mosses (up to 23% of frequency) probably incidentally while feeding (McLaren et al., 2021), and anecdotally fungi (**Fig. II.4**).

A significant proportion of terrestrial meat, especially predated or scavenged ungulates, is included in the diet (**Fig. II.4**). Ungulate predation occurs mostly on neonates making *Uam* a major threat to their survival, but with weak effect on adult mortality (**Fig. II.6**). However, ungulates can also outcompete *Uam* for plant resources (Côté, 2005). In the presence of big cats or wolves, *Uam* remains often a major neonates' predator due to higher population density. Where in sympatry with *Uar*, *Uam* is however easily outcompeted, lowering its predation rate. Nevertheless, *Uam* predation is clearly an additive mortality factor affecting recruitment (Zager and Beecham, 2006), as shown by exclusion treatments (Yarkovich et al., 2011). *Uam* presence may also alter ungulate behaviour, making them more vigilant (Seamans et al., 2016 but see Chamaillé-Jammes et al., 2014) or using safer but less productive sites (Latham et al., 2011). Scavenging on carcasses is also a reliable meat source and

Uam is well-known to kleptoparasite Puma kills. Kleptoparasitism can alter Puma predation behaviour and cause energy loss (Allen et al., 2021a). However, antagonistic interactions with other predators at kill sites are also frequent, and *Uam* can be kleptoparasites by Wolf (Ballard et al., 2003). Whatever, *Uam* may leave few remains available, and may even hide carcasses at the expense of other scavengers (Allen et al., 2021b, 2015).

Uam also consumes small mammals including rodents, racoons or beavers (e.g. McLaren et al., 2021) that can lead to fear and risk perceptions towards *Uam* (Morris, 2005). Occasionally, *Uam* predates birds, bird nests (McLaren et al., 2021) and even the Gopher tortoise (*Gopherus polyphemus* Daudin 1801) (Murphy et al., 2017).

In coastal and riparian areas, *Uam* consumes anadromous fish and benefits from this pulse of resources. *Uam* can be the main salmon mortality cause (**Fig. II.7**) but is clearly outcompeted by *Uar* when co-occurring. Its subordinate position forces *Uam* to consume alternative, less energetic resources (Service et al., 2019). However, *Uam* affects fish recruitment where *Uam* captures vast numbers of fish before spawning (**Fig. II.7**). Moreover, by catching the largest individuals, depending on stream morphology (Andersson and Reynolds, 2017), *Uam* appears to exert a selective force on fish traits (Reimchen, 2000). Then, by discarding carcasses, *Uam* also leaves lots of flesh, benefitting aquatic biota (Reimchen, 2017). Occasionally, algae or aquatic invertebrates complete the Uam diet (e.g. Fox et al., 2015).

Proteins and other nutrients also come from invertebrates, especially colonial hymenoptera. Myrmecophagy in particular seems to occur when or where protein-rich resources are scarce. *Uam* thus consumes large quantities of defenceless ants and partially or totally destroys their nests (Noyce et al., 1997) with potential implications for their dynamics. This regulation can benefit plants in plant-

ant-aphid interactions (Grinath et al., 2015). *Uam* also occasionally consumes dragonflies (Moeller et al., 2017), cicadas (Lundgren et al., 2022), or scorpions (López-González et al., 2009).

II.5.3.2 Associated engineering effects

Uam conifer debarking causes important damage, sometimes entirely girdling the tree. This initiates wood decay, providing resources to saproxylophagous species (**Fig. II.8**). Similar consequences may occur when *Uam* climbs trees and breaks branches to access masts (Kuhn and Vander Wall, 2007). *Uam* disturbs the soil when destroying ant nests in mounds, logs, stumps or under rocks (Noyce et al., 1997). In Arizona, *Uam* foraging on cicada nymphs produces large zones of overturned soil, which may affect local vegetation (Lundgren et al., 2022). *Uam* also digs for roots, cone caches (Kendall 1983) or mammal burrows (Graber and White, 1983) with potential similar effects on vegetation.

Uam disperses many seeds (**Fig. II.8**) over long distances through endozoochory (Willson, 1993) and germination trials show that gut passage of seeds may increase germination rate for some plants (Rogers and Applegate, 1983). Herbaceous seeds are also consumed while grazing (Graber and White, 1983) and probably dispersed, whereas hard mast is destroyed by chewing (Kuhn and Vander Wall, 2007). *Uam* releases large constrained faeces concentrated in seeds, but mitigated by secondary seed users (Enders and Vander Wall, 2012) or precipitation. Cázares and Trappe (1994) suggest that *Uam* mycophagy may help dispersing spores.

Uam moves substantial salmon carcasses up to hundred meters from the stream. Carcasses partially consumed become available to scavengers. Vertebrates and invertebrates rely on these carcasses, depending on where they are deposited (Collins and Baxter, 2014). As for *Uar*, flesh and nutrients' transfer may benefit scavengers, plants and cascades to the whole ecosystem (**Fig. II.8** and see *Uar* section).

II.5.3.3 Unassociated engineering effects

Uam wounds woody plants by marking behaviour (**Fig. II.8**) or building canopy nests (Hwang et al., 2002) with potential implication for tree fitness.

(Cipollini and Cipollini, 2011) noted that *Uam* wallowing in wetlands can severely disturb bulrush (*Scirpus ancistrochaetus* Schuyler) patches. This behaviour may induce the transport of barbed achenes, in line with (Kulbaba, 2004) showing *Uam* fur and body shape favours epizoochory.

Uam hibernates in dens of different types, generally excavated or natural cavities, agglomerated vegetation or brush piles. Usually built in one week, dens are wide, high, deep, often with a tunnel between chamber and outside (Linnell et al., 2000). *Uam* commonly builds more than one den, and the soil disturbance can be substantial. All year long, *Uam* also uses resting sites and day beds (Bard and Cain, 2020).

II.5.4 Lesser-studied bears

Hma is "*one of the least known bear species*" (Sethy and Chauhan, 2018), which feeds mainly on invertebrates, fruits, and sometimes on vertebrates (Augeri, 2005; Fredriksson et al., 2006; Sethy and Chauhan, 2018; Steinmetz et al., 2013; Wong, 2002). Termites are frequently consumed and *Hma* appears to regulate colonies, with repercussions for the ecosystem (Kemmerer and Wong, 2015). *Hma* climbs trees (Sasaki et al., 2005) for fruits and wild bees (Hwang et al., 2021; Ngoprasert et al., 2011; Wong, 2002). *Hma* builds resting nests in the canopy (Padmanaba et al., 2013), sometimes severely wounding trees (e.g. Fredrikkson, 2005) but also benefiting saproxylophagous species (Kemmerer and Wong, 2015). *Hma* also excavates plant parts or soil invertebrates (Sethy and Chauhan, 2018; Wong, 2002) that may induce important soil disturbance. Frugivore, *Hma* also disperses numerous seeds over hectometres (McConkey and Galetti, 1999).

Another Asiatic bear, *Mur,* depends on fruits and invertebrates, but also ungulates for its diet (Joshi et al., 1997; Palei et al., 2020; Rather et al., 2020). *Mur* excavates soil for roots (Laurie and Seidensticker, 1977) and mounds or underground nests to feed on ants and termites (Bargali et al., 2004; Davidar, 1983), which may disturb the soil. Like *Hma*, *Mur* climbs trees for honey and fruits, it also marks and wounds trees through scratching and rubbing (Laurie and Seidensticker, 1977), behaviours that may affect tree fitness. Significant fruit consumption (Akhtar et al., 2004) leads to abundant diaspore transport over long distances (Raju and Jonathan, 2010; Sreekumar and Balakrishnan, 2002).

Little evidence exists on the South-American *Tor* (e.g. (Cáceres-Martínez et al., 2020; Chávez et al., 2021). *Tor* feeds on plants rather than animals (Cáceres-Martínez et al., 2020; Peyton, 1980) but its diet varies with human proximity (Hernani-Lineros et al., 2020). The succulent heart of bromeliads and fruits are main foodstuffs (Bernátková et al., 2021). As other frugivores, *Tor* disperses seeds over long distances through endozoochory and improves certain plant germination (Figueroa, 2013; Rivadeneira-Canedo, 2008). While foraging for epiphytes and fruits (Goldstein, 2004), *Tor* wounds or even falls trees creating light gaps with potential ecosystem repercussions (Sandoval-Guillén and Yánez-Moretta, 2019). *Tor* also digs up for food and disturbs the soil (Peyton, 1980). Trees can be wounded when *Tor* rubs or marks them (Filipczyková et al., 2017; Kleiner et al., 2018) or builds a nest in the canopy (Peyton, 1980). As well as soil that can be disturbed when *Tor* builds beds on the ground (Peyton, 1980).

II.6 Discussion

The information we gathered on the interactions of omnivore bears in ecosystems provides a clearer picture of the diverse trophic and non-trophic interactions triggered by a group of apex omnivores and their potential cascading effects within ecosystems. Following Wilby et al. (2001), we visually

conceptualised the most important interactions of three major bear species (*Uth*, *Uar and Uam)* in different ecosystem compartments. These concept maps provide a comprehensive picture of the diversity of interactions that an omnivore can trigger. Our review reveals the extent of the trophic and non-trophic interactions and highlights the variability in the number, intensity and type of interactions within an omnivore group in particular. Considering pure trophic interactions, omnivore bears may be a significant cause of mortality for ungulates and salmon but little is known on their effect on invertebrates, small mammals' population dynamics or hard mast-bearing tree reproduction. Furthermore, omnivore bears can alter prey behaviour, co-consumers strategy or habitat use, even if results are not always congruent. The non-trophic interactions associated with omnivory, including endozoochory, salmon carcasses displacement, deadwood production, canopy opening, or soil disturbance could be described as forms of ecosystem engineering. Indeed they can improve seedling recruitment, understory and riparian forest productivity, sustain deadwood community, or even alter soil nutrient availability. However, some interactions such as endozoochory should be less biased towards fleshy-fruit bearing plants, like most studies on endozoochory (Green et al., 2022), to better characterise their effect on plant community (Beckman and Sullivan, 2023). In contrast, considerably less is known about non-trophic interactions not associated with trophic behaviour. Bears can transport seeds in their fur, disturb the soil to manage dens or daybeds, but no references really demonstrated their effects on the ecosystem, except daybeds that may favor germination (García-Rodríguez and Selva, 2021).

In a recent review on keystone species (Shukla et al., 2023), the authors showed that for mammals such a status is often associated with engineering rather than consumption interactions. However, omnivores have rarely been described as such. Jones et al. (1997) pointed out that sea otters, because they affect engineer species dynamics, are keystone species, species involved in trophic and non-trophic interactions. Our results underlined bears as important ecosystem modifiers (i.e. engineers) and also significant consumers, capable of controlling prey population and triggering cascading

effects. Following this line, we argue omnivorous bears should be considered keystone species, because they not only trigger strong interactions, but also a myriad of interactions of varying strength. A previous review focusing on the salmon-ecosystem already pointed out the potential status of *Uar* and *Uam* as keystone species (Levi et al., 2020). Our review considered all possible interactions involving different bear species in various conditions, so it is clear that their potential keystone effect is context dependent.

In fact, certain interactions have only been described in *Uar* and *Uam* (e.g. top-down control of ungulate prey populations, Zager and Beecham, 2006) or only in *Uth* or *Tor* (e.g. creation of light gaps, (Takahashi et al., 2015). Similarly, within the same species, many interactions are not described in several populations. Bears from North America are well documented for their crucial role in riparian forest productivity, whereas other populations are significant insects consumers or scavengers. We could attribute this either to the absence of these interactions or a lack of proof, maybe reinforced by the fact that studies showing no effect are not published. This should be even more important for species with few references retrieved (e.g. *Mur*, *Tor*, *Hma*). Based on our literature review, we observed that bears from North America, Europe and Eastern Asia are much more studied than bears anywhere else, a pattern shared with other works (Say-Sallaz et al., 2019). Publications in english are notably less numerous for *Tor*, *Mur*, *Hma* species, and this pattern was probably accentuated by missing articles in local languages or not referenced in WOS. We assume it is also true for other well-studied bears (e.g. Russian reports in (Niedzialkowska et al., 2019) or some populations (e.g. eastern asia *Uth*). As our study is a first step towards a comprehensive view of interactions by omnivores, here bears, the inclusion of non-english written articles may provide valuable additional evidence. Also, our findings may have been affected by articles not identified with our search equations.

Based on our review, we see several avenues of future research to strengthen our hypotheses. We found several studies on non-trophic interactions, if we combine all bear species. But, for each interaction and associated engineering, there were only few associated publications, generally focusing on a single species or population. Studying non-trophic interactions at various sites and investigating their effects on the ecosystem is clearly needed. In the light of current evidence, non-trophic interactions not associated with omnivory seem non-negligible but without real quantification and assessment of their effect on the ecosystems. Trophic interactions to the contrary are well documented but specific studies may lack for some preys (e.g. insects, small mammals), or some highly digestible items, like mosses or fungi, which remain cryptic, anc can be potentially dispersed (Glime, 2021; Vašutová et al., 2019). Technological advances in fecal eDNA metabarcoding should improve their detection in diets (Mumma et al., 2016) as already used in brown bear (De Barba et al., 2014; García-Rodríguez et al., 2021b; Nawaz et al., 2019). The use of frequency of occurrence to describe the diet may raise questions for accurate quantification , relative volume may be more informative, even if sensitive to digestibility (Bojarska and Selva, 2012).

Our literature review and representation of intra- and interspecies interactions shed new light on how omnivorous bears interact with their abiotic and biotic environment. We suggest a central role in the ecosystem through multiple trophic and non-trophic interactions of varying strength, not far from keystone organisms and at least interesting targets for ecosystem conservation. However, because of their omnivorous diet and opportunistic nature, it appears necessary to study population of each species in diverse ecosystems. In line with McLeod and Leroux (2021) on food webs, and in order to correctly assess the ecological role of omnivores, we need to consider interactions with the entire ecosystem. Furthermore, some omnivores have already been described as keystone organisms (Diehl, 1992; Schmitt et al., 2020) and we believe that approaches similar to ours would bring light on other smaller-sized omnivores (Shukla et al., 2023). A better standardized characterization and understanding of omnivores in ecosystems would allow us to improve their management,

conservation and the associated ecosystems. Our study paves the way for future meta-analyses on omnivore roles in ecosystems and highlights the need to consider their full interactions' spectrum to properly picture their functional role.

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Part 2 – Brown bear diet

A colourful insight into the omnivorous diet of the brown bear.

Chapter III - Do sex, age or ecological needs shape an endangered brown bear population diet? New insights from faecal metabarcoding.

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Results presented at the ***International Wildlife Congress*, Lillehammer (Norway)** - 1 to 4 September 2025.

III.1 Résumé

Contexte : Les stratégies de conservation se focalisent généralement sur la mégafaune et les espèces clés de voûte. Dans les écosystèmes tempérés, l'ours brun apparaît comme une espèce de la mégafaune pouvant être considérée comme clé de voûte. Cependant, la plupart des études qui se sont intéressées à ses interactions trophiques se sont basées sur des analyses coproscopiques des fèces généralement réalisées à la loupe binoculaire. Cette approche se heurte à la difference de digestibilité des éléments consommés, qui est d'autant plus variable chez un animal omnivore. Un second point sur le régime de l'ours brun, reside dans le peu d'études ayant examiné conjointement l'effet de l'âge et du sexe sur le régime. Par ailleurs, les études se basent souvent sur les saisons climatiques pour définir le régime de l'ours brun dans le temps, alors que les périodes écologiques de l'ours (reproduction, hyperphagie,..) régissent davantage les mouvements et les stratégies de fourragement.

Méthodes : Dans cette étude, à partir d'une collection de fèces d'ours brun de différentes classes d'âge, de mâles et de femelles récolltées dans les Pyrénées pendant plusieurs périodes écologiques (reproduction, pré-hyperphagie, hyperphagie), nous avons étudié son régime alimentaire utilisant le metabarcoding de l'ADN environnemental fécal (ADNe). L'utilisation de l'ADNe permet de détecter des espèces difficilement détéctables, souvent du au fait d'une forte dégradation à l'issue de la digestion. Nous avons utilisé quatre marqueurs pour identifier les plantes, les champignons, les arthropodes et les vertébrés présents dans les fèces.

Résultats : Nous avons pu mettre en évidence que le régime de la population pyrénéenne d'ours brun est majoritairement composé de plantes (~90% de fréquence d'occurrence dans les fèces) comme la plupart des populations du sud de l'Europe. Également, les vertébrés et les arthropodes complètent le régime avec notamment des ongulés sauvages (9%) et domestiques (7%) et des hyménoptères coloniaux (23%). Nous avons détecté un effet de la période écologique avec moins d'arthropodes

consommés pendant la période d'hyperphagie, mais aussi une forte variabilité dans les types de plantes consommées avec un pic de consommation de plantes herbacées, de fruits charnus et de fruits secs respectivement durant la période de reproduction, de pré-hyperphagie et d'hyperphagie. Cela s'explique par la disponibilité des ressources mais aussi par les besoins de l'animal. Nous observons aussi que les femelles consomment plus de plantes et moins de vertébrés sauvages que les mâles, ce qui est probablement lié à des probabilités de rencontre de proies ou de charognes plus faibles chez les femelles ou une habilité moindre à prédater des ongulés. Grâce au metabarcoding nous avons également mis en évidence la plus grande diversité de champignons consommée chez un Ursidé avec 21 genres identifiés produisant des champignons consommables (comme les truffes, bolets, russules). Cependant, nous n'avons pas observé d'effet de l'âge sur le régime alimentaire probablement dû à un échantillonnage déséquilibré ne permettant pas de détecter d'effet.

Conclusions : Cette étude a fourni un régime détaillé de l'ours brun et a mis en lumière les variations existantes entre sexes et périodes écologiques. La période écologique semble pertinent pour étudier le régime alimentaire et favoriser les comparaisons entre populations, notamment pour une espèce avec une distribution mondiale comme l'ours brun. Cette étude permet également de mettre à jour notre connaissance du régime de l'ours brun dans les Pyrénées.

Mots clés : Ursidé, omnivore, mycophagie, predation, frugivory, arthropods

III.2 Abstract

Conservation strategies usually focus on megafauna and keystone species to protect habitats. In temperate ecosystems, brown bear appears as one of the potential megafauna keystone species thanks to its omnivorous diet. However, most of the trophic interactions' studies used coproscopic analyses that generally miss highly digested items and rarely investigated the effect of sex, age and individual. In addition, the diet was frequently investigated according to climatic seasons, while Bear Ecological Periods - BEP - (e.g. mating, hyperphagia) really drive individual movement and foraging. In this study, we collected brown bear faeces of different age class and sex across BEP from a critically endangered population. We used metabarcoding and four markers specific to plants, fungi, arthropods and vertebrates to investigate the brown bear diet in the Pyrénées mountains. The diet was mainly composed of plants but also of arthropods, vertebrates and fungi. Pyrenean brown bear consumed significantly fewer arthropods during hyperphagia than other BEP, and exhibited preferences for different plant life forms during mating (diversified herbs), pre-hyperphagia (fleshy-fruits) and hyperphagia (dry-fruits). Females consumed plants more often than males, which in turn consumed more wild vertebrates. We highlighted the most diverse level of mycophagy (21 genera) of an omnivore Ursid thanks to metabarcoding. We showed the high variability of this brown bear population diet among BEP and sexes, but not among age-classes. This detailed diet study provides new insights for brown bear conservation, and invites similar approaches on other animals.

Keywords: Ursid, omnivory, mycophagy, predation, frugivory, arthropods

III.2 Introduction

Conservation strategies often target pivotal species with significant impacts on the ecosystem functioning. These keystone species usually belong to the megafauna (Shukla et al., 2023). However, the first step to propose an effective conservation strategy is to properly understand species' trophic interactions and ecological needs across its life cycle. In temperate areas, megafauna are diverse including canids, felids, bovids, cervids, suids, or ursids. The ursids count for the most abundant large carnivore species in the world (Ripple et al., 2014b), among which brown bear (*Ursus arctos*) distribution cover the entire temperate zone (IUCN). Brown bear is a typical omnivore that consumes diverse food types at various trophic levels (e.g. plants, insects, vertebrates) and triggers various forms of ecosystem engineering after foraging (e.g. endozoochory), turning it into a potential keystone species (Levi et al., 2020; Pauly et al., 2025b).

Basically, brown bear's diet can be highly biased towards plants with local and temporal predominance of fleshy-fruits, hard mast or herbs, but also towards meat consumption of terrestrial vertebrates (e.g. wild, domestic ungulates but also smaller mammals, Edwards et al., 2011) constituting a substantial part of the diet as shown in its northern range (Bojarska and Selva, 2012). Locally, arthropods such as colonial hymenoptera complete the diet (Bojarska and Selva, 2012), and elsewhere, the return of salmons to freshwater provides key resources for the brown bear (Mowat and Heard, 2006). Over the year, brown bears exhibit distinct timing of activities such as mating, hyperphagia or winter dormancy, representing typical ecological periods that may shape the diet. Indeed, these bear ecological periods (hereafter BEP) drive individual movement and foraging strategies (Penteriani et al., 2025, 2022), and in relation to resource phenology shape feeding opportunities. Yet, most studies investigated brown bear diet according to climatic seasons and therefore food availability (e.g. (Pereira et al., 2021; Vulla et al., 2009; but see (García-Rodríguez et al., 2021b; Naves et al., 2006).

Besides the spatio-temporal variability of brown bear diet, intra-population variation can be explained by sex, age or individual preferences. For instance, adults are the most active during the best period for salmon fishing in coastal British Columbia (Klinka and Reimchen, 2002), and males consume more fish than females in North America (Mowat and Heard, 2006). The consumption of wild terrestrial meat is also more frequent in adult males than females in the Canadian Arctic (Edwards et al., 2011), while similar consumption of herbs is reported for both sexes (in Himalaya: Nawaz et al., 2019; in Croatia: Pereira et al., 2021). However, among plant resources, hard mast availability is usually restricted to small areas, in which adults can be dominant in Spain (Ruiz-Villar et al., 2019). More broadly, females with cubs may avoid prime bear habitats to limit the risk of infanticide by males (Steyaert et al., 2012). However, part of the variability may also be explained by individual foraging preferences (Edwards et al., 2011).

In fact, studying the diet of an omnivorous species with a flexible diet is particularly challenging. Most of the studies describing brown bear diet were based on coproscopic analyses using visual identification (Pauly et al., 2025b) subject to the variable digestibility of food items and our ability to identify altered food items (e.g. Spaulding et al., 2000). Conversely, some less digested food items (e.g. fibrous plants) may be overestimated in the diet (Lagalisse et al., 2003) while highly digested ones (e.g. mosses, fungi) may be overlooked and rarely reported (e.g. Pereira et al., 2021). Nevertheless, faeces are also a pool of DNA sequences (i.e. environmental DNA) sourced from ingested food, which combined with advances in metabarcoding (Taberlet et al., 2018) greatly contributed in detailing animal diet (Ando et al., 2020). For endangered species, this noninvasive, time- and cost-effective approach appears appropriate (Ando et al., 2020). It was used only three times for brown bear, with a focus on plants in Himalaya (Nawaz et al., 2019), and plants, vertebrates and invertebrates in Slovenia (García-Rodríguez et al., 2021b) and Italy (De Barba et al., 2014) .

Hence, the use of a marker specific to fungi has never been tested to investigate brown bear mycophagy.

In this study, we analysed the content of faeces in the critically-endangered population of European brown bears (*Ursus arctos arctos*) in the Pyrénées (IUCN, 2017), accounting for sexes, different age-classes and collected within different BEP. We used a metabarcoding approach with four markers specific to plants, fungi, arthropods and vertebrates. We first hypothesised an effect of BEP especially on the frequency of vertebrate and plant food items in the diet due to the short availability period of weak body condition preys and nutritious plant phenology (García-Rodríguez et al., 2021b; Niedzialkowska et al., 2019) and brown bear movement variations among BEP (Penteriani et al., 2025, 2022). We also hypothesized an effect of the sex, with a more diverse and carnivorous diet expected for males than for females due to greater distances travelled (Penteriani et al., 2025, 2022) and the greater male ability to predate wild vertebrates (Mowat and Heard, 2006), both offering a greater prey encounter probability and food spatial variability. We finally expected a difference in the diet among age-classes related to reproduction and dominance relationships (Ruiz-Villar et al., 2019), thus predicting less rich food items for subadults.

III.4 Materials and Methods

III.4.1 Study site and population

Our study was conducted in the Pyrénées, a mountain chain (36,600 km^2) shared between France, Andorra and Spain, peaking at 3,400 meters above sea level. Forest covers more than 40% of the landscape and is dominated by hard mast trees. Above the timberline, large open areas are covered by fleshy-fruited shrubs and herbaceous plants. Pyrénées host a highly diverse flora, including

endemics, and megafauna species such as the brown bear, wild and domestic ungulates and mesocarnivores.

The local brown bear population was on the edge of extinction in the 1990s and has, since then, been subject to five phases of Slovenian bear translocations, initiating a partial demographic recovery (Vanpé et al., 2022) but still with genetic concerns (Auclair et al., 2025). In 2023, the population amounted to at least 90 individuals covering about 7,200 km² (Sentilles et al., 2025).

III.4.2 Faeces collection and metabarcoding

We collected 148 very fresh brown bear faeces (< 48h) from 2017 to 2023 covering different BEPs, with the help of dogs trained to detect bear faeces (Sentilles et al., 2021). We divided the year in six different BEPs: Winter dormancy (hibernal period of brown bear), Post-winter dormancy (hibernation recovery), Mating (reproduction period with high movement rate), Pre-hyperphagia (muscle recovery), Hyperphagia (massive consumption of aggregated resources), Pre-winter dormancy (Period of den searching) (**Fig. III.1**). Those BEP timings were defined based on local expertise and long-term monitoring of this population. We collected the outer part of the faeces composed of brown bear epithelial cells to identify the individual and the sex through genotyping and sex-markers (Vanpé et al., 2022). Thanks to the intensive monitoring of this population (Sentilles et al., 2025), individual identification helped to determine the age-class and reproductive status at the time of the faeces release. Brown bears were thus classified as “cub” (<1 year), “subadult” (1-5 years for males, 1-3 years for females) and as “adults” when older than subadults. The inner part of the faeces was collected to perform metabarcoding analyses using four universal markers (Taberlet et al. 2018) to detect plants (Sper01, trnl region), fungi (Fung02, ITS1 nuclear), arthropods (Arth02, 16S mtDNA) and vertebrates (Vert01, 12S mtDNA) taxa (see Appendix III.S1 for metabarcoding details). Only fungi producing edible fruit bodies were kept in the analysis to be parsimonious with brown bear real

mycophagy. After metabarcoding and data curation, we thus ended up with 126 samples with DNA sequences, including 72 females and 44 males distributed in 9 cubs, 23 subadults and 79 adults (**Fig. III.1**). For the diet analysis, we only considered the mating (n=43), pre-hyperphagia (n=35) and hyperphagia (n=45) BEP resulting in a sample size of 123 faeces samples. Results from pre- (n=1) and post-winter (n=2) dormancy are also presented.

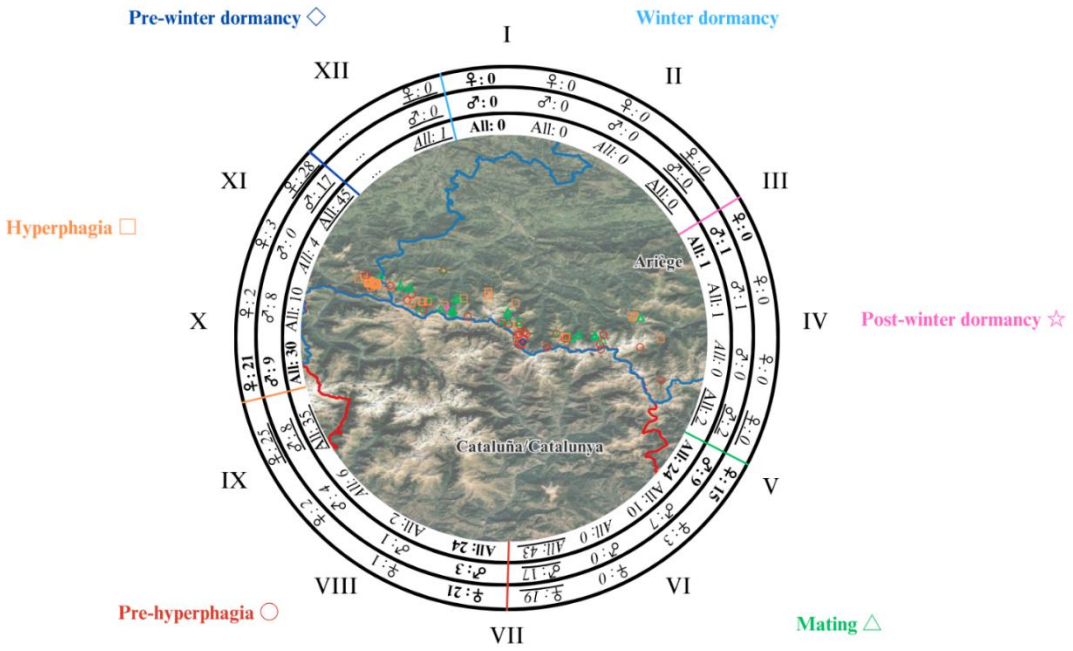

Figure III.1: Year-round spatial and temporal distribution of the brown bear faeces collected (n=127) in each of the six bear ecological periods, according to sexes (♀: Female, ♂: Male, All: both sexes and undetermined individuals) and age categories (**Adult** in bold, subadult in normal text, *cubs* in italics, and <u>All</u> combined underlined). Roman numerals indicate months (from I January to XII December). The blue line delimits the French administrative departments, in red the Spanish autonomous communities, and to the East the border with Andorra. Some faeces are not assigned to age or sex. One faeces of post-winter dormancy and two of hyperphagia are not visible on the maps as they were collected to the East (Ariège department) and the West of the Pyrénées (Hautes Pyrénées and Pyrénées-Atlantiques department).

III.4.3 Diet approach

III.4.3.1 Food types

We first analysed the diet using the frequency of occurrences (*FO*) of at least 250 reads from the four food types: plants, fungi, arthropods and vertebrates. We interpreted the absence of a food type in a sample, as a non-consumption, fully aware it may be due to metabarcoding failures.

III.4.3.2 Food items

Secondly, we analysed the diet based on the genera identified (i.e. Food items) by metabarcoding using the four markers. A food item was considered present if it occurred in a sample with at least 250 reads.

Among the reads not annotated at the genus level, 76% of them belong to Apiaceae or Poaceae families (i.e. dry-fruited herbs). To limit this potential loss of information, we decided to include the MOTUs annotated to both families as two additional food items. However, MOTUs annotated to genera of these two families were also included independently. Thus, the selected food items cover almost all of the sequences detected for plants (95.4%), vertebrates (99.3%) and invertebrates (79.9%), but much less for fungi (4.4%), but fungi sequences were not annotated at family level either (4.8%).

III.4.3.3 Diet analysis

Beforehand, we checked the spatial auto-correlation of our 123 samples using Moran test and did not detect any (p=0.51).

First, we tested the effect of BEP, sex and age class on the presence or absence of a givenfood type (plants, fungi, arthropods, vertebrates) (n=123 samples), using different Firth's Bias-Reduced Logistic Regressions (i.e. one per food type). We used this model because in one of the categories we only had successes (presence of a food type) and no failures (absence of a food type, i.e. complete separation of data). We excluded the effect of age class in the final model due to an absence of effect and a substantial increase in the number of parameters weakening the model.

Secondly, we investigated the food item diversity based on the bipartite interaction network linking food items and faeces (representing a bear individual for a specific BEP of a given sex within a particular age-class) using a subdataset with food items and sex information (n = 109). According to the unequal sample distribution per sex and BEP we conducted a bootstrap resampling method using eight samples per sex in each of the three BEP (i.e. the minimum collected) to build a sub-network (n= 48 samples). We did not have sufficient samples per age-class to include it in re-sampling. To estimate the diversity of food items, we calculated the degree (i.e. number of food items within faeces), *d* of Blüthgen (i.e. specialization of each faeces within the network, Blüthgen et al. 2006) and the species strength of food items (i.e. sum of dependencies of each item) within the sub-network. We resampled 1,000 times and averaged the degree and *d* of each faeces sample and species strength of each food item. We tested the effect of BEP, sex and age as fixed factor and year of sample and bear individual as random factors on the degree using a negative binomial model to account for overdispersion and on *d* using a quasibinomial model, which deals with data underdispersed. Based on AIC and BIC score, the BEP and sex fixed effects were kept in both final models.

Thirdly, we investigated the difference in the food item composition among BEP and age-classes and between sexes using a dissimilarity matrix approach. We performed a Permanova on the matrix according to BEP, sex and age-class. If significant, we used five variables to identify the drivers of

the difference observed: number of dry-fruited herbs, fleshy-fruited shrubs, dry-fruited trees, domestic and wild vertebrates.

Finally, we investigated the food item composition according to the plant life form (i.e. dry-fruited herbs, fleshy-fruited shrubs or dry-fruited trees) and the meat origin (domestic *vs* wild). For the former we investigated the effect of BEP, sex and age-class as fixed factors and year of sample collection and brown bear individual as random factor on the presence or absence (expressed in *FO*) of plants according to their life form using a binomial model. Based on AIC and BIC score the final model contained only BEP and sex as fixed effect. For the latter, we investigated the effect of BEP, sex and age as fixed factor and year of sample and brown bear individual as random factor on the on presence or absence (expressed in *FO*) of vertebrates according to origin using a binomial GLMM. We considered *Ovis* as domestic *Ovis arie*s due to the rarity of mouflons *Ovis gmelini* in our study area. Based on AIC and BIC score the final model contained only BEP and sex as fixed effect and the year as random factors. No specific analysis were conducted on fungi and arthropod item composition.

All analyses were performed with R (v.4.3.2). We used several packages, *logistf* (v.1.26.0, Heinze et al., 2003) to compute Firth's model and *performance* (v.0.12.3, Lüdecke et al., 2021) to calculate the R^2. For network analysis, we used *bipartite* (v.2.20, (Dormann et al., 2008) to calculate metrics. We used *glmmTMB* (v.1.1.9, Brooks et al., 2017) for negative binomial, quasibinomial and binomial GLM and GLMM computation and *MuMIn* (v.1.48.4) to calculate the R^2 using delta method (Barton, 2024). To perform NMDS, Permanova and fit drivers we used *vegan* (v.2.6-8, Oksanen et al., 2009). Figure 1 was computed using QGIS (v.3.30) and the others using *ggplot2* (v.3.5.1) (Wickham, 2011) and associated with *ggvenn* (v.0.1.10) for figure 2. We computed each figure to be understandable to colour-blind people.

III.5. Results

We found 13,369 OTUs and 21,066,708 reads in the 126 samples, mostly obtained using the plant marker (see supplementary here: https://doi.org/10.57745/V04NIG).

III.5.1 Food type consumption

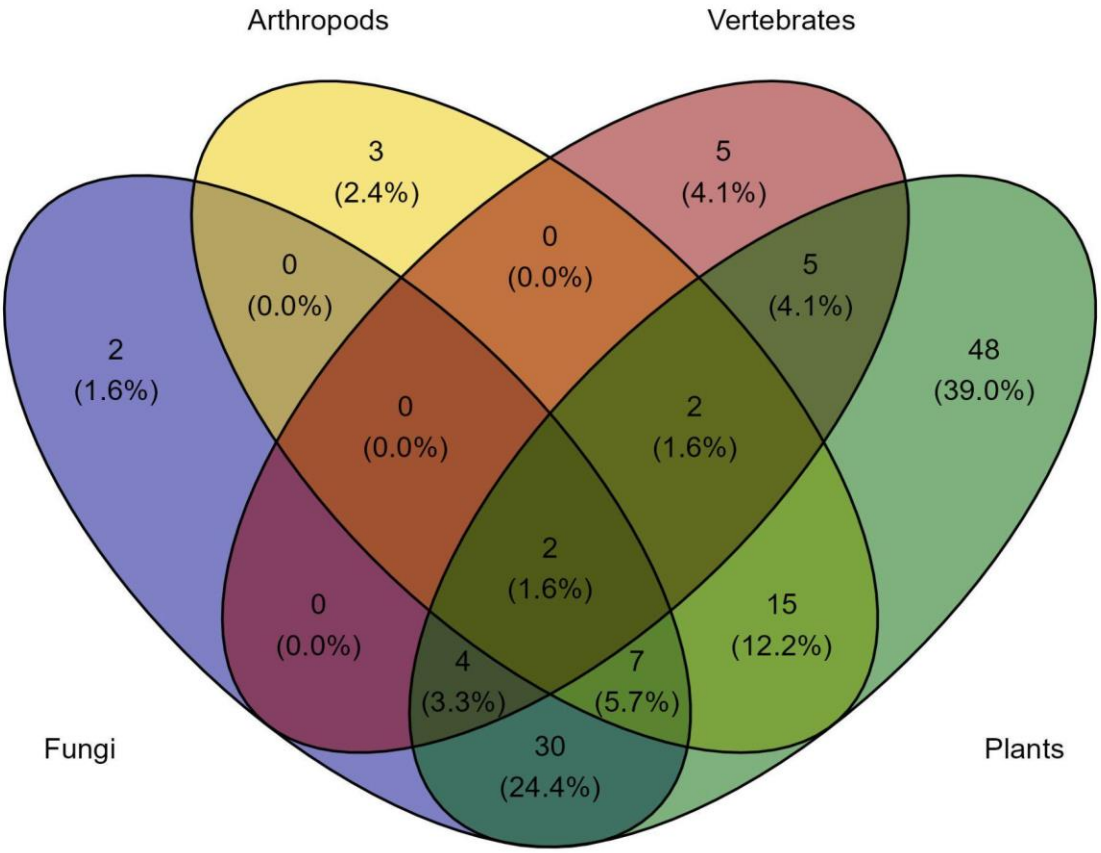

Figure III.2: Venn diagram with the occurrence of each of the four food types found in the 123 Brown Bear faeces, combining mating, pre-hyperphagia and hyperphagia periods.

Most of the faeces were composed of one (n=58) or two (n=50) food types, and less frequently of three (n= 13) or all the four (n=2) food types (**Fig. III.2**). We observed significant differences among food types in faeces collected from mating to hyperphagia (n=123, Firth's model: Pseudo-R^2 of McFadden= 0.42). We found more faeces containing plants (92%, n=113) than fungi (37%, n=45, t-

ratio=5.75, $p < 0.01$), arthropods (24%, n=29, t-ratio=6.72, $p< 0.01$) or vertebrates (15%, n=18, t-ratio=7.29, $p < 0.01$) across BEP. Faeces containing fungi were significantly more frequent than faeces containing vertebrates (t-ratio=3.17, p=0.01) and marginally than faeces containing arthropods (t-ratio 2.09, p=0.08). We observed no differences in the *FO* of faeces containing arthropods *vs.* vertebrates.

We showed that each food type *FO* varies among mating (n=43), pre-hyperphagia (n=35) and hyperphagia (n=45) (Firth's model: Pseudo-R^2 of McFadden = 0.42 **Fig. III.3.A**). We found plants marginally at higher *FO* during mating (98% of occurrences) compared to pre-hyperphagia (83%, t-ratio=2.30, p=0.07), whereas no difference was found between hyperphagia (91%) and the two other BEP. Conversely, we found arthropods at a significantly higher *FO* during mating (30%) and pre-hyperphagia (37%) than during hyperphagia (7%, t-ratio=3.06, p=0.01 and t-ratio = 2.30, p = 0.04 respectively) while there was no difference between pre-hyperphagia and mating. For vertebrates and fungi, we only observed non-significant trends (mating=23% and 35%, pre-hyperphagia=12% and 29% and hyperphagia=11% and 44% respectively).

We also observed that food types *FO* varied between females (n=72) and males (n=42) (Firth's model: R^2=0.42; **Fig. III.3.B**). Females significantly consumed plants (*FO*= 96%) more often than did males (86%, t-ratio=2.53, p=0.01). Conversely, males consumed vertebrates (24%) marginally more frequently than females (10%, t-ratio=1.80, p=0.07). Finally, we found no significant differences in arthropod and fungi consumption between males (26% and 31% respectively) and females (19% and 43% respectively).

We could not find any significant effect of age-class on the food types *FO*. Adults (n=78), subadults (n=22) and cubs (n=9) consumed plants (92%, 86%, 100% respectively), fungi (41%, 41%, 22%,

respectively), arthropods (19%, 32%, 11%, respectively). Only adults and subadults consumed vertebrates (18%, 9% respectively).

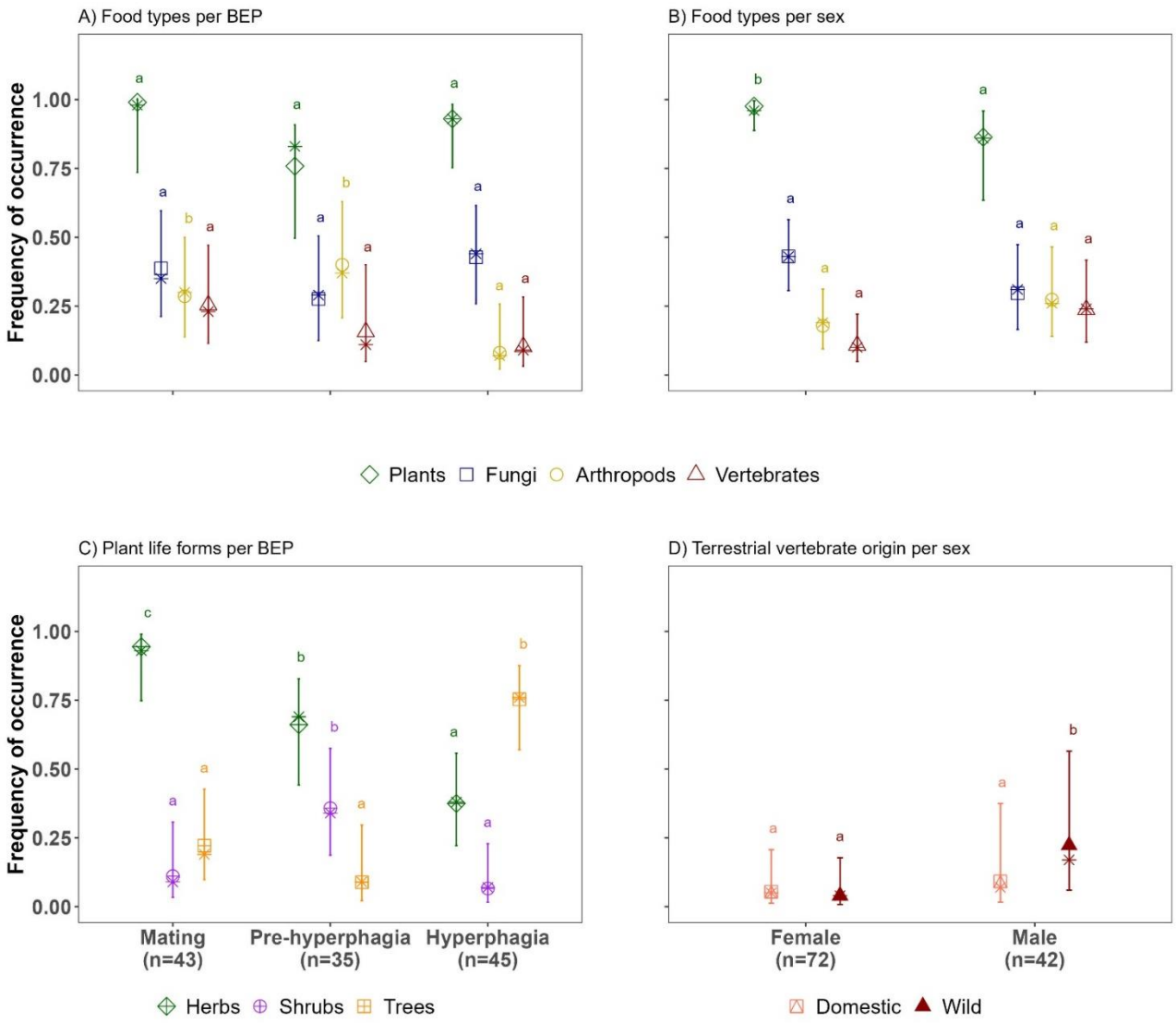

Figure III.3: Predicted frequency of occurrence (median and standard error symbolised by open symbol and bar) per food type (Plants: darkgreen, #006400; Fungi: darkblue, #00008B; Arthropods: gold, #CDAD00 ; Vertebrates: darkred #8B0000) according to the bear ecological period BEP (Mating; Pre-hyperphagia; Hyperphagia) (A) and the sex of the individual (B) in the top row. In the bottom left (C), per plant life form (Herbs: darkgreen, #006400, Shrubs: purple #A020F0 and Trees: darkorange #FF8C00) according to the bear ecological period BEP. In the bottom right (D), per terrestrial vertebrate origin (Domestic: coral, #FF7256; Wild: darkred #8B0000) according to the sex of the individual in the bottom row. For subfigure A) and B), results are based on a Firth model using food type, BEP and sex as fixed factors, for C) and D) results are based on two separate GLM

binomial. The letters indicate the significant differences among BEP (A) or sexes (B) and the stars (✳) the observed mean

III.5.2 Food item diversity

We identified 79 different food items (including Apiaceae and Poaceae) consumed across the (three) BEP (see details here: https://doi.org/10.57745/V04NIG). Among them, we identified 50 plants including 44 dry-fruited herbs, four dry-fruited trees and two fleshy-fruited shrubs. We also retrieved 21 fungi, one domestic and four wild vertebrates and three arthropods, all hymenopteran (**Fig. III.4**). During post-winter dormancy, one faeces contained only *Sus* (food item only found once) and the other seven herbaceous plant items (including Apiaceae and Poaceae). The sole pre-winter dormancy faeces contained only *Fagus* (**Fig. III.5**).

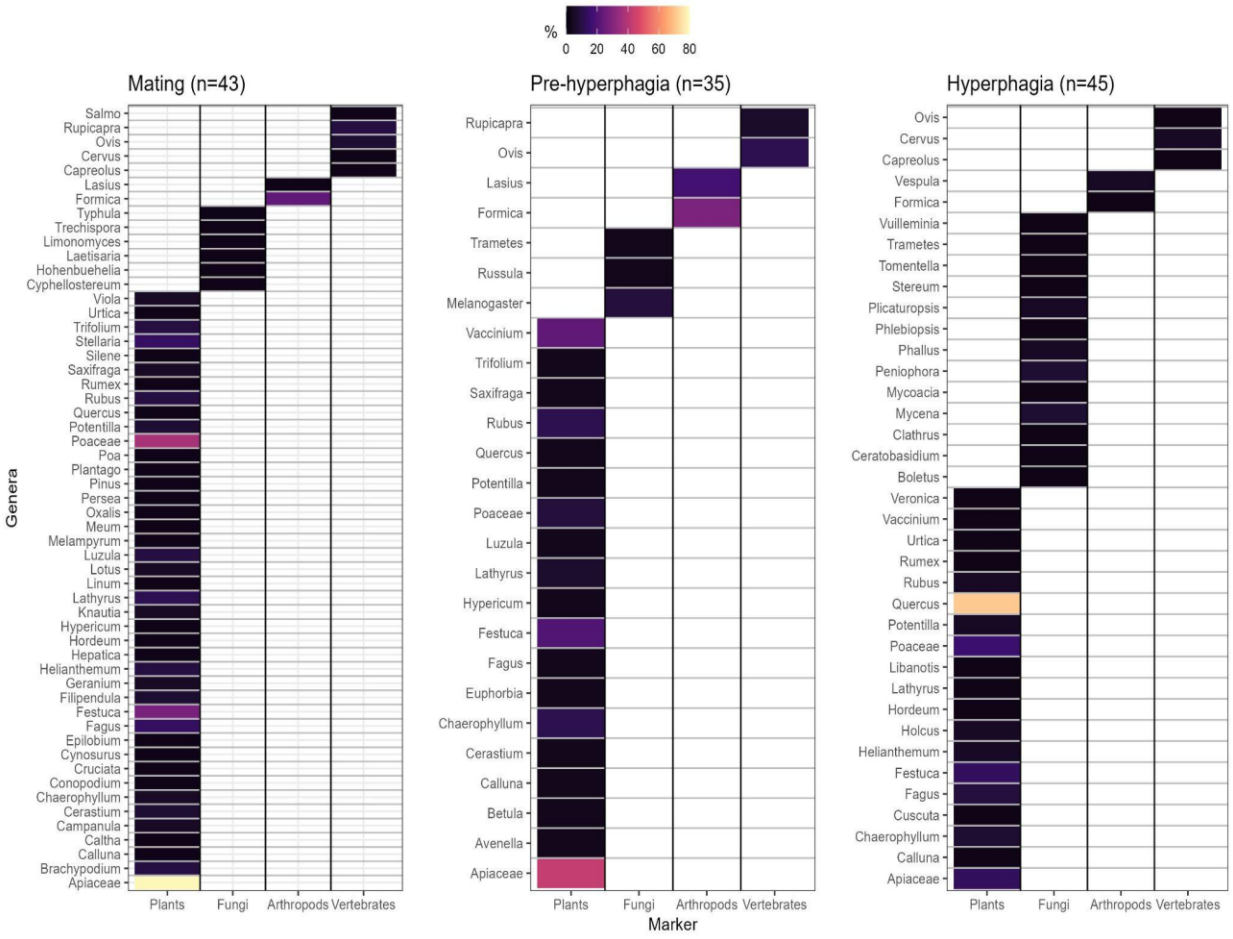

Figure III.4: The food items consumed per food types (Plants, Fungi, Arthropods, Vertebrates) and Bear Ecological Period (BEP) with sample size between brackets. Colour intensity represents the increasing percentage of occurrence within each BEP.

Based on interaction network analyses using the subdataset with sex information (n = 109), we found significant differences among BEP on the number of food items (GLM negative binomial, R^2=0.17), with significantly more items during mating (4.2 items) than during pre-hyperphagia (2.6, t-ratio=2.63, *p*=0.02) or hyperphagia (2.4, t-ratio=3.41, *p*=0.01), but no significant differences between pre-hyperphagia and hyperphagia. In addition, the number of food items did not differ significantly between sexes (males: 3.1 vs. females: 3.0), but we found a marginal effect during hyperphagia with more items per male (3.0) than female faeces (2.0, t-ratio=1.84, *p*=0.07). We did not detect an effect of age-class and it was not included in the final model (adults=2.9, subadults=3.4, cubs=3.2). Furthermore, we observed no effect of BEP on *d* of Blüthgen (GLM Binomial, R^2=0.10), with similar specialization during mating (*d*=0.35), pre-hyperphagia (0.32) and hyperphagia (0.35) or between females (0.34) and males (0.34) across BEP. However, during hyperphagia we observed significant higher specialization by females (0.28) than males (0.43, t-ratio= 2.01, *p*=0.04). We did not detect an effect of age-class on specialization and it was not included in the model based on AIC and BIC score (adults *d* = 0.35, subadults *d* = 0.29, cubs *d* = 0.37). Based on this subnetwork, 76 food items were retrieved in faeces, and we identified eight taxa (10% of the food items) with the highest species strength value: Apiaceae (8.6), *Quercus* (8.0), *Formica* (3.7), *Festuca* (2.6), *Ovis* (2.5), Poaceae (2.1), *Lasius* (1.5), *Fagus* (1.5) (**Fig. III.5**).

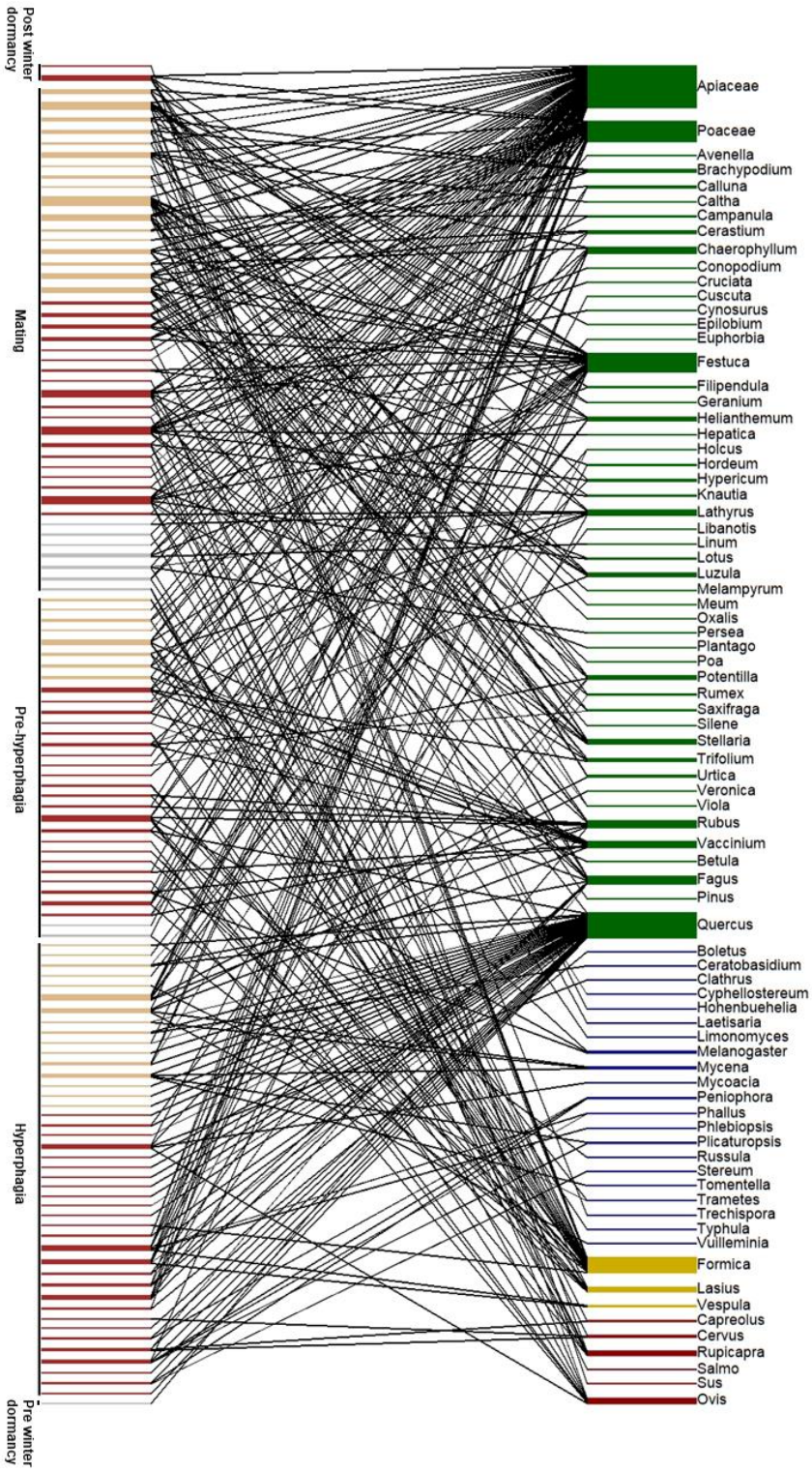

Figure III.5: Bipartite interaction network between food items consumed (top) and their occurrences in brown bear faeces (bottom). Food items are colour-coded for plants (darkgreen, #006400), fungi (darkblue, #00008B), arthropods (gold, #CDAD00) and vertebrates (darkred #8B0000). Faeces are colour-coded according to male (brown, #A52A2A) female (blurywood, #DEB887) and undetermined (grey, #BEBEBE). Bear Ecological Periods are indicated at the bottom. The width of the boxes (a food item or faeces) is proportional to the number of links.

III.5.3 Food item composition

Based on the dissimilarity matrix, we removed two singletons that increased stress and similarity (one female sample during **mating** and one during hyperphagia). We observed a significant effect of the BEP (**Fig. III.6**) on the food item composition between mating and pre-hyperphagia (Permanova, F-value=2.56, p=0.004), mating and hyperphagia (Permanova, F-value=17.41, p=0.001), and pre-hyperphagia and hyperphagia (Permanova, F-value=13.30, p=0.001). We identified three significant drivers of those differences, the consumption of herbs (R^2=0.11, p=0.001), trees (R^2=0.40, p=0.001) and domestic vertebrates (R^2=0.24, p=0.001), whereas the consumption of wild vertebrates as driver of those differences remained marginal (R^2=0.50, p=0.064) and the consumption of fleshy-fruited-bearing shrubs plant has no effect. We observed no effect of sex or age-class on food items composition.

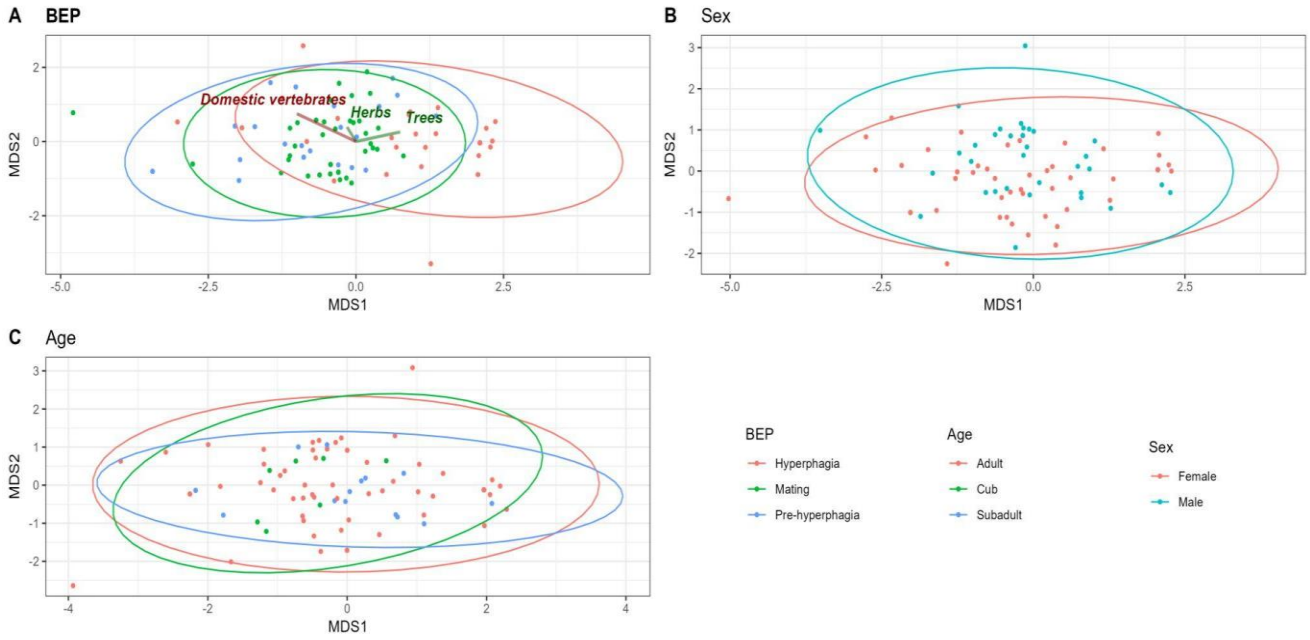

Figure III.6: Similarity of food item composition according to the Bear Ecological Periods (BEP), the sex and the age of brown bears. The bold title represents significant differences between groups based on a Permanova (p>0.05). In such cases, the arrows represent the food items driving the significant differences using the number of herb, shrub, tree, domestic vertebrate and wild vertebrates species per faeces samples.

Among samples composed of plants (n=113), we identified plant food items in 91% of those samples. Based on plant life forms, we observed significant differences among them (GLM Binomial: R^2 = 0.41). From mating to hyperphagia, herbs occurred significantly at higher *FO* (66%) than trees (37%, t-ratio=4.60, $p<0.01$) and shrubs (16%, t-ratio=6.72, $p<0.01$), and tree at higher *FO* than shrubs (t-ratio=2.40, $p=0.02$). We observed significant differences among BEP (GLM Binomial: $R^2=0.41$, **Fig. III.3.C**), herbs *FO* was significantly higher during mating (93%) than during pre-hyperphagia (69%, z-ratio=2.45, $p=0.02$) and hyperphagia (38%, z-ratio=4.23, $p<0.01$), and significantly higher during pre-hyperphagia than during hyperphagia (z-ratio=2.45, $p=0.02$). Fleshy-fruited shrubs were significantly more frequent during pre-hyperphagia (34%) than during mating (9%, z-ratio=2.32, $p=0.04$) and hyperphagia (7%, z-ratio=2.95, $p=0.01$), with no difference between mating and hyperphagia. Finally, dry-fruited trees were significantly more frequent during hyperphagia (76%) than during mating (19%, z-ratio=4.47, $p<0.01$) and pre-hyperphagia (9%, z-ratio=4.92, $p<0.01$), with no significant difference between mating and pre-hyperphagia. Females and males did not differ in the consumption of herbs (62% and 67%, respectively), shrubs (19% and 12%, respectively) or trees (39% and 40%, respectively). Similarly, among adults, subadults and cubs did not differ in their consumption of herbs (63%, 59%, 89%, respectively), shrubs (14%, 14%, 56%, respectively) and trees (40%, 41%, 22%, respectively). We also identified five families (Boraginaceae, Hyacinthaceae, Iridaceae, Onagraceae) with no genus identified.

Among samples containing fungi (n=45), we identified fungi items (genus level) in 48% of those samples. The most consumed genus of fungi were Mycena, Melanogaster and Peniophora (n=3), Phallus, Plicaturopsis and Trametes (n=2). Brown bear consumed wood saprotroph (n=9), ectomycorrhizae (n=4) or plant pathogen (n=4), soil saprotroph, litter saprotroph and lichenized fungi (n=1). No fungi was only identified at family level.

Among samples containing arthropods (n=29), we identified arthropod items in 90% of those samples. Three taxa were identified: *Formica* (n=21), *Lasius* (n=7) and *Vespula* (n=2). *Formica* were consumed during each BEP, *Lasius* during mating and pre-hyperphagia, whereas *Vespula* only during hyperphagia. Each sex- and age-class consumed hymenopterans. We also identified Aphidae and Psychodidae in faeces.

Among samples containing vertebrates (n=18), we identified vertebrate items in 88% of those samples including wild (n=11, *Cervus, Capreolus*, *Rupicapra* and aquatic *Salmo*) and domestic vertebrates (n=8, *Ovis*) in similar proportions (GLMM binomial with year of faeces as random effect, R^2 marginal=0.20, R^2 conditional=0.36). However, wild vertebrates were consumed in higher frequency by males (n=7 of 42 faeces) than females (n=3 of 72 faeces, z-ratio=2.350, p=0.02), whereas domestic vertebrates were found in similar proportions in both males and females (n=3 and 4 respectively) (**Fig. III.3.D**). Adults and subadults consumed vertebrates twice, whereas females with cubs did not consume vertebrates. Furthermore, we found Anatidae (i.e. ducks) in a single male sample.

III.6 Discussion

We showed that the critically endangered Pyrenean brown bear population diet is mainly plant based and secondarily composed of arthropods, vertebrates and even fungi, in agreement with previous Pyrenean studies (Berducou et al., 1982; Lagalisse et al., 2003) and more broadly in other populations of low latitudes (Bojarska and Selva, 2012; Vulla et al., 2009). We identified targeted food resources including herbs, hard mast trees, ants and ungulates, illustrating the omnivorous diet. This study updated and broadly detailed the knowledge of its diet, adding new information on mycophagy. We benefitted from a long-term ongoing project to study its diet among BEP, age-classes and sexes, accounting for individual identification.

We highlighted important differences among BEP with significant consumption of diversified herbs and arthropods during mating and pre-hyperphagia, and a quasi-exclusive consumption of hard-mast trees during hyperphagia, as shown by others (García-Rodríguez et al., 2021b; Naves et al., 2006) but never in this population. The almost exclusive consumption of various herbs during mating is probably related to the consumption of large quantities of vegetation in order to reach requirements in macronutrients (Coogan et al., 2014), few alternative resources or mating needs that do not drive foraging for rich resources (Penteriani et al., 2025, 2022). During pre-hyperphagia, we found a peak of fleshy-fruited shrubs consumption combined with other resources that may result in an optimal balance of protein, fat and carbohydrates (Coogan et al., 2014), ideal for this period of muscle and body recovery. Whereas hard mast are consumed for their high fat content and spatial aggregation during hyperphagia (Coogan et al., 2018; Ruiz-Villar et al., 2019). Accordingly, the preservation of *Vaccinium* spp. or oak forests in the Pyrénées is a key component for the brown bear conservation. We also observed trends with higher *FO* for fungi during hyperphagia and vertebrates during mating. For vertebrates, the temporal pattern can be explained by the high mobility during mating (Penteriani et al., 2025, 2022) associated with diversified resources available, including carcasses or weak preys (Niedzialkowska et al., 2019). Obviously, another main driver of these dietary differences was the plant phenology. In this sense, the presence of hard-mast trees during mating can be related to the consumption of cambium, young leaves or fruits from previous fructification. Fungi consumption appears as opportunistic, with few occurrences but high diversity, and may represent a significant and effective source of nutrient including unique elements such as Selenium, which are not accessible in other food items but are key elements in muscle health (Elliott et al., 2022). However, despite considerable effort to target real mycophagy, it is possible that some of the fungi were not consumed deliberately. Finally, ants were especially consumed during mating and pre-hyperphagia and wasp during hyperphagia, which may be related to opportunistic consumption to meet energy requirements,

particularly in terms of lipids (Coogan et al., 2014), or to the seasonal availability of pupae (e.g. *Ursus thibetanus* myrmecophagy, Fujiwara et al., 2013).

Brown bear diet seems to be shaped by sex differences with more herbivorous females while males preying more upon wild animals, in agreement with our second prediction. Higher meat consumption by males confirms previous studies in Europe (Pereira et al., 2021), North America (Edwards et al., 2011; Mowat and Heard, 2006) or Asia (Nawaz et al., 2019). It can be explained by higher energy requirements or predation ability for males (Mowat and Heard, 2006). The fact that females and males both similarly predate defenseless ewes in our study strengthen this idea. The higher herbivory by females contrasts with previous studies (Nawaz et al., 2019; Pereira et al., 2021). Some authors suggested this difference may be explained by the vegetation alone being sufficient to meet energy requirements (Mowat and Heard, 2006), however others stated it could be due to the fear of infanticide and the use of second choice habitats by females (Steyaert et al., 2012). This is consistent with our observation that no faeces contained meat for females with cubs. We did not find any difference between sexes on fungi consumption, contrary to Yellowstone NP where females consumed more false-truffles than males monopolising richer resources (Fortin et al., 2013). We did not detect any age effect on the die (Pereira et al., 2021), which may be related either to sufficient resources that limit competition or to the few faeces of cubs and sub-adults compared to adults. Exclusion of subadults by adults has already been reported in fruit rich oak forests (Ruiz-Villar et al., 2019).

All of those trophic interactions triggered by the brown bear may lead to several associated engineering processes (Pauly et al., 2025b). By consuming several plants of different life forms, brown bear ingests and disperses many seeds in our study site (Lalleroni et al., 2017; Pauly et al., 2024) and elsewhere (García-Rodríguez et al., 2021a). Similarly, consumption of fungi, especially mycorrhizae, can induce similar spore dispersal as shown for other vertebrates (Correia et al., 2018; Vašutová et al., 2019). In contrast, the low proportion of wild ungulates consumed (through predation

or scavenging) suggests that brown bear predation is probably not an important mortality factor in the Pyrénées, as observed elsewhere (Zager and Beecham, 2006). However, the consumption of domestic ungulates, although rare in the diet, has implications for local stakeholders (Ouvrier et al., 2025). The consumption of *Salmo salar* in our study is intriguing, and it is hard to determine whether it comes from anadromous fish, lake fish or fish remains, but it echoes the keystone interaction between bear and salmon in North America (Levi et al., 2020). Finally, ant consumption may reduce local defense of ants to aphids, beneficial to plants (Grinath et al., 2015).

Part of our diet results could also be explained by our metabarcoding approach and the choice of the markers. The combined use of markers such as trnl and rbcl for plant items could have improved our results (Botha et al., 2024) and some of the plants consumed may be missed, as shown in a previous study in Asia (Nawaz et al., 2019). However, in this study, we were particularly cautious using very fresh faeces, but also with our assignment methods, the read threshold and the use of one parsimonious taxonomic level, contrasting with other studies (García-Rodríguez et al., 2021b; Nawaz et al., 2019). For example, using the Inse01 marker, García-Rodríguez et al. (2021b) identified 48 taxa, most of them being coprophagous insects (i.e. potential sample contamination). However, the use of such an arbitrary read threshold may be also a source of bias within and among studies (Drake et al., 2022). Furthermore, the use of different taxonomic levels to describe the diet also raises concerns, with artificial segregation or similarity among faeces or in the functional interpretation of the diet. In fact, the genus level is more sensitive to the reference database and the marker resolution than the family level, which can at the same time bias the results and provide robust functional information of the diet. Metabarcoding of faecal eDNA also bears limitations to estimate the amount of each food item, a metric relevant to describe the diet (Bojarska and Selva, 2012). A trade-off would probably be to combine metabarcoding and coproscopic approaches to obtain more precise diet information.

Our study highlighted within one population various findings from different studies and sites, meaning a plant-based diet with sexual and BEP differences. The use of BEP that are more related to habitat use and animal movement may favour among-site comparisons for this worldwide distributed species, and it could be used for other species with a well-defined biological cycle. We gained knowledge on the important diversity of fungi consumed, a cryptic food item with potential ecological implications, suggesting the need to include them in future brown bear diet studies. Our detailed diet description according to sex and age-class also means that conservation programmes for brown bear could be better framed by focusing on key resources, which depend on climate and land use and may thus shift with global change for this opportunistic species (Lucas et al., 2025). In this context, the differences observed in the diet between sexes or BEP may also be altered with climate change and food distribution variation (Lucas et al., 2025). Moreover a thorough understanding of trophic and associated engineering interactions appears crucial to understand ecosystem functioning and thus effectively conserved ecosystems, be it for brown bear or other species.

III.7 Acknowledgments

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Part 3 - The dispersal of diaspores by brown bears

(From left-top to bottom-right) Brown bear faeces full of Rubus sp.; Rubus sp seed retrived from faeces; Rubus sp. seed tested with Tetrazolium; Rubus sp seedling germinated from faeces.

Chapter IV- Inferring endozoochory from ingestion to germination through biological filters: brown bear faeces as a case study.

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IV. 1 Résumé

Contexte : La dispersion des diaspores (e.g. graines ou spores) est reconnue comme un mécanisme clé dans la dynamique des plantes. Parmi les mécanismes de dispersion, l'endozoochorie peut représenter un voyage risqué pour les diaspores. En effet, l'endozoochorie est le résultat d'étapes successives commençant par l'ingestion d'une diaspore, puis sa résistance à la mastication et au passage dans le transite digestif et enfin à sa germination potentielle une fois relâchée dans la fèces. L'endozoochorie, qui est particulièrement étudiée, a été inférée par de nombreuses méthodes, notamment basées sur des observations de comportements frugivores, sur des diaspores récupérées dans des fèces ou par des mises en germination en conditions controlées. Cependant, la plupart de ces méthodes ne prennent en compte que partiellement les différents filtres associés à l'endozoochorie (ingestion, mastication, tube digestif, fèces). Par conséquent, l'effet combiné des méthodes et des filtres considérés peut conduire à une inférence biaisée de l'endozoochorie.

Méthodes : Dans cette étude, nous avons utilisé une collection de 52 fèces d'ours brun (*Ursus arctos*) pour comparer cinq méthodes inférant l'endozoochorie et qui considèrent partie ou totalité des filtres associés à l'endozoochorie. Deux méthodes utilisées prennent en compte le filtre de l'ingestion et utilisent le métabarcoding de l'ADN fécal pour identifier les fruits charnus (i) ou les plantes consommées pendant leurs périodes de fructification (ii). La troisième méthode (iii) est basée sur les propagules intactes récupérées dans les fèces, tenant compte des filtres de l'ingestion et de la mastication. Une autre méthode (iv) est basée sur la germination à partir de fèces désagrégées, tenant compte des filtres de l'ingestion, de la mastication et du transit digestif digestif. La dernière méthode (v) était basée sur la germination à partir de fèces agrégées permettant de tenir compte des quatre filtres liées à l'endozoochorie. Nous avons comparé le nombre de taxons, la communauté et les formes de vie des plantes, inférés par chacune des méthodes.

Résultats : Nous avons inféré le plus grand nombre de taxons dans la méthode (iii), mais les méthodes basées sur la germination (iv ; v) ont permis d'inférer une plus grande diversité de formes de vie des plantes (plantes à fruits charnus, à fruit secs, mousses et fougères). Nous avons identifié peu de taxons en commun entre les méthodes, probablement dû à la détectabilité liée à chaque méthode et au caractère hétérogène des fèces. Les méthodes basées sur le métabarcoding (i ; ii) ont détecté peu de taxons.

Conclusions : Les méthodes basées sur le métabarcoding (i ; ii) pourraient représenter un outil intéressant comme première approximation de l'endozoochorie tout en détaillant le régime alimentaire. La méthode (v) apparaît comme la plus fiable et réaliste car elle considère l'ensemble des filtres et a permis de détecter une grande diversité de formes de vie. Les autres méthodes représentent aussi de bon outils mais leurs résultats nécessitent plus de prudence compte tenu des filtres endozoochores considérés. Enfin, nous invitons les études futures à intérpréter leurs résultats en fonction des filtres de l'endozoochorie considérés et de la détectabilité des plantes liée à la méthode utilisée.

Mots clés : Filtres biologiques, Fougère, Germination, Metabarcoding, Mousse, Teste de viabilitié

IV. 2 Abstract

Diaspore (e.g. seed and spore) dispersal is recognized as a key mechanism in plant dynamics, including endozoochory, which can be a risky journey for diaspores. Endozoochory is achieved when diaspores are consumed and may germinate after the mastication, the gut and faecal matrix passage, all representing filters for diaspores. Nevertheless, endozoochory is a highly studied mechanism through numerous methods, notably based on the observation of frugivorous behavior, diaspores retrieved in faeces or germination experiments. However, most of those methods consider partially the endozoochorous filters (ingestion, mastication, gut, faeces). Hence, the combined effect of the methods and filters consideration may lead to biased inference of endozoochory. In this study, we used a collection of 52 brown bear (*Ursus arctos*) faeces to highlight five methods inferring endozoochory. Two methods consider the ingestion filter and used metabarcoding of fecal eDNA to identify fleshy fruits (i) or plants during fruiting periods (ii). The third method (iii) was based on the intact propagules retrieved in faeces, considering ingestion and mastication filters. Another method (iv) was based on the germination from disaggregated faeces, considering up to the gut passage filter. The last method (v) was based on the germination from aggregated faeces, considering the four filters. We compared the number of taxa, the community and the plant life forms inferred among methods. We inferred the largest number of taxa in method (iii), but the germination-based methods inferred the most diverse plant life forms. We identify few shared taxa among methods. The metabarcoding-based methods might be an interesting tool as first approximation of endozoochory while detailing the diet. The method (v) appeared as the most reliable. Overall, we invite future studies to mitigate their interpretations according to the filters of endozoochory considered and plant detectability related to the method used.

Keywords: Biological filters, Ferns, Germination, Metabarcoding, Mosses, Viability test

IV.3 Introduction

Plant population dynamics in ecosystems are determined by many biotic and abiotic mechanisms, among which diaspore (e.g. seed or spore) dispersal across the landscape is crucial (Beckman and Sullivan, 2023). Indeed, diaspore dispersal is a key mechanism for the colonization or the escape from harsh environments due to competition, predation, or pathogens. Diaspores can be dispersed by various vectors either abiotic (e.g. the wind, anemochory) or biotic (i.e. zoochory) (Howe and Smallwood, 1982). For instance, vertebrates may transport diaspores on long distance by epizoochory through adhesion to their fur, hoof or feathers or endozoochory through ingestion and excretion by defecation or regurgitation (e.g. Baltzinger et al., 2019).

Endozoochory by vertebrates has received considerable attention in past decades (e.g. Nogales et al., 2024) and if it was related to frugivores and fleshy fruits ingestion in the first place (i.e. endozoochorous dispersal syndrome, Van der Pijl, 1982), other guilds and plant types are now documented as involved in this dispersal mechanism. In particular, large herbivores (Baltzinger et al., 2019) and omnivores (García-Rodríguez et al., 2021a) have been well studied, and numerous evidence of dry-fruited plants (Lalleroni et al., 2017; Pauly et al., 2024), ferns (Lovas-Kiss et al., 2018; Pauly et al., 2024) or mosses (Parsons et al., 2007; Pauly et al., 2024) dispersal exist. However, endozoochory has been studied and inferred in many different ways, either based on frugivorous behavior, diaspores retrieved in faeces or germination experiments as shown in review on islands (Nogales et al., 2024), seed dispersal networks (Dáttilo, 2025) or palms (Marques Dracxler and Kissling, 2022). Similar observations can be done if we focus on a given species, such as brown bear (*Ursus arctos*), for which endozoochory was inferred either by monitoring diaspores retrieved in faeces (Lalleroni et al., 2017), germination of diaspores extracted from faeces (Tavşanoğlu et al., 2021), or germination experiments using intact faeces (Pauly et al., 2024). And yet, although all these

studies deal with endozoochory, we can legitimately wonder whether they all provide a reliable inference of this complex mechanism (Dáttilo, 2025).

Endozoochory is a risky and hazardous process for the plant diaspores, which pass through at least four successive filters to be dispersed (i.e. described hereafter), and numerous methods consider only partially these filters. For instance, the first filter is the effective ingestion of diaspores, which can be inferred by visual observation of frugivory (e.g. Harrer and Levi, 2018) or through eDNA faecal metabarcoding to detect fleshy fruits (endozoochorous syndrome, e.g. Sato et al., 2025)). Once eaten, diaspores are often masticated (i.e. second filter) and potentially broken, drawing the limit between diaspore dispersal and predation (Janzen, 1971). The study of intact diaspores retrieved from faeces enable a consideration of this filter (Lalleroni et al., 2017). Subsequently the diaspores are within the gut (i.e. third filter), that may cause abrasive detrimental effect on diaspore or enhance their viability through the action of digestive acids (Traveset and Verdú, 2002). Studies testing diaspore viability (e.g. using tetrazolium, Farmer et al., 2017) or germination experiment of diaspores retrieved in faeces (Tavşanoğlu et al., 2021; Tsunamoto et al., 2024) properly consider the filters up to the gut passage. Finally, when the animal defecates, the diaspores can be constrained for germination by the faecal matrix through chemical or mechanical constraints (Jiménez-Martín et al., 2025; Mancilla-Leytón et al., 2012; Pauly et al., 2024), and germination experiments based on intact faeces permit to assess this filter (e.g. Jiménez-Martín et al., 2025; Mancilla-Leytón et al., 2012; Pauly et al., 2024). In addition, germination and establishment stages also depend on the quality of the releasing site (García-Rodríguez and Selva, 2021; Karimi et al., 2020; Schupp et al., 2010) and on secondary dispersal events (Culot et al., 2015; Ishikawa, 2011; Pauly et al., 2025c). Nevertheless, according to these four filters (ingestion, mastication, gut passage and faeces), a partial consideration of at least one of them in the study of endozoochory may lead to biased results.

Typically, the use of different methods to infer endozoochory complicate comparisons among studies but we argue that it is exacerbated by the variability in the inference reliability according to the endozoochorous filters considered (Dáttilo, 2025). For instance, several studies based on target plant and using captive animals, highlighted more intact diaspores (up to the mastication filter) than germinated diaspores (up to the gut passage filter) (Grande et al., 2013; Mancilla-Leytón et al., 2011; Rubalcava-Castillo et al., 2023; Tsunamoto et al., 2024), illustrating the inference variability according to the filters considered. In this regard, the combined effect of the method and the filters considered can lead to biased results, with varying degrees of confidence. Both can affect particularly the results of the number of plant taxa retrieved and the type of plant life form and dispersal syndrome inferred. For the latter, is particularly important, as dispersal syndrome are not fully reliable for endozoochory, especially for omnivores and herbivores (Green et al., 2022). In this context, the investigation of endozoochory inference according to different method, could be particularly relevant.

Therefore, we investigated the inference of endozoochory according to five different methods that consider part or all of the four endozoochorous filters (i.e. ingestion, mastication, gut passage, faecal matrix). To this purpose, we used 52 brown bear faeces collected in the Pyrénées (South-West Europe), a well-known plant disperser (García-Rodríguez et al., 2021a) of different plant life-forms (Pauly et al., 2024) We performed two methods based on faecal eDNA metabarcoding that consider only the ingestion filter, a first one (i) relying on the ingestion of plants with a fleshy fruit syndrome, and a second one (ii) relying on all plants ingested during their fruiting periods (i.e. propagules ingested). We performed a third method (iii) that consider up to the mastication filter, based on intact diaspores retrieved from the faeces. The fourth method (iv) was based on germination experiment from disaggregated faeces, method that considers up to the gut passage filter. We additionally used a Tetrazolium test as an alternative of germination experiments. Finally, we inferred endozoochory using a fifth method (v) based on germination experiments from intact and aggregated faeces that considers all the four filters of the endozoochory process. For each method, we investigated the

number of taxa and plant life forms inferred. Furthermore, as our study was based on a comparison of methods, we also provided information related to their applicability. We hypothesized a different number of taxa retrieved among methods and predicted that methods considering only the ingestion filter will provide the largest number of taxa. We also hypothesized that most of the taxa are shared between at least two methods. Finally, we hypothesized that methods based on germination (iv and v) and metabarcoding (only ii) will enable the inference of cryptic taxa dispersed as very small diaspores or spores, which can be missed through visual observation (method iii).

IV.4 Materials and Methods

IV.4.1 Faeces collection

We collected 52 fresh (less than 48h-old) brown bear faeces between 2017 and 2022 in the French part of the Pyrénées (18,000 km²) using dogs trained to detect brown bear faeces (Sentilles et al., 2021). We searched faeces from March to November, corresponding to the activity periods of brown bear (i.e. excluding winter dormancy). We searched faeces systematically on identified feeding areas (hosting soft or hard mast plants) and opportunistically following recent brown bear sightings, livestock depredations or apiaries damages. Faeces were stocked in a freezer at -18°C. Metabarcoding for methods (i) and (ii) was performed during December 2022. The diaspore extraction for method (iii) was performed in spring 2024. The germination experiments of methods (iv) and (v) were performed simultaneously between April and October 2023, results already being published (Pauly et al. 2024).

IV.4.2 Metabarcoding procedure

The metabarcoding was conducted at the Molecular biology microbiology facility of the Centre de Recherche sur la Biodiversité et l'Environnement (CRBE) laboratory in Toulouse (France) in December 2022 using a 15-g portion extracted from the core of the faeces collected in the field or in the laboratory after collection. We used the trnL marker to detect the plants ingested (see Supplementary for details on the metabarcoding procedure) and a reference sub-database on the plant species present in the Pyrénées, extracted from Genbank to obtain a better assignment accuracy at the species level. The 15-g portion allowed the identification of the plant composition of the entire faeces.

IV.4.2 Method (i): Metabarcoding and the fleshy-fruited plants ingested

Metabarcoding provides information on the presence of plants in faeces, regardless of the part consumed. Here, based on endozoochorous dispersal syndrome (Van der Pijl, 1982), we consider fleshy-fruited plants as consumed for their fruits. We thus inferred endozoochory based on fleshy-fruited plant occurrences in the diet using metabarcoding results. This method only considers the ingestion filter. We considered all taxa (species or genera) producing only fleshy fruits.

IV.4.3 Method (ii): Metabarcoding and plants ingested during fruiting periods

Here, we consider all the plants retrieved in faeces based on metabarcoding results, and inferred endozoochory for plants ingested during their fruiting period (i.e. diaspore ingestion). This method only considers the ingestion filter. To collect the information of the fruiting period, we used three sources: 1) FLORAPYR (https://atlasflorapyrenaea.eu), a Pyrénées flora database; 2) Tela Botanica (https://www.tela-botanica.org), a collaborative database managed by French botanists and 3) Pl@ntNet (https://plantnet.org), a database encompassing fruit observations by observers in the Pyrénées, as a form of citizen science. Based on months of fructification recorded in databases, we

determined the main fruiting period for months when the three databases were congruent. Otherwise, we considered the remaining months reported as secondary fruiting periods. We did not perform this approach at the genus level because interspecific variation of fruiting periods can be too wide. Hard mast species of Fagaceae (e.g. *Quercus* sp.) were discarded as their diaspores are generally destroyed by mastication (but see Lalleroni et al., 2017).

IV.4.4 Method (iii): Seed extraction

The third method (iii) inferred endozoochory based on the intact diaspores retrieved in the faeces. This method considers the ingestion and mastication filters. We used 5 g of fresh matter per individual faeces to extract the intact diaspores, similarly to Lalleroni et al. (2017) who used 5 g of dry matter. We passed each faeces through three successive sieves (with a mesh of 4.00, 0.80 and 0.08 mm, respectively) and water washed them to break down the faecal parts, remove macroelements, and collect large diaspores and fruits. We then collected the filtered material to search for smaller diaspores. We dried the filtered material to prevent mold formation, and sorted all intact diaspores under a binocular magnifying glass. The diaspores retrieved were identified using reference books (Cappers et al., 2006; Cappers and Bekker, 2013) and counted up to 100 (as some fruits, such as *Vaccinium* sp. fruits, may contain an extremely high number of seeds).

IV.4.5 Method (iv): Seed germination from disaggregated faeces

Here, we inferred endozoochory based on the germinated plants identified using a germination experiment on disaggregated faeces. This method considers the ingestion, mastication and gut passage filters. This method and its results were extracted from a previous study using the same samples (Pauly et al., 2024). We collected 75 g of fresh matter from each faeces, which were passed through the same successive sieves as method (iii) and water washed to disaggregate the faeces and remove macroelements that were not seeds or fruits. The disaggregated material was then deposited

on a potting soil (blond sphagnum peat moss and coarse perlite, ©Klasmann/ Dielmann) and a wipe (i.e. cotton gauze for medical use) under the potting soil, in a rectangular pot measuring 13 x 9 x 4.5 cm (length by width by height). We left the pots under a greenhouse for 209 days (from 5 April 2023 to 31 October 2023), with frequent watering. After 121 days, we randomly changed pots position to limit the effect of placement. We monitored each sub-sample every four days to map and count the new and dead seedlings. To control for external and potting soil contamination, we veiled the experiment during the *Asteraceae* sp. and *Salicaceae* sp. fruiting periods, and used 20 control pots with potting soil only. These control sub-samples were placed at the same time and in the same greenhouse than faecal samples. We annotated the germinated plants to the finest taxonomic level based on morphological criteria (Hanf and Martin, 1970; Muller, 2013). For some plants whose premature death prevented reliable identification, we assigned a probable identification (mostly based on the cotyledons only). We also inventoried and identified all the mosses and liverworts in each sub-sample just after the end of the 209-day monitoring period, because the identification required disruptive extractions of the substrate.

We also performed a viability tetrazolium test as an alternative to germination experiments on plant taxa extracted with the method (iii). We decided to conduct this test on taxa with at least 50 seeds retrieved to properly estimate the effect of gut passage. On those plants, we randomly selected 50 seeds per taxa during summer 2025 and followed the Tetrazolium test procedure outlined in the dedicated handbook (Miller and Peter, 2010).

IV.4.6 Method (v): Seed germination from aggregated faeces

The fifth method (v) inferred endozoochory based on the germinated plants identified using a germination experiment on aggregated faeces. This method considers the ingestion, mastication, gut passage and faeces filters. This method and its results were extracted from a previous study using the

same samples (Pauly et al., 2024). We collected another 75 g sample of fresh matter from each faeces, which was left intact and naturally aggregated, keeping the structural complexity of the faeces. The intact aggregated faeces were similarly deposited and monitored as for the fourth method (iv) in the same place, at the same time and with the same protocol.

IV.4.7 Comparison of the methods

We compared the plant detectability among methods using a GLMM Poisson on the number of taxa with the method as fixed factor, the faeces sample as random factor and the relative weight of method as an offset term. The relative weight corresponded to the proportion of faeces used per method and faeces. For this analysis, we removed unidentified taxa or uncertain identification. In a second analysis, we compared plant communities dispersed based on a dissimilarity matrix using a permutation test and by calculating the turnover and nestedness among methods. For this purpose, for a given method that identified a taxa at the species level (e.g. *Rubus idaeus*), an occurrence at the genus level was recorded if that genus had been identified at that taxonomic rank by another method (e.g. *Rubus*). Finally, we qualitatively described for each of the methods the ability to detect different plant life forms, and applicability related to the time, expense (except agent salary) and expertise required.

We performed all data analyses on R studio (v.4.3.2). For the GLMM and R^2 calculation, we used respectively *glmmTMB* (v.1.1.9) (Brooks et al., 2017) and *MuMIn* (v.1.48.4) (Barton, 2024) packages, and for dissimilarity matrix test and turnover calculation we respectively used *vegan* (v.2.6.8) (Oksanen et al., 2009) and betapart (v.1.6.1) (Baselga and Orme, 2012) packages. We realized the figures 1-4 on R Studio and figure 5 using Canva.com.

IV.5 Results

Based on metabarcoding of faecal eDNA, we identified 5,919 OTUs (Operational Taxonomic Units) including 12,945,186 reads. Of these 5,919 OTUs, 5785 were annotated to family level (nearly 100% of reads annotation, n=12,939,806 reads), 624 to genus level (87.7% of reads annotation, n=11,351,326 reads) and 297 to species level (1.4% of reads annotation, n=175,219 reads). Thanks to the BLAST performed, we enhanced the taxonomic annotation of 13 OTUs (180,621 reads; including three species annotation: *Conopodium majus*; *Rubus idaeus* and *Meum athamanticum*). Most of the annotations were hard mast bearing Fagaceae (2,132 OTUs, 87.1% of annotation, n=11,257,894 reads). We thus identified 53 different taxa including 19 species, 23 genera and 11 families (see details in supplementary).

IV.5.1 Method (i): Metabarcoding and fleshy fruits ingested

According to the metabarcoding results and the method (i), we identified three fleshy-fruited plants considered as dispersed by endozoochory. Those plant species were scattered in 27% (14/52) of faeces samples, *Vaccinium myrtillus* (9/52), *Vaccinium uliginosum* (4/52) and *Rubus idaeus* (5/52).

IV.5.2 Method (ii): Metabarcoding and plants ingested during fruiting periods

On the 19 plant species identified in the diet by metabarcoding, we found information on the fruiting period for 16 of them permitting endozoochory investigation according to the method (ii) (data lacking for *Cynosurus cristatus*, *Salvia pratensis* and *Nepeta cataria*). Among those 16 species, we counted three fleshy-fruited shrubs, 12 dry-fruited herbaceous plants and one hard-mast woody plant (and not considered as dispersed). According to the method (ii), we identified nine species consumed during their fruiting periods and inferred as dispersed by endozoochory (three fleshy-fruited and six dry-fruited plants). Those species were scattered in 29% of faeces samples (15/52). Most of the

fleshy-fruited plants (90% of samples) were ingested during their fruiting period (main and secondary), whereas dry-fruited plants (46% of samples) were ingested mostly outside their fruiting period (**Fig. IV.1**).

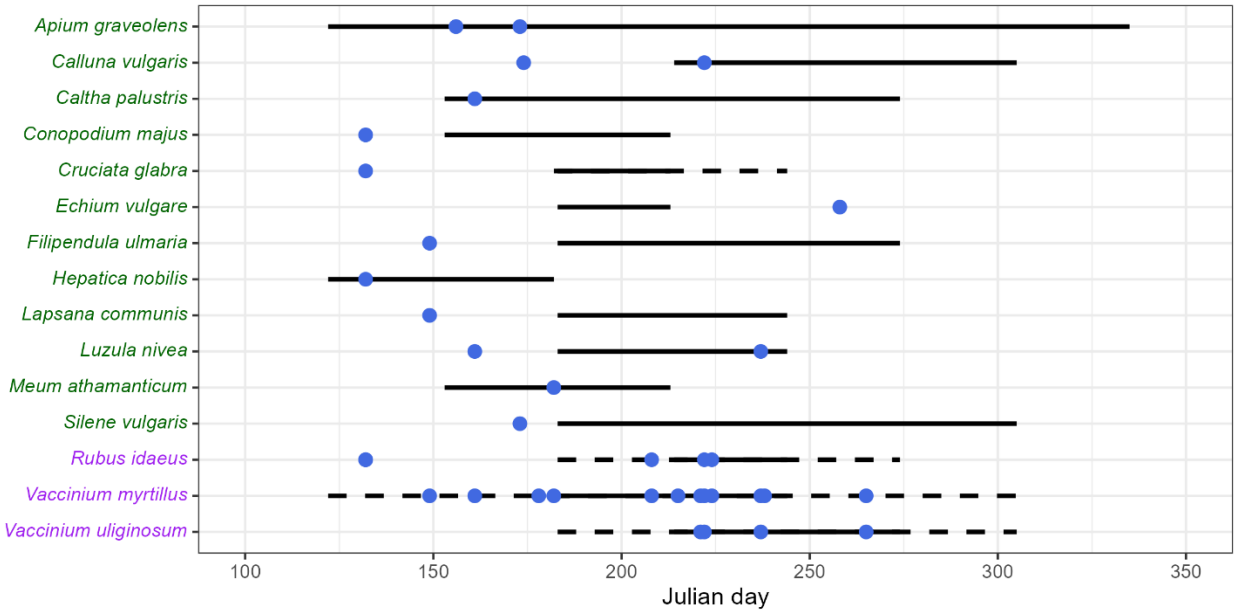


Figure IV.1: Occurrence of species (Y axis) identified in brown bear faeces (blue dots: #4169E1) during the year (X axis in Julian day). For each species, the black solid line corresponds to the main fruiting period, while the black dotted line corresponds to the secondary fruiting periods; a species retrieved outside of these periods was not considered as dispersed. Dry-fruited plants are written in green (#006400), fleshy-fruited in purple (#800080).

IV.5.3 Method (iii): Seed extraction

We extracted in total 1,478 intact diaspores in 58% (30/52) of the faeces samples, belonging to 27 different taxa and according to the method (iii) were considered as dispersed by endozoochory. We identified nine taxa at species level, 13 at genus level and five at family level. We found 66 diaspores from 15 different herbaceous plant taxa scattered in 28% (14/52) of the samples. We found at least 1,405 diaspores from six fleshy-fruited taxa (*Ribes alpinum*; *Rosa canina*; *Rubus* sp.; *Vaccinium* sp.; *Sorbus* sp. and *Juniperus* sp.) scattered in 37% (19/52) of the samples and most of them were *Vaccinium* sp. (69%) and *Rubus* sp. (30%). We found only one diaspore from a dry-fruited shrub (*Calluna vulgaris*). We finally retrieved six diaspores from four dry-fruited woody plants scattered

in 6% (3/52) of the samples, including two taxa producing small diaspores (*Betula pendula* and *Betula pubescens*) and two producing larger diaspores (*Abies* sp.; *Pinaceae* sp.).

IV.5.4 Method (iv): Seed germination from disaggregated faeces

Those results were extracted from a previous published study (Pauly et al. 2024). Based on the germination experiment from disaggregated faeces (n=52), we detected plants (angiosperms, mosses and ferns) in 42% of faeces samples (22/52), all considered as dispersed by endozoochory according to the method (iv). We observed the emergence of 164 angiosperm seedlings in 27% (15/52) of the samples and identified taxonomically 121 out of the 164 seedlings. We thus identified seven angiosperms including one tree (*Betula* sp.), two fleshy-fruited shrubs (*Rubus idaeus* and *Vaccinium myrtillus*) and four herbaceous taxa (*Holcus lanatus*; *Oxalis corniculata*; *Persicaria hydropiper* and one *Asteraceae* sp.). *Vaccinium myrtillus* is the species that germinated the most (n=5/52) and represented most of the seedlings identified (n=114/121), whereas other taxa only counted one or two seedlings. We also observed 43 unidentified seedlings, but most of them were probably *Vaccinium* sp. (88%, n=38/43). Furthermore, we detected one fern species (*Dryopteris carthusiana*) with three sprouts scattered in 6% (3/52) of samples and four mosses at the end of the monitoring (*Leptodictyum riparium*; *Ptychostomum dichotomum*; *Ceratodon purpureus*; *Barbula convoluta*) scattered in 17% (9/52) of samples.

As an alternative to germination experiment from disaggregated faeces, we performed Tetrazolium viability tests on 50 *Rubus* sp. and 50 *Vaccinium* sp. diaspores extracted and determined that 41% and 21% respectively of the diaspores tested were still viable. For non-viable diaspores, we noted that the embryo was either aborted or intact but non-viable.

IV.5.5 Method (v): Seed germination from aggregated faeces

Those results were extracted from a previous published study (Pauly et al. 2024). Based on the germination experiment from aggregated faeces (n=52), we detected plants (angiosperms, mosses and ferns) in 25% of faeces samples (13/52), all considered as dispersed by endozoochory according to the method (v). We observed the emergence of 85 angiosperm seedlings in 19% (n=10) of the samples and identified taxonomically 41 out of the 85 seedlings. We thus identified three angiosperms including one tree (*Betula* sp.) and two fleshy-fruited shrubs (*Rubus idaeus* and *Vaccinium myrtillus*). *Vaccinium myrtillus* represented most of the germinations (n=5) and seedlings (n=39), whereas the two other taxa only counted one seedling. We also observed 44 unidentified seedlings, but most of them were probably *Vaccinium* sp. (93%, n=41/45). Furthermore, we detected one fern species (*Dryopteris carthusiana*) with three sprouts in one sample (2%). We also identified two mosses at the end of the monitoring (*Pseudoscleropodium purum*; *Ceratodon purpureus*) scattered in 6% (3/52) of samples.

IV.5.6 Comparison of methods

IV.5.6.1 Taxa diversity

Among all the methods used we identified potential plant dispersal in 78% of the samples (41/52) corresponding to 56 taxa. This included eight fleshy-fruited shrub taxa (*Rubus idaeus*; *Vaccinium myrtillus*; *Vaccinium uliginosum*; *Ribes alpinum*; *Rosa canina*; *Juniperus* sp.; *Rubus* sp. and *Vaccinium* sp.), one fleshy-fruited tree (*Sorbus* sp.), one dry-fruited shrub (*Calluna vulgaris*), 35 dry-fruited herbaceous plants (see details in supplementary), three dry-fruited tree taxa (*Betula pendula*; *Betula pubescens; Betula* sp.), two hard-mast tree taxa (*Pinaceae* sp., *Abies* sp.), one fern (*Dryopteris carthusiana*) and five mosses (*Barbula convoluta; Ceratodon purpureus; Leptodictyum riparium; Pseudoscleropodium purum; Ptychostomum dichotomum*).

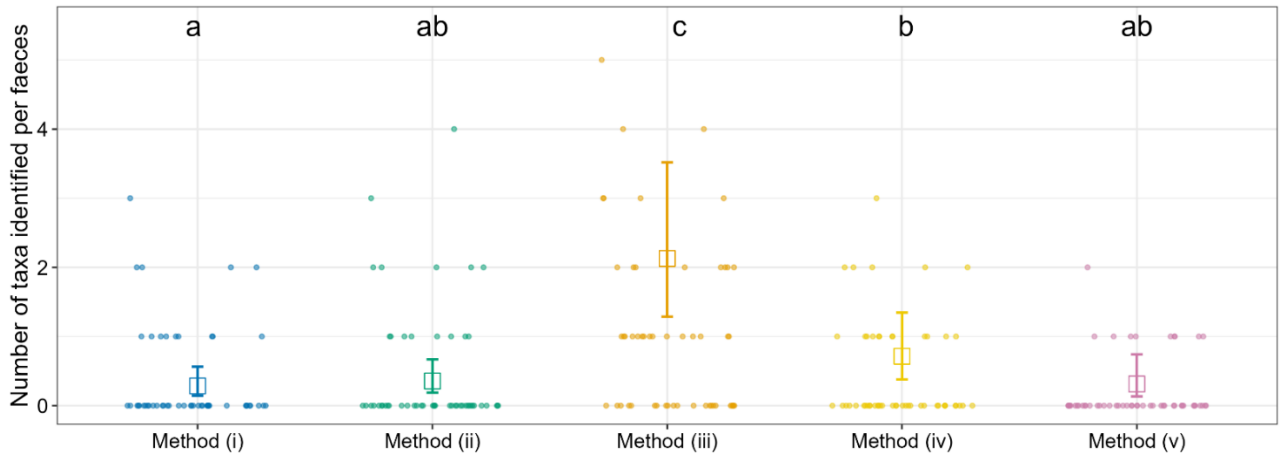


Figure IV.2: Modelled mean and standard error (square and error bar) based on GLMM Poisson and observed (points) plant taxa inferred as dispersed through endozoochory by brown bear according to five different methods (i.e. (i) Fleshy fruits based on metabarcoding, (ii) Plants during fruiting periods based on metabarcoding, (iii) Seed extraction, (iv) Disaggregated faeces and (v) Aggregated faeces). Different top letters indicate significant differences among methods.

Based on the number of plant taxa inferred as dispersed by endozoochory in each method, we observed significantly more taxa inferred in the method (iii) than in the other four methods (GLMM Poisson, R^2 marginal = 0.21, R^2 conditional = 0.45). Conversely, the method (i) inferred significantly less taxa than the method (iv) (**Fig. IV.2** and see **Table IV.1** for detailed results).

Table IV.1: Pairwise results of GLMM Poisson using lme4 and emmeans packages on R.

[1]Model: #of taxa detected ~ Method + (1| Faeces Sample),offset=relative weight per method

Pairwise	Ratio	Standard error	z-ratio	*p* value
Method (i) - Method (ii)[2]	0.800	0.2400	-0.744	0.9462
Method (i) - Method (iii)	**0.134**	**0.0349**	**-7.718**	**<.0001**
Method (i) - Method (iv)	**0.399**	**0.1200**	**-3.057**	**0.0190**
Method (i) - Method (v)	0.907	0.3410	-0.258	0.9990
Method (ii) - Method (iii)	**0.167**	**0.0403**	**-7.431**	**<.0001**
Method (ii) - Method (iv)	0.499	0.1410	-2.454	0.1014
Method (ii) - Method(v)	1.134	0.4110	0.348	0.9969
Method (iii) - Method (iv)	**2.981**	**0.7180**	**4.534**	**0.0001**
Method (iii) - Method (v)	**6.776**	**2.2400**	**5.797**	**<.0001**
Method (iv) - Method (v)	2.273	0.8220	2.269	0.1550

[1]Model used. The relative weight per method corresponds to the weight used per method relative to the weight of the faeces.
[2] Method (i) =Metabarcoding and the fleshy-fruited plants ingested; Method (ii) =Metabarcoding and plants ingested during fruiting periods; Method (iii) =Seed extraction. Method (iv) =Seed germination from disaggregated faeces; Method (v) =Seed germination from aggregated faeces
[3]In bold: Statistically significant results

IV.5.6.2 Taxa composition

Based on the plant inferred as dispersed by endozoochory in each method, we detected a significant difference in plant composition among methods based on the dissimilarity matrix analysis (Permanova, F-value=3.2604, p=0.001 and R^2=0.13). The composition obtained with method (iii) was significantly different from all others, while no significant dissimilarity was detected between metabarcoding-based methods (i) and (ii) or between germination-based methods (iv) and (v). The method (v) was significantly different from metabarcoding-based methods (i; ii), whereas the method (iv) was not different from metabarcoding-based methods (**Table IV.2** for comparison details). All faeces combined, we calculated a high turnover (0.80) and nestedness (0.99) among methods.

Table IV.2: Statistical results based on permutation test on dissimilarity matrix per method.

Pairwise comparison	F-value	*P* value	R^2
Method (i) - Method (ii)[1]	0.9168	0.476	0.03284
Method (i) - Method (iii)	**5.583**[2]	**0.001**	**0.11733**
Method (i) - Method (v)	**5.3008**	**0.001**	**0.15016**
Method (i) - Method (iv)	1.9892	0.085	0.08292
Method (ii) - Method (iii)	**4.5698**	**0.001**	**0.09607**
Method (ii) - Method (v)	**3.7675**	**0.001**	**0.10836**
Method (ii) - Method (iv)	1.2136	0.272	0.05012
Method (iii) - Method (v)	**3.2472**	**0.002**	**0.06594**
Method (iii) - Method (iv)	**2.0861**	**0.027**	**0.05204**
Method (v) - Method (iv)	1.2249	0.258	0.04499

[1]Method (i) =Metabarcoding and the fleshy-fruited plants ingested; Method (ii) =Metabarcoding and plants ingested during fruiting periods; Method (iii) =Seed extraction. Method (iv) =Seed germination from disaggregated faeces; Method (v) =Seed germination from aggregated faeces
[2]In bold: Statistically significant results

In details, two taxa were identified in all the five methods (*Vaccinium* sp. and *Rubus* sp.) (**Fig. IV.3**). Those two taxa were identified at species level (*Vaccinium myrtillus* and *Rubus idaeus*) in methods (i), (ii), (iv) and (v), whereas the method (iii) only reached the genus level. *Betula* sp. was shared by methods (iii), (iv) and (v). The moss species *Ceratodon purpureus* and the fern species *Dryopteris carthusiana* were exclusively identified in methods (iv) and (v). One species (*Vaccinium uliginosum*) was only identified in both methods (i) and (ii), another one (*Calluna vulgaris*) in both methods (ii) and (iii) only, and a last taxon (*Asteraceae* sp.) in both methods (iii) and (iv) only. In contrast, five taxa were found exclusively in method (ii), 23 exclusively in method (iii), six exclusively in method (iv) and one exclusively in method (v) (**Fig. IV.3**).

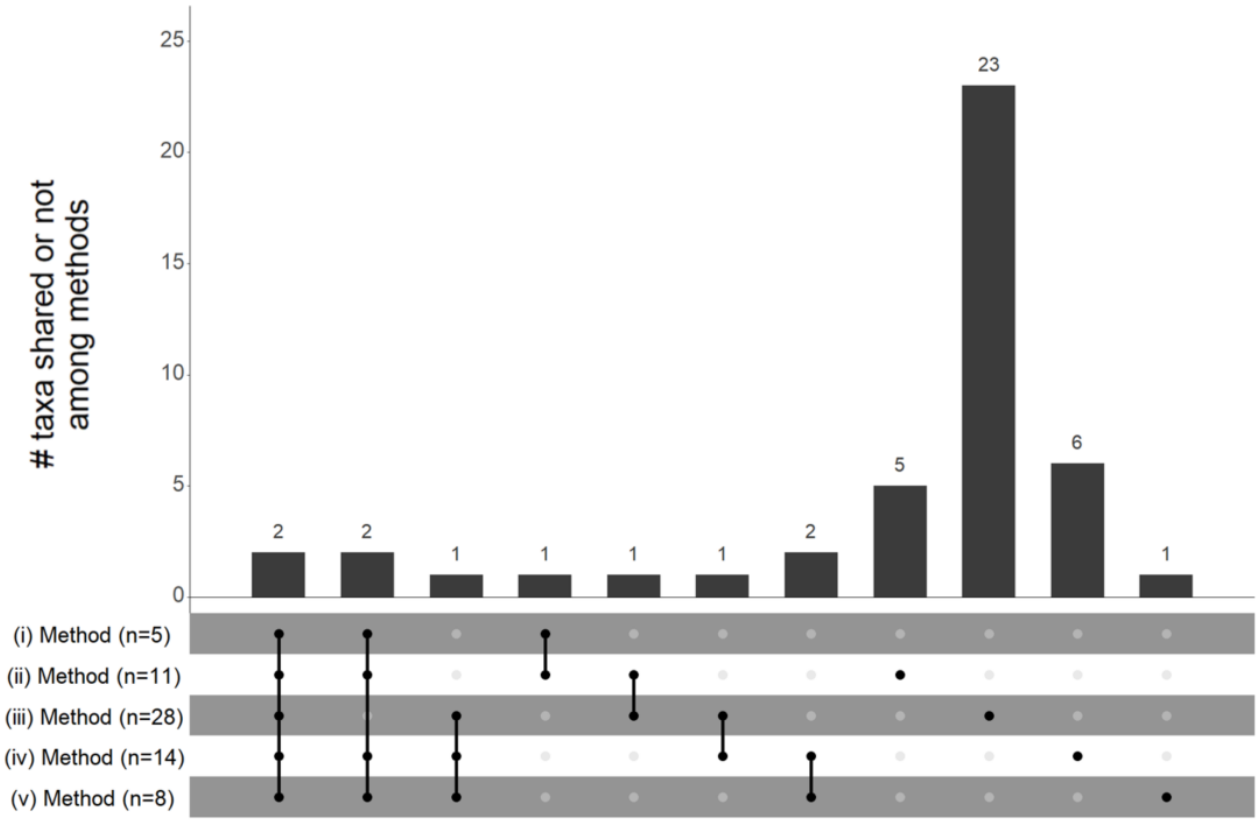


Figure IV.3: Number of taxa inferred per method (between brackets) and shared (connected black dots) or not among the five methods (i.e. (i) Fleshy fruits based on metabarcoding, (ii) Plants during fruiting periods based on metabarcoding, (iii) Seed extraction, (iv) Disaggregated faeces and (v) Aggregated faeces). The bar of the histogram represents the number of taxa shared by a unique combination of methods.

Concerning *Vaccinium* sp. and *Rubus* sp. that were retrieved in each of the five methods, they were found respectively in 16 and 10 of the 52 faecal samples, with method (iii) inferring most of the dispersal events (80% and 94% of total detection, respectively, **Fig. IV.4**). In two of the 52 faecal samples, we detected *Vaccinium* sp. in each method , which was not the case for *Rubus* sp. The method (ii) refined results of the method (i) by removing two *Rubus* sp. occurrence. The methods (iv) and (v) provided the lowest detection, with *Vaccinium* sp. retrieved in 31% and *Rubus* sp. in only 10% of of the faeces.

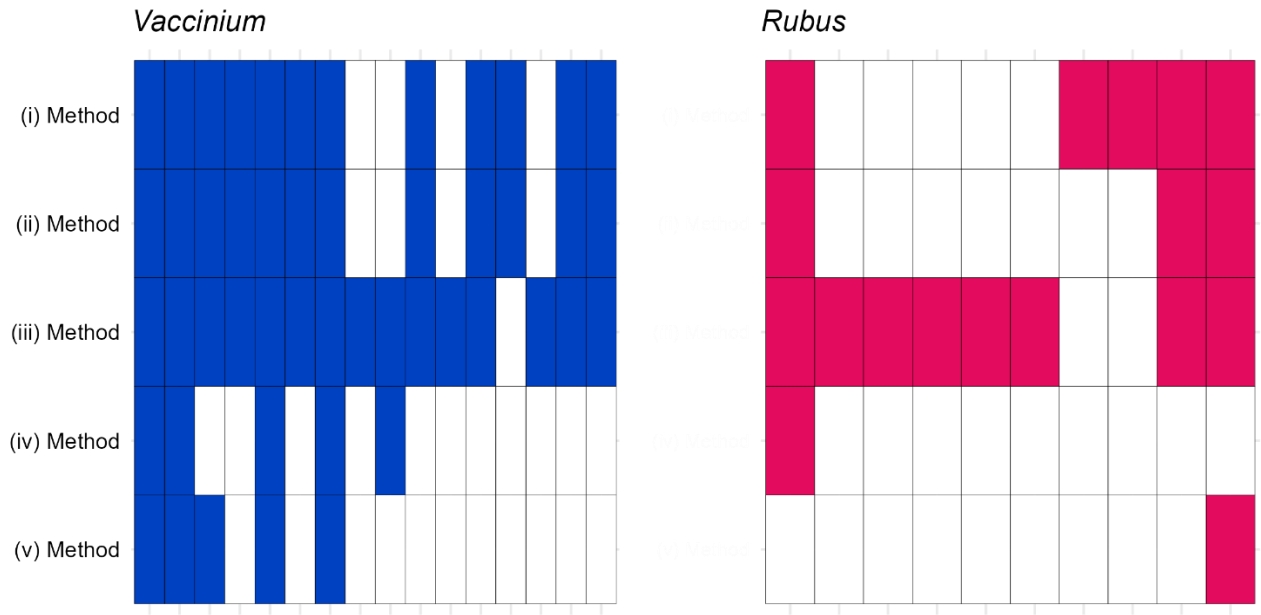
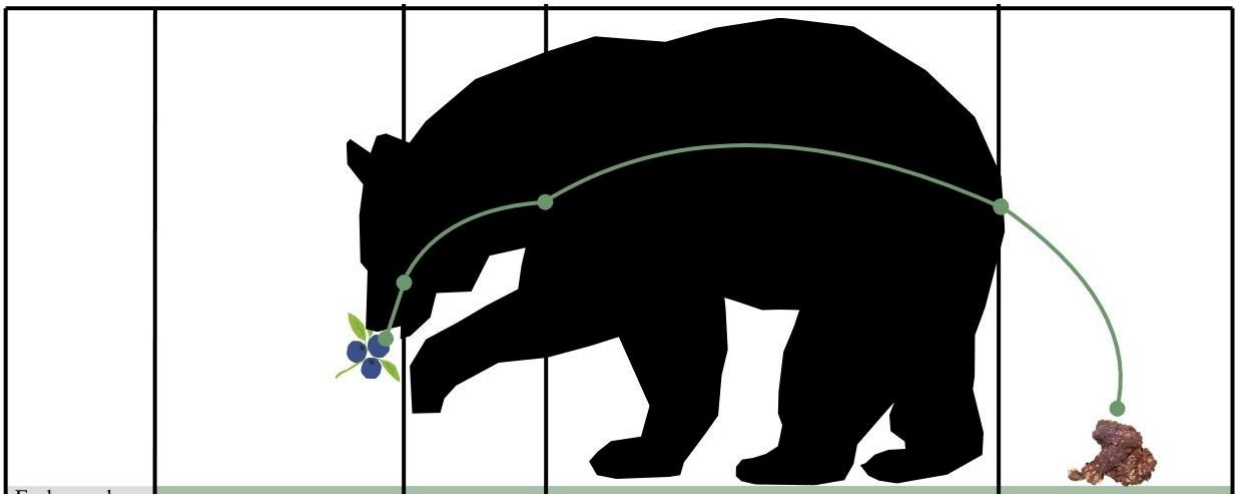


Figure IV.4: Occurrence of *Vaccinium* sp. and *Rubus* sp. (filled cell) per method (lines) and sample (columns) with *Vaccinium* sp. (n=16) or *Rubus* sp. (n=10) seeds retrieved. The methods were (i) Fleshy fruits based on metabarcoding, (ii) Plants during fruiting periods based on metabarcoding, (iii) Seed extraction, (iv) Disaggregated faeces and (v) Aggregated faeces.

IV.5.6.3 Life form detection, time, cost and expertise required

All the methods allowed the inference of fleshy-fruited plants. The methods (ii), (iii), (iv) and (v) allowed the inference of dry-fruited plants, while only the methods (iv) and (v) permitted the inference of mosses and ferns (**Fig. IV.5**). In terms of time, the methods (iii) was the fastest, whereas the germination-based methods (iv) and (v) were the longest. In terms of cost, the methods (i) and (ii) were the most expensive (extraction and sequencing costs), whereas the methods (iii), (iv) and (v) were relatively cheap if we exclude available binocular or greenhouse (only functioning and watering cost). In terms of expertise, the methods (i) and (ii) required a high level of expertise (molecular tools and bioinformatics). In contrast, (iii), (iv) and (v) required only taxonomic expertise which can be facilitated by the use of handbooks (**Fig. IV.5**).



Endozoochory filters	Ingestion	Mastication	Gut passage	Faeces
Methods used	(i) Metabarcoding (ii) Fruiting periods	(iii) Seed extraction	(iv) Seed germination from disaggregated faeces	(v) Seed germination from aggregated faeces
Plant life-forms detected	(i) Ff plants (ii) Ff plants , Df herbs	Ff plants Df herbs and trees	Ff plants, Df herbs and trees, Ferns, Mosses	Ff plants - Df herbs - Df trees - Ferns - Mosses
Time	(i) Weeks to Months (ii) Weeks to Months	Weeks	Months	Months
Cost	(i) Thousand(s) (Extraction, sequencing) (ii) Thousand(s) - Idem		Hundred (Greenhouse functioning and watering)	Hundred (Greenhouse functioning and watering)
Expertise	(i) High (ii) High	Medium	Low	Low

Figure IV.5: Chronology of the four different filters that seeds face from the consumption to the release in the fecal matrix, with the appropriate method(s) to handle each successive filter (i.e. (i) Fleshy fruits based on metabarcoding, (ii) Plants during fruiting periods based on metabarcoding, (iii) Seed extraction, (iv) Disaggregated faeces and (v) Aggregated faeces.). We also represented the plant life-forms detected (*Ff* plants = Fleshy-fruited plants; *Df* herbs = Dry-fruited herbs; *Df* trees = Dry-fruited trees; Ferns and Mosses), the time spent, the cost in euros, and the level of expertise, ranked from low to high, required for each method. The silhouette was obtained freely from Canva.com.

IV.6 Discussion

In this study, we used brown bear faeces to conduct five methods to infer endozoochorous dispersal according to the filters of endozoochory (ingestion, mastication, gut passage, faeces). We highlighted the variability in the inference of endozoochory according to the combined effect of the methods and

filters considered. First, contrary to our hypothesis, among the many different taxa inferred as dispersed by endozoochory we found only few taxa shared among methods. This difference could be related to the use of different sample masses from heterogeneous faeces, which probably biased the comparison. However, we detected more overlap among methods for plant life forms detection, with fleshy-fruited plants inferred in each methods, dry-fruited plants inferred in each methods except the method (i), and mosses and ferns inferred only in methods (iv) and (v). Although the greatest detection of plant life forms by germination-based methods confirmed our hypothesis, the absence of moss and fern in metabarcoding-based methods contradicted it. The absence of detection was probably related to the marker used (Taberlet et al., 2018). Furthermore, significant different number of taxa were detected among the methods, with method (iii) resulting in the largest number of taxa inferred despite the use of only 5g of faeces material, which contradicted our hypothesis. This result may be related to the filters of endozoochory, as the method (iii) did not consider the filters of gut passage and faeces, some of the diaspores retrieved can be intact but non-viable. On the opposite, it may be related to the requirements of diaspore germination not met for many diaspores, the low detectability of metabarcoding or the intrinsic heterogeneous nature of the faeces. Nevertheless, considering that method (v) was the only to consider all the endozoochorous filters and inferred the greatest diversity of life form, it appeared as the most reliable and complete method to infer endozoochory.

The metabarcoding-based methods (i) and (ii) considered only the ingestion filter of the endozoochory process. Those methods were risky as they were based on the occurrence of a plant that was ingested either as diaspore, shoot, leaf or root, which may not indicate endozoochory at all. This is why the method (i) was only based on the consumption of fleshy-fruited plants (endozoochorous syndrome,- Van der Pijl, 1982). The results for *Vaccinium* or *Rubus* show that the inferences of the method (i) were congruent with other methods most of the time. However, metabarcoding also missed other fleshy-fruits retrieved in method (iii) including *Sorbus* sp.; *Ribes* sp.; *Rosa* sp. and *Juniperus* sp. We could explain this lack of detection by the incomplete reference

sequence database or the length of the marker, which constrained taxonomic annotation. Based on metabarcoding, we also introduced a new method (ii) using fruiting periods data of all plants retrieved in faeces to infer potential diaspore ingestion. This method permitted to go beyond the endozoochorous syndrome (Green et al., 2022) and allowed the investigation of dry-fruited plant dispersal. We thus highlighted the dispersal by endozoochory of six dry-fruited plants, among which one was inferred in other methods (but probably more if the entire faeces was considered). Furthermore, using fruiting periods also refined the inference of fleshy-fruited plants, by revealing the occurrence of *Rubus* in two faeces outside its fruiting period, which is consistent with methods (iii), (iv) and (v). This method could be improved with enhancement of plant detection by metabarcoding, and more precise information on the fruiting period (e.g. fruiting periods of the year of faeces collection). Although expensive, imperfect and risky in terms of endozoochory inference, the use of metabarcoding may be used as an interesting tool in first approximation of endozoochory (especially for fleshy-fruited plants) while providing detailed information on the animal diet (García-Rodríguez et al., 2021b; Nawaz et al., 2019; Pauly et al., 2025a).

Based on the method (iii) highlighting intact diaspores retrieved in faeces, we inferred the largest number of taxa dispersed by endozoochory. Yet, this method may still miss tiny diaspore or spore dispersal as based on visual observation, even though it may be possible but required higher expertise and more time (e.g. Cázares and Trappe, 1994). In the same way, the results may be overestimated due to intact but potentially non-viable seeds. Moreover, visual identification encounters some limits for taxonomic annotation, as few morphological criteria exist to discriminate plant species (Cappers et al., 2006; Cappers and Bekker, 2013). Dáttilo (2025) suggested that barcoding on extracted intact seeds can be a powerful tool to refine such results. Nevertheless, the method (iii) is less expensive than metabarcoding, faster than germination experiments (and not sensitive to seed germination requirements) and require medium level of expertise to identify diaspores. In this regard, the method

(iii) was useful to infer endozoochory, despite the missed flora (mosses, ferns) and that did not consider the detrimental effect of the gut passage and the faecal matrix.

The germination-based methods (v) and (vi) tested the viability of seeds through germination and thus considered the gut passage (Traveset and Verdú, 2002). These methods permitted the detection of cryptic dispersal (mosses or ferns, Pauly et al., 2024). Such dispersal inference can also be due to contamination occurring between the defecation and the collection or from airborne origin. We limited this contamination by the use of very fresh faeces and that most species were not present near the greenhouse or in the controls (Pauly et al., 2024). For instance, endozoochorous dispersal of mosses and ferns has already been documented in other monogastric mammals respectively in flying fox *Pteropus conspicillatus* (Parsons et al., 2007) and wood moose *Apodemus sylvaticus* (Arosa et al., 2010). A recent review argued that endozoochory by large mammal could even be of ecological relevance for these plants (Brock, 2025). Nevertheless, germination experiments are also sensitive to diaspore requirements for germination that may bias the results (Karimi et al., 2020). As an alternative to germination experiments from disaggregated faeces, we performed Tetrazolium test on *Rubus* and *Vaccinium* diaspores and proved quickly that most of the seeds were viable. On one hand, Tetrazolium tests may counter seed dormancy or other requirements and provide similar results than germination experiments at a faster rate. On the other hand, it requires important expertise, handling diaspores and potentially destroying them. This can induce bias, and be time-consuming according to the number of diaspore retrieved (Miller and Peter, 2010; Soares et al., 2016). Therefore, the use of Tetrazolium offers an interesting but potentially riskier alternative to germination experiments.

Germination experiments from aggregated faeces was the only method used that considered the four filters of endozoochory. Contrasting with the original study (Pauly et al., 2024), we did not observe significant differences between germination methods “Disaggregated faeces”(iv) and “Aggregated faeces” (v) in the number of taxa detected. This was probably related to the statistical model used or

to the smaller sample size here. Nevertheless, the significant differences observed in this previous study highlighted the importance of the faecal matrix in the inference of endozoochorous dispersal, as reported elsewhere (Enders and Vander Wall, 2012; Jiménez-Martín et al., 2025; Mancilla-Leytón et al., 2012). To disaggregate brown bear faeces in the Pyrénées, dung beetles seem to be the main biotic agent, while inducing secondary dispersal (Pauly, Vanpé, et al., 2025), but other agents can be observed such as small mammals (e.g. Enders and Vander Wall, 2012). Neglecting the faecal matrix filter may overestimate endozoochory but also overlook the crucial activity of faecal visitors and secondary dispersers in the plant dispersal process (Culot et al., 2015; Ishikawa, 2011), all the more relevant for animals releasing large faeces (Stricklan et al., 2020).

We acknowledge that our comparative approach was not perfect as we used different sample masses from heterogeneous faeces, which may explain the high turnover in taxa identified among methods. The use of similar masses, particularly for method (iii), could have revealed more similarities among the methods. In the same way, the passage in the freezer (-18°C) or the greenhouse monitoring may have biased germination ability and the results of methods (iv) and (v). Our study suggests that germination from aggregated faeces provides a reliable method for inferring, but remained biased according to germination requirement. In the same way, to better quantify the endozoochorous filters, feeding experiments with identified amount of seeds, as previously done for target plants (Grande et al., 2013; Mancilla-Leytón et al., 2011; Rubalcava-Castillo et al., 2023; Tsunamoto et al., 2024) or animal materials (Lovas-Kiss et al., 2024), may provide interesting results especially according to plant life forms. Furthermore, the methods used here are not the only ones for inferring endozoochory, other such as the germination of seeds extracted on potting soil (e.g. Tavşanoğlu et al., 2021) or in Petri dishes (e.g. Lovas-Kiss et al., 2023), can properly infer endozoochory while not considering the faeces filter. Finally, diaspores journey does not end with the release in the faecal matrix as the presence of secondary dispersers (Andresen and Urrea-Galeano, 2022) and the releasing site quality are both crucial to the germination and establishment success (Schupp et al., 2010).

This study encourages greater caution and nuance for the inference of endozoochory according to the method used and the filters considered. We draw particular attention in the plant life form detectability and confidence of inference. In this sense, the comparison among studies on endozoochory must look beyond simple methodological differences, but also consider the different filters tackled in these methods. Our results also suggest that the methods could complement each other to limit the biases of each. Finally, it may be interesting to analyses the most significant filters for different plants as performed in previous studies, in order to gain a more accurate understanding of the endozoochorous dispersal process and reduce part of the black box.

IV.7 Acknowledgments

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Chapter V - Endozoochorous plant dispersal by the brown bear (*Ursus arctos*) in the Pyrénées: angiosperms but also ferns and mosses and the importance of disaggregation agents

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V.1 Résumé

Contexte : Les écosystèmes tempérés montagneux sont particulièrement sensibles aux changements globaux et notamment aux changements climatiques. Dans ce contexte, les agents zoochores et particulièrement endozoochores permettent aux plantes de se disperser sur de longues distances, un mécanisme crucial pour que les plantes puissent suivre le déplacement de leurs niches écologiques. L'ours brun apparaît comme un agent unique dans ce contexte du au fait de son écologie et de sa biologie qui se traduit par des déplacements importants et un grand domaine vital, ainsi qu'un régime alimentaire très varié incluant des angiospermes, mais aussi des fougères et des mousses. Cependant la plupart des études s'étant intéressées à l'endozoochorie par l'ours brun ont rarement examiné la dispersion potentielle de tous les angiospermes (i.e. pas uniquement à fruits charnus) et aucune sur la dispersion d'autres plantes non-angiospermes. De plus, la dispersion endozoochore induit différents filtres et notamment la matrice fécale qui peut être une barrière mécanique ou chimique à la germination, mais cette dernière n'a été que rarement considérée. Inversement, la fèces peut aussi être un fertilisant favorisant la croissance des plantules.

Méthodes : Dans cette étude, nous avons évalué l'endozoochorie par l'ours brun dans les Pyrénées et l'effet de la matrice fécale sur le succès de la dispersion à partir du nombre d'espèces et de plantules ayant germé, et de la croissance des plantules. Pour cela nous avons conduit une expérience de germination dans une serre pendant sept mois à partir de 87 fèces fraîches d'ours brun. Chaque fèces a été divisée en deux traitements (*brute versus filtrée*) pour quantifier l'effet de la matrice fécale sur la germination et la croissance des plantules. La fèces *brute* consiste en une matrice fécale intacte,

structurée et composées de macro-éléments (e.g. cailloux, glands concassés,..), à l'inverse la fèces *filtrée* correspond à une fèces que nous avons déstructurée et lessivée pour enlever les macro-éléments et les nutriments. Les fèces des deux modalités ont été laissées plus de 200 jours, avec un arrosage fréquent, et les plantules ont été suivies tous les 4 jours, puis mesurées à 15 et 30 jours après germination (hauteur de tige et nombre de feuilles vraies).

Résultats : Nos résultats montrent que l'ours brun ne disperse pas que des plantes à fruits charnus mais aussi des plantes à fruits secs et pour la première fois démontrée chez les Ursidés, des mousses et des fougères. Nous avons aussi mis en avant que la matrice fécale agit comme un filtre important sur la germination avec significativement moins de plantules et d'espèces dans les fèces *brutes* que dans les fèces *filtrées*. En revanche, nous n'avons pas trouvé d'effet de la fèces sur la croissance des plantules, potentiellement dû à peu de nutriments disponibles dans les fèces, ou au contraire suffisamment de nutriments presents dans le terreau utilisé.

Conclusions : Notre étude montre le rôle de l'ours brun dans la dispersion des plantes qui ne produisent pas de fruits charnus, suggérant que le spectre de dispersion par cet animal est bien plus large que supposé jusqu'ici. Nous montrons également que la matrice fécale est determinante pour l'endozoochorie, au même titre que sa désagrégation par des agents biotiques ou abiotiques pour une dispersion efficace.

Mots clés: Endozoochorie, *Ursus arctos,* Fougère, Mousse, Dispersion des plantes, Ingénieur de l'écosystème

V.2 Abstract

Endozoochory by megafauna enables temperate mountain plants to disperse over long distances. As an endozoochorous agent, Brown bear may play a unique role through its biology and ecology especially because of its very diverse diet (angiosperms, ferns, mosses). However, few studies have been conducted on the dispersal of all angiosperms and none on ferns or mosses. Also, the fact that the faecal matrix could represent a barrier for the germination of dispersed seeds due to various physical or chemical constraints, has often been neglected. In this study, we investigated endozoochory by the European brown bear and the faecal matrix effect on germination success. We conducted a seedling emergence monitoring experiment in greenhouse during seven months to assess seed dispersal potential based on 86 faeces. Each sample was split into two treatments (raw vs. filtered faeces), to test the effect of the faecal matrix on seedling germination and growth. We found that brown bear dispersed not only fleshy-fruited plants, but also dry-fruited plants, and for the first time among Ursids, ferns and mosses. We also pointed out that the faecal matrix acts as an important barrier for germination with little effect on growth. These results highlight the role of brown bears in the dispersal of non-fleshy-fruited plants, and suggest that the spectrum of plant species potentially dispersed by brown bear is wider than formerly thought. They also stress the importance of faeces disaggregation on seed dispersal outcomes, a mechanism mediated by abiotic or biotic agents.

Keywords: Endozoochory; *Ursus arctos*; Fern; Moss; Plant dispersal; Ecosystem engineers

V.3 Introduction

The role of seed dispersal in the dynamics of plant communities is increasingly considered as a critical process (Ozinga et al., 2009; Schupp et al., 2010). Seed dispersal enables plants to escape from sub-optimal abiotic (e.g. nutrient limitation) and biotic (e.g. competition) conditions (Howe and Smallwood, 1982; Venable and Brown, 1993; Willson and Traveset, 2000). Human activity confronts plants with additional threats such as rapid climate change, habitat loss and fragmentation and invasive species. Climate change is an even greater threat in montane biomes (Rangwala and Miller, 2012), moving altitudinal zonation higher up in altitude (Walters and Miller, 2001). In this context, plant dispersal over long distance appears crucial (Cain et al., 2000) and animal mediated seed dispersal appears as a key process (Jordano, 2017; Nathan et al., 2008) regardless of the plant syndromes (Green et al., 2022). Seeds can be passively transported by animals on external parts of their body, e.g on fur (epizoochory) or through fruit or seed consumption that are later excreted with faeces (endozoochory). Numerous endozoochorous agents have been described including birds, ungulates, small and large carnivores, or even lizards. Ungulates have been extensively studied for their role in the dispersion of herbaceous seeds and non-fleshy fruits by endozoochory (Baltzinger et al., 2019). On the other hand, birds, lizards and carnivores are well documented for their role in the dispersion of fleshy fruits (García-Rodríguez et al., 2022; Nakashima and Do Linh San, 2022; Valido and Olesen, 2019; Wenny et al., 2016) even if dispersal of other plants has been reported such as dry fruits or ferns (Green et al., 2008; Lovas-Kiss et al., 2018; Otani, 2002). Within the community of seed dispersers, large mammals appear as the best candidates for dispersing large numbers of seeds in a single faeces (Baltzinger et al., 2019; García-Rodríguez et al., 2022; Tochigi et al., 2022) and over long distances (Jordano, 2017; Nathan et al., 2008).

In temperate mountains, most of the large seed dispersers are herbivores such as Cervidae (Goldfuss) or Bovidae (Gray), but also omnivores including Suidae (Gray) and Ursidae (L.). Ursids stand out

due to their unique ecology, in particular the widely distributed brown bear (*Ursus arctos*, L. Ursidae). Indeed, brown bear is an apex consumer, with a monogastric system with long gut retention time (Elfström et al., 2013; Patten, 1993; Tsunamoto et al., 2024), a high mobility (Lalleroni et al., 2017; Patten, 1993; Tsunamoto et al., 2024) and a very omnivorous flexible diet across sites and seasons (Mowat and Heard, 2006; Niedzialkowska et al., 2019; Vulla et al., 2009). Throughout the year, brown bear consumes fleshy fruits, hard mast, herbs, ferns and mosses (Elgmork and Kaasa, 1992; García-Rodríguez et al., 2021b; Lagalisse et al., 2003). However, most studies on brown bear endozoochory have focused solely on the dispersal of fleshy fruited plants (García-Rodríguez et al., 2021a; Harrer and Levi, 2018; Tsunamoto et al., 2024) and herbs (Karimi et al., 2018; Lalleroni et al., 2017; Tavşanoğlu et al., 2021). Indeed, despite their well-documented accidental or intentional consumption by brown bear, no investigation has been conducted on moss or fern dispersal. Yet, endozoochory of mosses and ferns by other vertebrates has been demonstrated (Arosa et al., 2010; Lovas-Kiss et al., 2018; Russo et al., 2020) as well as by invertebrates (Boch et al., 2016, 2013).

Germination success of diaspores dispersed by endozoochory depends notably on the gut passage (Schupp et al., 2010). Depending on the species dispersed, brown bear gut passage can be negative, null or positive (Auger et al., 2002; Nowak and Crone, 2012; Tavşanoğlu et al., 2021; Traveset and Willson, 1997; Tsunamoto et al., 2024). In these studies and other endozoochorous studies by large mammals (Lee and Lee, 2020; Picard et al., 2016) the faecal matrix was artificially disaggregated or seeds were extracted from the faecal matrix before testing for seed germination potential. This handling eliminated the role of the faecal matrix as a potential barrier for germination. However, one study on the dispersal of three plant species by American Black Bear (*Ursus americanus*, Pallas Ursidae) (Enders and Vander Wall, 2012) and others reports on other large seed dispersers (Mancilla-Leytón et al., 2012; Miller, 1995; Stricklan et al., 2020) showed that seeds embedded in large faeces presented a lower germination rate, which stresses the fact that faeces can represent a harsh environment for germination. Conversely, faeces can represent a fertile environment rich in nutrients,

which potentially enhances seedling growth once seeds have germinated (Traveset et al., 2007, 2001). We therefore question the overall intrinsic effect of the faecal matrix on seed dispersal considering both germination and later growth stages as an important step in the dispersal process.

In this study, we assessed the pool of species potentially dispersed throughout the year including all plant life forms by Eurasian brown bear (*Ursus arctos arctos*) to estimate the whole potential of plant dispersal. We expected herbaceous angiosperms to be dispersed throughout the year and fleshy fruits mainly in the summer, according to the bear diet and the plant fruiting periods. We expected that moss, fern and dry-fruit bearing woody plants to be sporadically dispersed according to accidental or occasional consumption. We also expected very few or no large hard mast bearing species dispersal due to the mastication filter (Lalleroni et al., 2017; Tavşanoğlu et al., 2021). We also tested the effect of the faecal matrix either as a barrier to seed germination or as a fertiliser to seedling growth. We expected that the faecal matrix should negatively affect plant germination but could subsequently boost seedling growth.

V.4 Materials and methods

V.4.1 Study site

Our study was conducted in the Pyrénées, a mountain chain (36,600m²) shared between the south of France, Andorra and the north of Spain, peaking at 3,400 meters in altitude. Forest covers more than 40% of the landscape and is dominated by hard-mast bearing trees. Above the timber line, large open areas are covered by fleshy-fruited shrubs and herbaceous plants (Martin et al., 2012). The mountain chain hosts a wide variety of plants, including endemic species (Ninot et al., 2017) and several potential seed dispersers including brown bear, small carnivores (e.g. European Pine Marten *Martes*

martes, L. Mustelidae), birds (Eurasian Jay, *Garrulus glandarius* L. Corvidae) but also wild (e.g. Wild Boar *Sus scrofa* L. Suidae) and domestic (e.g. cattle *Bos Taurus* L. Bovidae) ungulates.

V.4.2 Study population

The total brown bear population of the Pyrénées included 79 individuals in 2022 and was therefore considered as critically endangered (Sentilles et al., 2024). It is still growing, benefiting from successive (in 1996, 2006, 2016 and 2018) translocations of Slovenian brown bears. In 2022 the population range covered more than 5700 km² from east to west of the Pyrénées (Sentilles et al., 2023). Based on coproscopic investigations, this population is known for consuming mostly plant resources such as forbs, berries and hard mast. Animals such as rodents, ungulates (domestic and wild) and invertebrates also contribute to its diet (Lagalisse et al., 2003).

V.4.3 Faeces collection

We collected bear faeces between 2017 and 2022 in the French part of the Pyrénées (18 000km²), with the help of a dog trained to detect bear scat (Sentilles et al., 2021), over the whole bear activity season. The faeces were searched systematically on identified feeding areas (hosting fleshy fruits or hard mast bearing plants) and opportunistically following recent sightings, livestock depredations, or damages on apiaries. The faeces collected were georeferenced and then conserved frozen until germination trial (-18°C degrees), such conservation conditions is optimal for orthodox species (i.e. species able to survive extreme cold or dry conditions), but not optimal for recalcitrant species, like Fagaceae (Dumort.) in the Pyrénées whose seeds are generally destroyed by chewing (De Vitis et al., 2020). We selected 86 faeces according to their freshness (less than one day old), the season, the location and the individual (based on genotyping of the external part of the faeces; Vanpé et al., 2022) to avoid pseudo-replications. We thus kept 11, 35, and 41 in spring, summer and fall respectively, according to meteorological season (**Fig. V.1**) (e.g. spring starts on March 1), which corresponds more or less to the period when the brown bear emerge from the den, the rut and the hyperphagia

periods. The faeces came from at least 31 genetically different brown bears and composed of different food items.

Figure V.1: Spatial and seasonal distribution of 86 brown bear faecal samples collected in the French Pyrénées according to meteorological seasons (e.g. spring starts on March 1st).

V.4.4 Germination trial

The germination trial was conducted under greenhouse conditions in Nogent-sur-Vernisson (Loiret, France) during 209 days from 05/04/2023 to 31/10/2023. The greenhouse was painted in white to limit overheating and operated with a system of shading and opening roof according to light and temperature conditions. Each faeces was split into two 75g portions of material according to our two treatments (i.e. two subsamples) to test the effect of the faecal matrix on germination and seedling growth with *a priori* the same level of seed density (**Fig. V.2**). The first treatment, i.e. the "raw faeces", corresponded to intact portion of faeces. The second treatment, i.e. the "filtered faeces", was the same portion of faeces artificially disaggregated and water leached through three successive sieves: 4, 0.8 and 0.08mm in order to subtract non-seed macro-elements (e.g. hard mast fragments)

and reduce the amount of nutrients. Both treatments were placed on potting soil (blond sphagnum peat moss and coarse perlite, ©Klasmann/Dielmann) and a wipe (i.e. cotton gauze for medical use) under the potting soil, in a rectangular pot measuring 13x9x4.5 cm (length by width by height). For faecal samples lighter than 150g but heavier than 75g (n=11), we only monitored the “raw faeces” treatment with 75g of material to only assess plant dispersal potential. For faecal samples that were lighter than 75g (n=10), we used all the material for the "raw faeces" treatment for the same reason. We therefore ended up with 86 “raw faeces” and 65 “filtered faeces”. The pots were then placed on a single tray and aligned in two sections (corresponding to the two treatments) of four columns, one section per treatment. After 121 days of monitoring, we alternated columns and rows to limit a confounding effect of placement in the greenhouse. Between the two sections, we placed a column of 20 control pots with the same substrate and without faecal material to check out for potential airborne or potting soil contamination. In addition, we periodically veiled the experiment to prevent external contamination, particularly during the Asteraceae (Bercht. & J.Presl) and Salicaceae (Mirb.) fruiting periods.

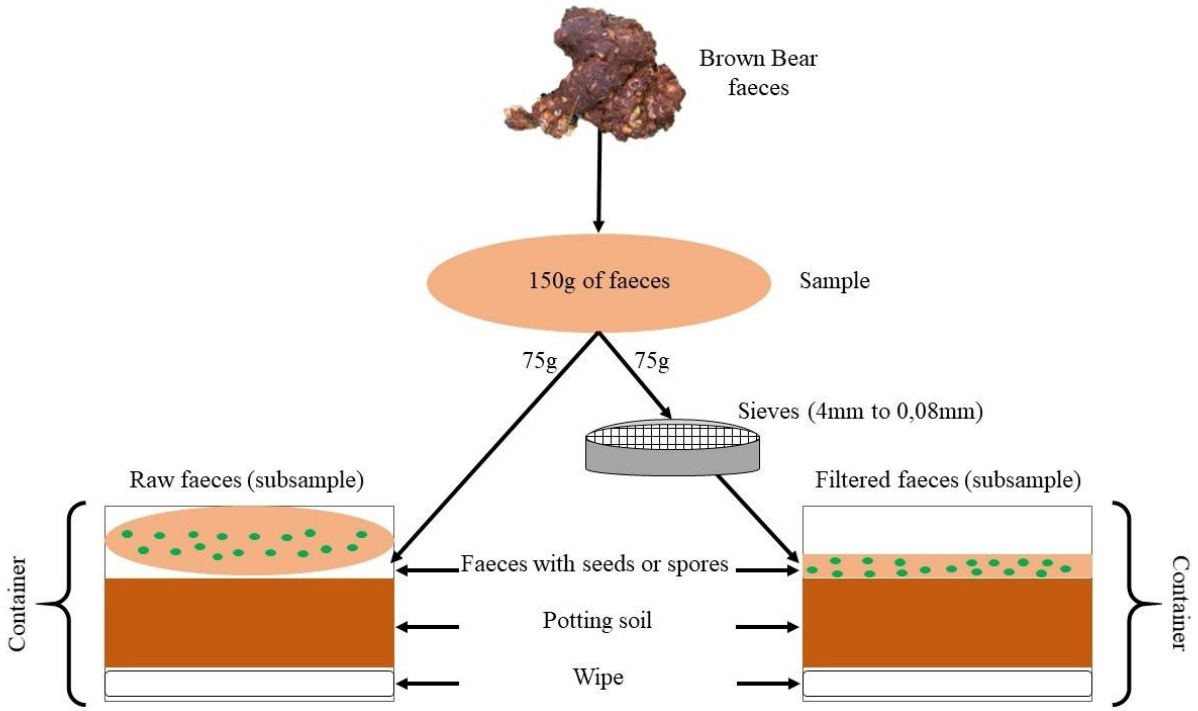

Figure V.2: Faeces monitoring for the germination experiment designed to test the effect of the faecal matrix on germination and growth. Each faeces was split in a “raw” (i.e. intact) and “filtered” (i.e. disaggregated) treatments.

We monitored every four days each sub-sample to map and count the new and dead emerged seedlings. In case of massive seedling germination (e.g. *Vaccinium myrtillus* L., Ericaceae), mapping was not feasible, making it impossible to clearly identify new and dead seedlings, in this case we just counted the number of seedlings. At each visit, we watered the tray around the sub-samples to avoid physical disturbance of the fragile seedlings and allow wetting from below thanks to the absorbent wipe. During summer, we watered the sub-samples every day. We assigned seedlings to the finest taxonomic level based on morphological criteria (Hanf and Martin 1970; Muller 2013). Some seedlings died before full identification confidence due to the lack of criteria according to the early-life stage. These cases were labelled "unconfirmed", along with the putative taxon. Dead and not identified seedlings were labelled "undetermined". As a precaution, we removed the seedlings once identified to limit competition with other seedlings, by cutting them at the basis of the stem to limit any disturbance to the substrate. We also inventoried and identified all the bryophytes and marchantiophytes in each subsample at the end of the monitoring, because that required extractions disruptive to the substrate. Plant species that were recorded in both controls and treatments were discarded as contaminations, the others as truly dispersed. Similarly, plants that were only recorded in samples with bear faeces but not listed in the Pyrénées flora database (FLORAPYR 2024) were considered as contamination. Plant of Pyrénées that only germinated in faecal treatments (either “raw” or “filtered”) were used to assess seed dispersal potential. Differences in germination between treatments were used to estimate the effect of the faecal matrix.

V.4.5 Trait measurements and qualitative seed dispersal estimation

To test the effect of the faecal matrix on seedling growth, we monitored two traits on: shoot length (in cm) and the number of true leaves per seedling (excluding cotyledons). These traits were monitored 15 and 30 days after germination.

For each plant species that was monitored and assigned as dispersed, we used botanical references (FLORAPYR, 2024; Prelli and Boudrie, 2001; Saule, 1991) to verify its altitudinal range and canopy dependence (open, close or both) in the Pyrénées. For some plant species, we also noted the association with watercourses (see in supplementary: https://doi.org/10.57745/CPS1V3). Then, we used the geographical coordinates that were recorded for each collected faeces to determine the altitude, habitat type (open, close or edge) and the presence of watercourses at less than 50 meters, using Google Earth (v. 10.49.0) and the database "Forêt" (v. 2_https://geoservices.ign.fr/bdforet). Hence, for each species, we checked if dispersal occurred within its altitude range and in a suitable habitat in terms of habitat openness and watercourse proximity.

V.4.6 Statistical analysis

To evaluate the effect of faecal matrix on germination, we compared the number of seedlings and the number of species per sub-sample between the two treatments among faecal samples with both treatments (n=65). Considering the large number of zeros (i.e. no germination), we ran a Hurdle model on a truncated Poisson distribution (Min and Agresti, 2005; Potts and Elith, 2006) with sample ID as a random factor. For these analyses, we decided not to combine the vascular plants with the mosses and to make separate models, since we could not quantify the number of seedlings for mosses. To evaluate the effect of faecal matrix on vascular plant growth, we worked on the same pool of samples and decided to keep only the data for seedlings with measurements at both 15 and 30 days, and presenting no inconsistencies. For the analysis, we only kept the species for which more than 10

seedlings were observed. The number of leaves was analysed using a GLMM with Poisson distribution with sample ID as a random factor. The shoot length was analysed using non-parametric Permutation mixed model with sample ID as a random factor as the conditions were not met for parametric approaches.

All statistical analyses were carried out on R studio (v.4.3.2) with the use, in the order of the previously announced models, of the packages 'glmmTMB' (v.1.1.9) (Brooks et al., 2017), 'lme4' (v.1.1-35.1) (Bates et al., 2015) and 'lmerPerm' (v.0.1.9) (Wentao, 2023). To calculate the R^2 of our models we used the package 'performance' (v.0.12.3) (Lüdecke et al., 2021) Figure 1 was computed with QGIS (v3.30), Figures 2 and 3 was computed with Microsoft office Professional plus 2016. Figure 4 was computed with R studio and ggplot2 package (Wickham, 2011) using geomsmooth function with non-parametric "loess" formula. All Figures should be readable by colour-blind people.

V.5. Results

V.5.1 Plant dispersal potential

All the species of plants identified during the experiment are found in the Pyrénées. Within bear faeces (n=86), 20 samples show angiosperm plant germination among which five species of herbaceous plants, two species of fleshy-fruited plants and one tree species germinated (**Table V.1**). Herbaceous plants germinated in faeces collected during the three seasons, but particularly in faeces collected in the fall (three taxa). Conversely, fleshy-fruited plants only germinated during summer (**Fig. V.3**). *Betula* sp. (L., Betulaceae) was found twice, once in spring and once in the fall. Salicaceae species, *Juncus effusus* (L., Juncaceae) and *Calluna vulgaris* (Salisb., Ericaceae) were considered as contamination as they were also observed in the control pots (**Table V.1**). Hard mast fragments from Fagaceae trees were found in faeces. In terms of number of seedlings, *Vaccinium myrtillus* was by

far the most abundant species with a total of 179 seedlings clearly identified, whereas we counted from one to six seedlings for the other germinating flowering-plants (**Table V.1**). Most of the angiosperms were dispersed within their altitudinal range (86%) and in a suitable site (71%) (Table V.1). *Vaccinium myrtillus* was dispersed in suitable habitats (open and close), as well as *Rubus idaeus* (L., Rosaceae) and *Holcus lanatus* (L., Poaceae) that was dispersed in suitable habitat (open). *Persicaria hydropiper* (Spach, Polygonaceae) was not dispersed in suitable habitat (close habitat far from a river). The only tree species, *Betula sp.* was dispersed in both suitable and non-suitable sites. Conversely, *Oxalis corniculata* (L., Oxalidaceae) was the only species dispersed outside its range in three out of four occurrences higher in altitude than its known altitude range and in all instances in unsuitable sites (see supplementary data https://doi.org/10.57745/CPS1V3).

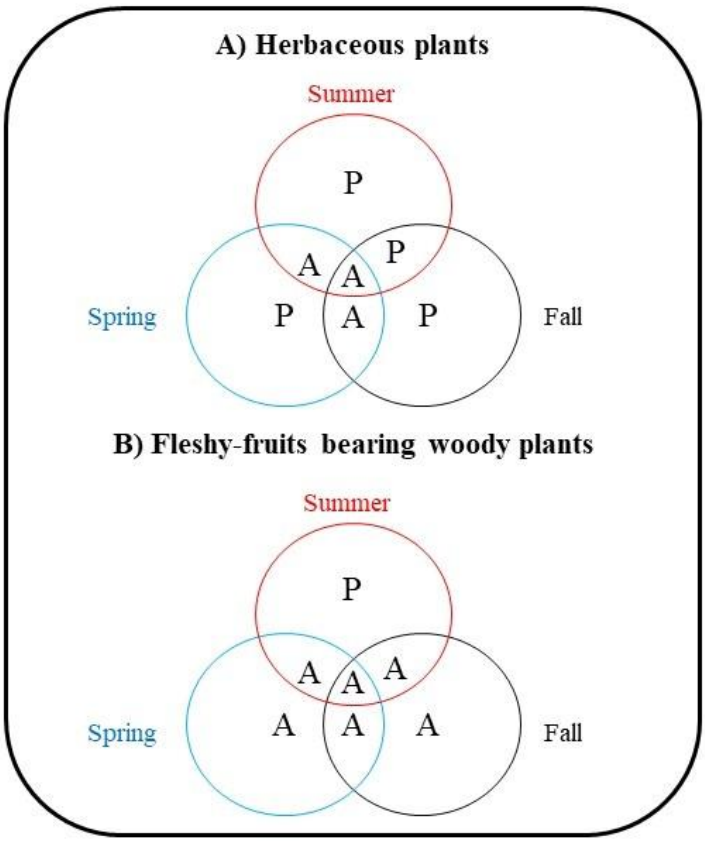

Figure V.3: Occurrence of germinated plant species (Presence = P; Absence = A) per season and shared among seasons (i.e. one circle = one season), according to their life form, herbs or woody plants with fleshy fruits.

We also reported the germination of a fern in fall and spring, *Dryopteris carthusiana* (H.P. Fuchs, Dryopteridaceae), which was dispersed within its range and in a suitable habitat in two out of four occurrences. At the end of the experiment, we reported the presence of 13 species of mosses in the samples, seven of which were only found in bear faeces. Among species that were only found in bear faeces, all were dispersed within their range and 55% in suitable habitats (**Table V.1**).

Table V.1: Number of plant germinations recorded within brown bear faeces (n=86) according to their life form, altitudinal range and the habitat suitability of their releasing site**.** (To be continued)

Taxa	**Life form**[1]	**#Seedlings**	**Contamination**[2]	**#Samples**	**Altitudinal range**[3]	**Habitat Suitability**[4]
			Flowering plants			
Betula sp.	T	2	No	2	2/2	1/2
Vaccinium myrtillus	S	179	No	11	11/11	11/11
Unconfirmed *V. myrtillus*	S	94	/[5]	11	/	/
Rubus idaeus	S	2	No	2	2/2	2/2
Persicaria hydropipper	H	1	No	1	1/1	0/1
Oxalis sp.	H	1	No	1	NA	NA
Oxalis corniculata	H	4	No	4	1/4	0/4
Holcus lanatus	H	1	No	1	1/1	1/1
Asteraceae	H	1	No	1	/	/
Undeterminated	U	14	*na*	13		
Salicaceae	T	18	Yes	14		
Salix sp.	T	20	Yes	18		
Populus tremula	T	89	Yes	43		
Calluna vulgaris	H	9	Yes	8		
Juncus effusus	H	1	Yes	1		
			Ferns			

Dryopteris carthusiana	F	6	No	4	4/4	2/4
Mosses and liverworts						
Aulacomnium palustre	M		No	1	1/1	0/1
Bryum dichotomum	M		No	2	2/2	2/2
Ceratodon purpureus	M		No	6	6/6	5/6
Leptodictyum riparium	M		No	6	6/6	0/6
Pseudoscleropodium purum	M		No	1	1/1	1/1
Tortula muralis	M		No	3	3/3	2/3
Streblotrichum convolutum	M		No	1	1/1	1/1
Amblystegium serpens	M		Yes	86		
Bryum argenteum	M		Yes	18		
Funaria hygrometrica	M		Yes	65		
Leptobryum pyriforme	M		Yes	7		
Marchantia polymorpha	M		Yes	5		
Ptychostomum pseudotriquetrum	M		Yes	39		

Note: [1]Life form: F = Fern; H = Herbaceous; M = Mosses; S = Shrub; T = Tree; U = Unknown
[2]Contamination specified if the species is found in the control pots without faeces (yes) or not (no)
[3]Plant dispersal within their altitudinal range based on the site of the faecal sample release (e.g. For the 2 samples containing germinated *Betula* sp., both faeces were located in the altitudinal range of *Betula* sp).
[4]Plant dispersal in a suitable habitat is based on the site of the faecal sample release and the ecological requirements of the plant (openness and depending on the species, presence of watercourse).
[5] /: No information

V.5.2 Faeces as an inhibitor of seed germination and a mild booster of seedling growth

When comparing the plants that germinated in faeces with both treatments available (n=65), the average number of species per sub-sample tended to be higher (hurdle model: p= 0.99) in filtered faeces (m=0.29, sd=0.52) than in raw faeces (m=0.14, sd=0.35). In addition, raw faeces had a higher probability of showing no species germinated at all than filtered faeces (hurdle model: p= 0.004, zvalue=2.8, R^2 = 0.97). The average number of seedlings per sample was significantly higher (hurdle model: p=1.47e^{-07}, zvalue=-5.3, R^2 = 0.88) in filtered (m=2.7, sd =10.4) than in raw faeces (m=1.3, sd =6.1). In details, four vascular plants germinated in both raw and filtered faeces and five species only in filtered faeces (**Table V.2**). Filtered faeces also tended (hurdle model: p= 0.99) to show slightly

more dispersed moss species per sample (m=0.19, sd=0.52) than raw faeces (m=0.06, sd=0.24). In addition, raw faeces had a higher probability of showing no mosses at all compared to filtered faeces (hurdle model: p= 0.003, zvalue=2.9, R^2 = 0.99). More precisely, one moss species (*Ceratodon purpureus,* Brid. Dicranaceae) germinated in both treatments, four species only in filtered faeces and one species only in raw faeces (**Table V.2**). *Ceratodon purpureus* germinated from the same sample in both treatments in two cases out of three. *Streblotrichum convulvatum* (P.Beauv., Pottiaceae) germinated in a sample with only "raw faeces" and was not included in this comparison.

Table V.2: Seedling abundance per plant species in the subset (n=65) of brown bear faeces with both the raw and filtered faeces treatments.

Species	**Raw faeces**			**Filtered faeces**		
	#Samples[1]	#Seedlings[2]	#Seedlings / sample[3]	#Samples	#Seedlings	#Seedlings / sample
Flowering plants						
Betula sp.	1	1	1.0	1	1	1.0
Vaccinium myrtillus	6	38	6.3	6	115	19.6
Unconfirmed *V. myrtillus*	4	34	8.5	5	40	8.0
Rubus idaeus	1	1	1.0	1	1	1.0
Persicaria hydropipper	0	0	0	1	1	1.0
Oxalis sp.	0	0	0	1	1	1.0
Oxalis corniculata	0	0	0	4	4	1.0
Holcus lanatus	0	0	0	1	1	1.0
Asteraceae	0	0	0	1	1	1.0
Total	8	74	9.5	16	165	10.5
Ferns						
Dryopteris carthusiana	1	3	3.0	3	3	1.0
Mosses						
Aulacomnium palustre	0			1		
Ceratodon purpureus	3			3		
Leptodictyum riparium	0			5		
Pseudoscleropodium purum	1			0		

Bryum dichotomum	0	2
Tortula muralis	0	1

Note: [1]#Samples: number of brown bear faeces samples containing seedlings from the given plant species.
[2]#Seedlings: total number of seedlings from the given plant species.
[3]#Seedlings/sample: Average number of seedlings per brown bear faeces with at least one seedling of the species germinated (i.e. *Vaccinium myrtillus* in "raw" treatment is 38 / 6 = 6.3)

Vaccinium myrtillus was the only species with more than 10 seedlings, with at least 115 and 38 seedlings in filtered and raw faeces, respectively (**Table V.2**, **Fig. V.4**). In faecal samples with both treatments (n=65), germination of *Vaccinium myrtillus* seemed to start earlier in the filtered than in the raw faeces (**Fig. V.4**). Regarding seedling traits, no significant difference was observed between treatments. However, shoot length of *Vaccinium myrtillus* on day 15 tended to be slightly higher in raw than in filtered faeces (Permutation mixed model: p= 0.96), with respectively 0.36 cm (sd=0.12) and 0.31 cm (sd=0.17) cm on average . On day 30, the average shoot length was 0.50 cm on average (Permutation mixed model: p= 0.82) in both raw (sd=0.13) and filtered (sd=0.17) faeces. The number of true leaves tended to be higher in raw than in filtered faeces on day 15, with respectively 0.9 leaves (sd=1.1) and 0.5 leaves (sd=0.7) (GLMM poisson: p = 0.13) on average. We observed the same trend on day 30 (GLMM poisson: p = 0.56), with 1.9 (sd=1.4) leaf and 1.7 leaf (sd=1.88) on average in raw and filtered faeces, respectively.

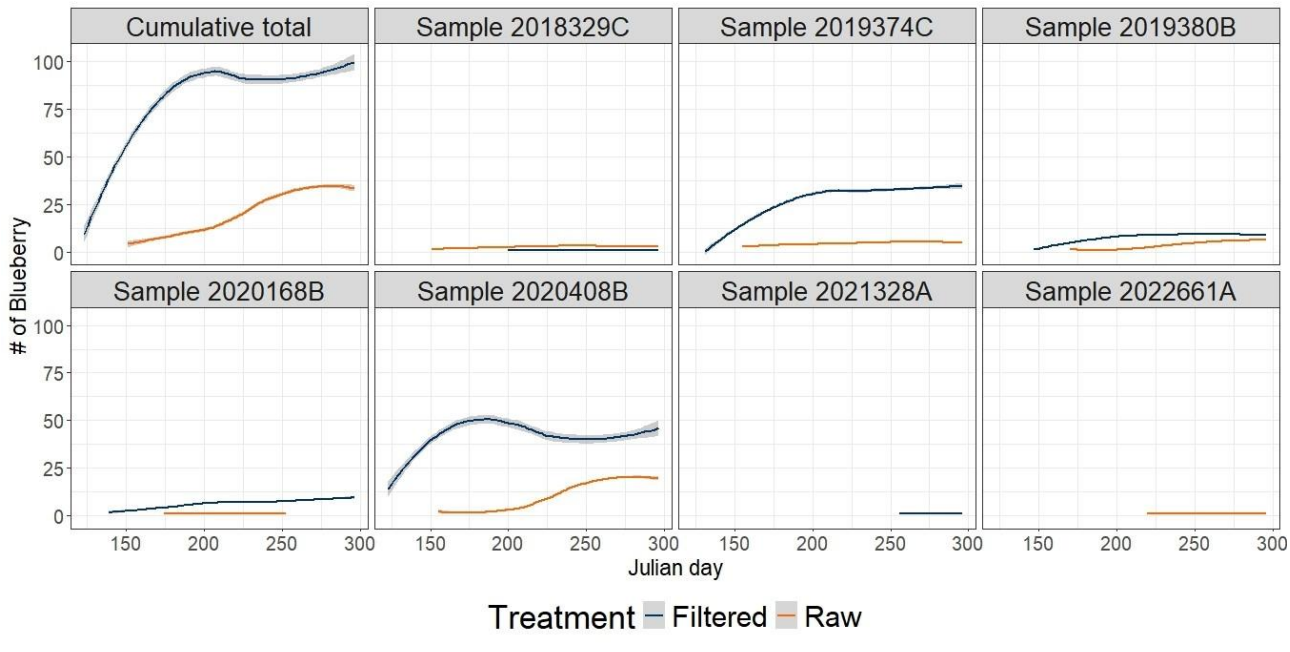

Figure V.4: Germination dynamics of blueberries (*Vaccinium myrtillus*) on all samples (Cumulative total) or per sample. The blue curves (#003366) represent the germination dynamics in the faeces from the ”filtered” treatment (i.e. disaggregated faeces) and the orange curves (#FF6600) in the faeces from the ‘raw’ treatment (i.e. intact faeces). Each curve is associated with a t-based approximation confidence interval in grey (#A9A9A9) based on loess method of ggplot2 package.

V.6 Discussion

We recorded eight different angiosperm species dispersed by brown bears in the Pyrenean landscape through endozoochory. These included five herbaceous species, two fleshy-fruit bearing species, and one tree species, which supports the paradigm that brown bear does not only disperse fleshy-fruit bearing species (Karimi et al., 2020; Tavşanoğlu et al., 2021). Our results showed a lower number of angiosperm species dispersed as compared to previous results obtained in the Pyrénées based on the identification of intact seeds observed in faeces. Indeed, Lalleroni and collaborators (2017) recorded potential seed dispersal of 30 taxa by brown bear in the Pyrénées. This difference can be explained by the absence of seeds in our faeces due to the bear omnivorous diet, the presence of intact but low-vigour or non-viable seeds (French, 1996; Mancilla-Leytón et al., 2012; Varela and Bucher, 2006), by ecological germination requirements that may have not been satisfied in our greenhouse conditions (Fernández-Pascual et al., 2021), or by biases induced by the age of our faeces and their conservation monitoring. However, similarly to results from Lalleroni and collaborators (2017) we found a majority of herbaceous species and fewer woody ones. As expected from their phenology, fleshy fruit bearing species are dispersed in summer, especially *Vaccinium myrtillus*, as part of a well-documented mutualist interaction between bears and fleshy-fruit bearing Ericaceae (García-Rodríguez et al., 2021a; García-Rodríguez and Selva, 2021; Harrer and Levi, 2018; Nowak and Crone, 2012; Steyaert et al., 2019). Herbaceous angiosperm species were dispersed through the year as we predicted based on brown bear diet in Pyrénées (Lagalisse et al., 2003). Their seeds are probably consumed accidentally with foliage consumption, following the “foliage is a fruit” hypothesis (Janzen, 1984). We also suggest that consumption of some herbaceous seeds may occur when bear

feeds upon hard mast on the ground during the spring or the fall. Similarly, we argue that the occurrence of *Betula* seeds in bear faeces after the fruiting period of this species can be explained by accidental consumption, as these seeds are characterized by a long residence time in the environment. We found no dispersion of hard-mast bearing trees, despite numerous fragments of seeds observed in faeces, because hard mast is generally destroyed by mastication.

For the first time to our knowledge, we demonstrated the potential dispersal of mosses and ferns by an Ursid species thanks to our germination experiment. One fern, *Dryopteris carthusiana,* germinated in bear faeces but not in control and represented the first evidence of potential fern dispersal by an Ursid species. This result is consistent with the diet of Eurasian brown bear, for which the consumption of *D. carthusiana* but also other ferns species has been documented throughout the year (García-Rodríguez et al., 2021b; Lagalisse et al., 2003). Although ferns are classically considered as being dispersed by abiotic agents such as wind or water (Mehltreter et al., 2010), some recent studies have reported fern dispersal after spore ingestion by monogastric mammals (Arosa et al., 2010; Brock and Collier, 2020), ruminants (Bråthen et al., 2007) or birds (Hervías-Parejo et al., 2019; Lovas-Kiss et al., 2018). We also reported seven moss species that were potentially dispersed by brown bear, probably linked with accidental consumption, as formerly reported in a study on bear diet (McLaren et al., 2021). Moss dispersal is also often considered to be dependent on abiotic vectors (Glime, 2021), but recent studies show that mosses can also be dispersed by bird endozoochory (Deregnier et al., 2024; Lázaro et al., 2021; Wilkinson et al., 2017), ruminant mammals (Bråthen et al., 2007) and monogastric mammals (Parsons et al., 2007) including humans (Dickson, 1997; Dickson et al., 2019). Our results confirm that zoochory may be an overlooked mean of dispersal for some fern and moss species.

In these studies moss or fern dispersal involved ingestion of spores (Arosa et al., 2010; Bråthen et al., 2007; Lovas-Kiss et al., 2018) or even fragments in the case of mosses, which regenerate once

excreted in faeces (e.g. (Parsons et al., 2007). All these results and ours suggest that endozoochory by mammals may be an effective mechanism for long distance dispersal of ferns and mosses (Boch et al., 2016), which are crucial organisms in many ecosystems (Eldridge et al., 2023; Mehltreter et al., 2010; Turetsky et al., 2010). However, we acknowledge that we cannot completely rule out the outer origin for ferns, mosses or angiosperms in brown bear faeces. Spores or diaspores may have been deposited on the faeces between defecation and faeces collection. This could be controlled only using the core of the faeces. However, as the faeces collected were very fresh (less than one day), the probability of such contamination remains low. During the experiment, fern spore may be airborne or present in the potting soil used, although this potting soil was supposed to be fern-clear (Picard et al., 2016) and we did not find any fern individuals in our 20 control. Similarly, mosses could be airborne as suggested by Jaroszewicz et al., (2011), but the presence of a same moss species (*C. purpureus*) in subsamples from identical faeces gave us confidence in the endozoochorous origin of this moss and potentially others. In addition, most of the mosses found in our bear scat samples were not found in the greenhouse vicinity.

In the plant dispersal process, the quality of the seed releasing site can be crucial for effective germination and plant growth, as part of the *"qualitative component"* of a dispersal event (Nevo et al., 2023; Schupp et al., 2017). In our study, most of the plant species (vascular plants, ferns and mosses) were dispersed within their altitudinal range. However, *Oxalis corniculata* was the only plant dispersed in higher altitude than recorded in Pyrénées, which suggests than brown bear can disperse plant within a given altitude range (Lalleroni et al., 2017; Patten, 1993; Tsunamoto et al., 2024) but also across altitude ranges, as demonstrated with *Ursus thibetanus* by Naoe et al. (2019, 2016). However, we can also be dubious about the endozoochorous origin of this weed plant present in the greenhouse vicinity. Overall, in our study, all native plant species dispersed by the brown bear were dispersed in suitable habitats in most cases, which suggest that brown bear is a qualitative seed disperser (see Schupp et al., 2017) as formerly suggested for *U. thibetanus* (Tochigi et al., 2022).

However, in our study, habitat description was restricted to large scale and at least on one variable (openness) and did not include the fine-scale description of the releasing site, which may also be crucial for plant germination. Indeed, García-Rodríguez and collaborators (2022) showed that brown bear often defecates in vegetation, which reduces *Vaccinium myrtillus* seed germination. Hence, these authors suggested that brown bear may be a poorer qualitative disperser as compared to other seed dispersers. However this effect could be mitigated by local abiotic conditions or animal secondary dispersers which visit bear faeces and potentially displace part of the seed pool (Enders and Vander Wall, 2012; Shakeri et al., 2018).

As expected, our results suggest that the faecal matrix seems to reduce plant germination, as reported in monogastric mammals (Enders and Vander Wall, 2012; Stricklan et al., 2020; Valenta and Fedigan, 2009) and ruminants (Mancilla-Leytón et al., 2012; Miller, 1995). We observed a higher number of species and seedlings and earlier germination in filtered faeces (disaggregated and washed to collect the seeds) compared to raw faeces (i.e. intact faecal matrix). In this sense, we argue that the faecal matrix plays the role of an additional barrier in the dispersal process, like mastication or gut passage probably due to dense matrix structure, mechanical or chemical inhibitor (Ramos et al., 2024). This effect appears especially important with mammals which release large and complex faeces, with a matrix structure that can impede germination (Stricklan et al., 2020). In addition, the positive effect of gut passage on germination of certain seeds (Nowak and Crone, 2012; Traveset and Willson, 1997; Tsunamoto et al., 2024) seems to be cancelled out by the negative effect of faecal matrix as suggest the results of a study on *U. americanus* (Enders and Vander Wall, 2012). However, in the field, faeces can be disaggregated by rain or secondary dispersers such as coprophagous insects or rodents, which may mitigate the negative effect of the faecal matrix structure. In this sense, these secondary dispersers may play an even more important role than generally thought in the whole dispersal process. Indeed, they may reduce intra-faeces seed competition (Milotić et al., 2019, 2018; Shakeri et al., 2018), break down physical barriers (Mancilla-Leytón et al., 2012; Milotić et al., 2019, 2018),

limit the action of potential inhibitors (Malo and Suárez, 1995; Traveset et al., 2007, 2001) or disperse a part of the seed pool (Enders and Vander Wall, 2012). Once germinated, seedlings could benefit from faecal matrix fertilizers (Traveset et al., 2007). We observed very light and non-significant differences in trait measurements (i.e. shoot length and number of true leaves) of *Vaccinium myrtillus* seedlings between both treatments. This suggests that the fertilizing effect of faeces was rather low or null, at least according to the duration of our experiment. Our results contrast with those of Traveset et al. (2001). They used fertilization subsidies on previously removed seeds rather than seeds within the faecal matrix, which may explain this difference. Our results could also be explained by the fact that seedlings were not nutrient-limited in our study. In any case, this inconstancy plaids for more experimental tests on the effect of faecal matrix, and more specifically its fertilisation potential.

Overall, our findings confirm that brown bear disperse herbaceous and woody plants, including fleshy-fruited and non-fleshy-fruited species. Our results also suggest that the brown bear may be a potential disperser of ferns and mosses, which is the first report for an Ursid species. More investigation is needed on endozoochorous non-angiosperm dispersal, with special caution on potential contamination control including potting soil, greenhouse and the period between defecation and collection. In contrast, our results suggest that large hard mast are consumed but destroyed, probably during the mastication process. Our study also supports the fact that brown bear is also a qualitative plant disperser, since all the native species recorded were dispersed within their range and in most of the cases, within a suitable habitat. However, fine-scale analysis based on abiotic and biotic factors using species distribution model (SDM) could greatly improve the analysis of the 'qualitative component' of such plant dispersal processes. Hence, we argue that brown bear is an effective plant disperser and Ursids in general should play an even more important role in the plant dispersal process than previously described (García-Rodríguez et al., 2021a; Karimi et al., 2018). In addition to our findings, the apex predator status of the brown bear could also modulate seed rain (i.e. the pool of seeds potentially dispersed) of other seed dispersal agents through ecology of fear, as demonstrated

in other species (Bartel and Orrock, 2021; Burgos et al., 2024) resulting in a complex effect on seed dispersal dynamics at the landscape scale. More broadly, we encourage future research to thoroughly investigate the whole spectrum of vascular and non-vascular plants dispersed by omnivores and other guilds.

Finally, our results highlight the importance of an overlooked barrier in the germination process, which is the potential inhibition of seed germination by the faecal matrix. This "filter" may be increasingly important as the size of the animal increases, and the faeces matrix structure is complex. In this context, secondary dispersers may play a key role, not only through secondary dispersal of faecal fragments with seeds, but also on the disaggregation of the faecal matrix, allowing better germination success for the seeds it contains. We recommend future studies on endozoochory to take into account the importance of this filter and of secondary dispersers in the plant dispersal process.

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Chapter VI - The role of brown bear in the potential co-dispersal of mycorrhizae, endophytes and pathogens together with their hosting plants

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VI.1 Résumé

Contexte : La mycophagie (i.e. la consommation de champignons) est un comportement variable chez les mammifères. Si certains sont particulièrement dépendants de cette ressource, d'autres vont la consommer de manière opportuniste. A l'inverse, certains champignons sont consommés de manière accidentelle par le biais de l'ingestion de plantes hébérgant des champignons. Ces animaux mycophages peuvent donc ingérer des propagules de champignons (spores, fragments mycéliens, sclérotes) et cela pourrait constituer un moyen de dispersion. En effet, certaines études ont montré la présence de spores viables de champignons dans les fèces de mammifères, confirmant ce potentiel de dispersion notamment pour des champignons ectomycorhiziens, qui sont d'une importance capitale pour les plantes leur permettant une meilleure captation de l'eau et des nutriments. D'autres mycorhizes ou champignons associés aux plantes peuvent être consommés et potentiellement dispersés comme les endophytes ou les pathogènes. Les endophytes non-mycorhiziens sont de plus en plus étudiés et leurs rôles dans la défense ou la croissance des plantes ont été bien documentés. La co-consommation de plantes et de champignons symbiotiques, mycorhiziens, endophytes ou pathogènes pourrait ainsi aboutir à des événements de co-dispersion et avoir des impacts importants dans le fonctionnement des écosystèmes. Ainsi, les consommateurs actifs de champignons et de plantes sont des acteurs légitimes à l'instar des omnivores comme l'ours brun.

Méthodes : Dans cette étude nous nous sommes intéressés à la consommation de champignons mycorhiziens, endophytes et pathogènes (notamment via la consommation de tissus végétaux colonisés) par l'ours brun, et la potentielle co-dispersion avec leurs plantes hôtes. Pour cela nous avons procédé par métabarcoding de l'ADN environnemental des fèces en utilisant deux marqueurs permettant d'identifier les champignons (Fung02) et les plantes (Sper01). Les champignons non coprophiles et symbiotiques identifiés ont été considérés comme potentiellement dispersés, et les plantes ont été inférées comme dispersées si de précédentes études l'avaient démontré.

Résultats : Nous avons pu identifier quatre taxons ectomycorhiziens, 21 endophytes et 44 pathogènes comme potentiellement dispersés par l'ours brun. Parmi les 44 pathogènes, huit sont aussi décrits comme endophytes. Le champignon ectomycorhizien le plus fréquent était la truffe *Melanogaster sp.*, alors que *Aureobasidium* sp., *Penicillium* sp. et *Cladiosporium* sp. sont les endophytes les plus fréquents, le dernier étant également le pathogène le plus fréquent. Nous avons observé la co-consommation et co-dispersion des mycorhizes à deux occasions et des endophytes à 16 occasions avec leurs plantes hôtes (*Quercus* sp. et *Festuca* sp.).

Conclusions : Cette étude questionne le rôle potentiel des grands mammifères dans la dispersion longue distance de la mycoflore bénéficiant à la flore locale. Elle permet aussi de nuancer le rôle souvent négatif de l'ours brun sur la dispersion des glands, en montrant la potentielle dispersion de leurs champignons ectomycorhiziens. Nos résultats montrent aussi la co-dispersion potentielle des champignons symbiotiques avec leurs plantes hôtes, pouvant être crucial dans la structuration des communautés. Cette étude a mis aussi en avant la dispersion de pathogènes, pouvant influencer l'assemblage des communautés de plantes. L'absence de champignons endomycorhiziens parmi les séquences obtenues souligne qu'une large partie des plantes consommées reste dispersée sans ses symbiotes, mais une recherche plus spécifique de ces champignons reste à réaliser. Enfin, démontrer la colonisation de ces champignons symbiotiques de plantes à partir de fèces de mammifères serait une expérimentation complémentaire pour valider ce phénomène de co-dispersion par l'ours brun.

Mots clés: Dispersion de champignons, co-dispersion, endozoochorie, *Ursus*

VI.2 Abstract

Mycophagy is a multifaceted behaviour spread among mammals that consume fungal fruiting bodies, or accidentaly ingest fungi included in another host or substrate. Following consumption, fungal propagules (spores, mycelial fragments, sclerotia) can be retrieved in animal faeces representing a potential dispersal event. So far, the few studies that investigated fungal dispersal through endozoochory have focused on the dispersal of ectomycorrhizal fungi but, other plant-associated mycorrhizae and fungi, such as endophytes or pathogens present in plant tissues, can be consumed by animals and potentially dispersed. In this study, we investigated mycorrhizae, endophytes and pathogens dispersed by an opportunistic mycophagous and omnivore large mammal, the brown bear. We also inferred joint dispersal of mycorrhizae and endophytes with their host plants. To do this, we performed metabarcoding and used fungal (Fung 02) and plant (Sper 01) markers on 148 fresh brown bear faeces from the Pyrénées population (South-West of Europe). We considered the fungi retrieved as potentially dispersed, whereas the plants detected were considered as potentially dispersed only if they were described in previous reports as dispersed by brown bear in the Pyrénées. We detected four ectomycorrhizal fungi, 21 endophytes and 44 pathogens potentially dispersed by brown bear, among which 8 taxa were considered both as endophytes and pathogens. The most frequently found mycorrhiza was the truffle, *Melanogaster sp.*, whereas *Aureobasidium* sp., *Penicillium* sp. and *Cladiosporium* sp. were the most frequent endophytes, and the latter was also the most frequent pathogen. We observed the co-occurence of mycorrhizal fungi and their host plants in two events and endophytes in 16 events (with *Quercus* sp. and *Festuca* sp.). This study highlights the potential role of large mammals in the long distance dispersal of the mycoflora benefiting local plants. Furthermore, we highlighted potential event of joint dispersal with their host plants. However, there is still a large majority of plants that were not detected together with their mycorrhizal symbionts. These first results based on metabarcoding nuance the negative role of brown bear on hard mast trees (mostly seed predated) through the dispersal of symbiotic fungi. This study also shows the potential dispersal of

pathogens that may greatly influence plant dynamics and assemblage. Furthermore, we invite future research to sequence other barcodes to target endomycorrhizal ones that have been probably been missed. Overall, this study is the first to investigate endozoochorous dispersal of such fungi and invites future research to test if dispersed plants do germinate with their co-dispersed fungi from omnivore faeces.

Keywords: Fungi dispersal, joint dispersal, plant symbionts, endozoochory, *Ursus*

VI.3 Introduction

Mycophagy by mammals has been quite documented, with 508 species involved in which rodents and primates are the most represented (Elliott et al., 2022). Fungi can be very rich in nutrients, contain unique elements (e.g. Selenium) and secret aroma, turning sporocarpe as an attractive food for mammals (Claridge and Trappe, 2005; Elliott et al., 2022). Nevertheless, mycophagous mammals can be categorised as obligate (high dependency to sporocarps, e.g Western red-backed vole, *Myodes californicus*), preferential (sporocarps are privileged resources, e.g. Northern flying squirrel, *Glaucomys sabrinus*), opportunistic (attractive sporocarps can be consumed, e.g. bears, Ursidae) or accidental (fungi are consumed along with other food items, e.g. dung beetles) (Claridge and Trappe, 2005). When sporocarps such as truffles are consumed, a massive amount of spores are ingested and can be released into faeces. Several pieces of evidence compiled in recent reviews show that spores in mammal faeces are still viable despite the passage in the digestive tract (Elliott et al., 2022; Paz et al., 2021; Vašutová et al., 2019) and are thus dispersed by endozoochory. Other forms of propagules such as mycelial fragments or sclerotia may also be involved in endozoochory events (Vašutová et al., 2019). Endozoochory appears much more effective in fungi LDD than wind does (Elliott et al., 2022), which rarely exceeds a few meters (Galante et al., 2011; Li, 2005). Among the fungi documented as dispersed through endozoochory by mammals, most of them are ectomycorrhizae (Elliott et al., 2022; Vašutová et al., 2019) related to the consumption of fruiting bodies. However, rare evidence exist on dispersal of arbuscular mycorrhizal fungi (Correia et al., 2019; Paugy et al., 2004; Vernes and Dunn, 2009), which are associated with at least 71% of plant species (Brundrett and Tedersoo, 2018), as well as ericoid mycorrhizal fungi that are associated with the Ericaceae plant family.

For instance, most plants depend on mycorrhizae for growth and survival (Simard and Durall, 2004), and plants dispersed over long distances require those fungi to establish (Correia et al., 2018). In this

context, the dispersal of mycorrhizae over long distances by large mammals is particularly relevant. However, mycorrhizae are also obligatory symbionts that depend on plants to establish. This means that the joint dispersal (co-dispersal) of plants with their associated fungi within the same faeces appears thus crucial for both partners (Correia et al., 2019). A recent study on birds showed the first evidence of joint dispersal of arbuscular mycorrhiza and its host plant following endozoochory, affecting plant and fungi distribution pattern (Correia et al., 2019), contributing to a process that remains barely investigated.

However, mycorrhizae are not the only fungi that interact with living plants. For instance, there are many endophytes, i.e. fungi inhabiting internal plant tissues with no apparent negative effects at least during part of their life (Petrini, 1991). Endophytes are widespread in plants and can be found in pteridophytes, bryophytes, gymnosperms or angiosperms (Rashmi et al., 2019). They are categorised either as grass-inhabiting (i.e. clavicipitaceous) or non-grass inhabiting (i.e. non-clavicipitaceous), and both are recognized in plant growth enhancement, resistance to herbivory or abiotic stress (Clay and Schardl, 2002; Hyde and Soytong, 2008; Verma et al., 2019), but also latent pathogen for some of them (e.g. (Slippers and Wingfield, 2007). In such a context, the dispersal of endophytes is also of ecological importance. The dispersal of clavicipitaceous endophytes is vertical through seeds (Saunders et al., 2010) whereas non-clavicipitaceae disperse horizontally (Bard et al., 2024), through air (Kaneko and Kaneko, 2004), litter (Herre et al., 2007; Kaneko and Kakishima, 2001), insects (Hannula et al., 2019) or even mammals (Fracchia et al., 2011). Contrary to ectomycorrhizae, endophyte ingestion by mammals appears accidental following root, leaf or stem consumption. Other fungi inhabiting plants may thus be consumed and potentially dispersed such as pathogen fungi. Very little is known on the dispersal of plant-pathogen propagules by mammals. A recent report showed that plant-pathogen fungi may be dispersed by endozoochory following ingestion of contaminated fodder by cattle (Kumar et al., 2022).

In this context, large mammals that consume and disperse plants over long distances may also disperse symbiotic endophytes, pathogens and mycorrhizae. Large omnivores appear as particularly relevant in co-consumption and potentially joint dispersal of plants and fungi as they can consume both types of resources. This is the case of Suids (e.g. (Baubet et al., 2004; Mysterud et al., 2024) or Ursids (**Chapter III**, (Elliott et al., 2022). For instance, wild boar (*Sus scrofa*) received particular attention in recent literature as a potential fungal dispersal vector (Aguirre et al., 2021; Livne-Luzon et al., 2017; Nuñez et al., 2013; Piattoni et al., 2014, 2012; Soteras et al., 2017) as well as a recognized plant dispersal vector (Karimi et al., 2018; Picard et al., 2015). However, despite numerous records on mycophagy by Ursids (e.g. (Fortin et al., 2013; Koike, 2010; Rathore et al., 2014), there is almost no evidence of fungal dispersal by bears (but one fungi taxa has been retrieved in *Ursus americanus* faeces, see (Cázares and Trappe, 1994). Yet, as mycophagous animals and recognized agent of plant dispersal through endozoochory (García-Rodríguez et al., 2021a), their role in fungal dispersal must be particularly relevant.

Here we assessed plant-associated fungi (mycorrhizae, endophytes and pathogens) dispersal by brown bear (*Ursus arctos*) in the Pyrénées (south west Europe) based on the detection of fungi using metabarcoding of faecal eDNA. Faecal eDNA metabarcoding can be an effective tool that improves the number of fungi detected compared to visual approaches (Soteras et al., 2017). Using a fungal marker, we thus expected to retrieve mycorrhizae (endo- and ectomycorrhizae), endophytes and pathogens in the faeces, following occasional or accidental consumption. We expected to detect endophytes and plant-pathogens more frequently than mycorrhizae due to the highly plant-based diet of brown bear in the Pyrénées (**Chapter III**). In addition, combined with a plant marker, we aimed to identify the host plants of endophytes and mycorrhizae that were co-consumed within the same faeces. Based on those co-occurrences, we then inferred potential joint dispersal based on previous evidence of seed dispersal by brown bear in the Pyrénées of the co-consumed plant retrieved. We expected joint dispersal events of both symbionts with hosting plants.

VI.4 Materials and Methods

VI.4.1 Study Site and population

Our study was conducted in the Pyrénées, a mountain chain (36,600 km^2) peaking at 3,400 meters above sea level and situated in South-Western Europe at the border of France, Andorra and Spain. The forest, which represents more than 40% of the landscape, is dominated by beech (*Fagus sylvatica*) and silver fir (*Abies alba*), but also includes oak (*Quercus* spp.), pine (*Pinus* spp.) chestnut (*Castanea sativa*), hazel (*Corylus avellana*), wild cherry (*Prunus avium*), Norway spruce (*Picea abies*), common ash (*Fraxinus excelsior*) or even white birch (*Betula pubsecens*) (Ninot et al., 2017). Above the timberline (about 1,800 m), large open areas are covered by fleshy-fruited shrubs and herbaceous plants, including rhododendron (*Rhododendron ferrugineum*), blueberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*), with alpine pastures and rocks at the summits (Ninot et al. 2017). Pyrénées host a highly diverse flora, including endemics, and megafauna species such as the brown bear, wild and domestic ungulates and mesocarnivores.

To avoid the extinction of the local brown bear population in the 1990s, translocations of a total of 11 bears originating from Slovenia were implemented from 1996 to 2018, initiating a partial demographic (Vanpé et al., 2022) but still poor genetic (Auclair et al., 2025) recovery. In 2023 the population amounted to at least 90 individuals covering about 7,200 km² (Sentilles et al., 2025).

VI.4.2 Fungi and plant detection using metabarcoding

The faeces samples and metabarcoding procedure were the same as the ones performed for the **Chapter III** but here, we only used Sper01 and Fung02 markers to detect, respectively, plants and

fungi (see Appendix for metabarcoding procedure details). The marker Fung02 is a universal marker for the detection of mycorrhizal fungi, as well as endophytes and pathogens. We considered genera as taxonomic level for analyses for plants and fungi as species level is too sensitive to the marker and the reference database. We functionally annotated each fungal genera using FungalTraits (Põlme et al., 2020) to identify mycorrhizal (ecto-, endo- and ericoide), non-mycorrhizal endophyte, and pathogen fungi. Fungi that were animal parasites or faeces saprotrophs as primary lifestyle but endophytes or plant pathogens as secondary lifestyle were discarded due to potential faeces contamination. Otherwise, mycorrhizal, non-mycorrhizal endophyte retrieved in the faeces were considered as fungal propagules. Only plant and fungal genera with at least 250 reads within a faeces sample were kept.

VI.4.3 Co-consumption and joint dispersal inference

Based on the co-occurrence of plant and fungal genera sequenced within the same faeces, we inferred co-consumption of fungi, either mycorrhizae or endophytes, and their hosting plant(s) using, respectively, a database on mycorrhizal plant status (Soudzilovskaia et al., 2020) and the numerous evidence compiled by (Rashmi et al., 2019) on the endophyte-plant associations. We also identified all the hosting plants present in the Pyrénées (using a local plant database [(FLORAPYR, 2025)]) of the endophytes retrieved. We could not investigate any pathogen-plant co-consumption due to insufficient information but we report their abundance in faeces.

All fungi retrieved in faeces were considered as potentially consumed and dispersed by brown bear, whereas for plants, we considered them as potentially dispersed by brown bear when they were previously described as dispersed by endozoochory in the Pyrenees. We were based on previous studies that investigated diaspores retrieved in faeces (Lalleroni et al., 2017) or seedling emergence

(**Chapter V**). Joint dispersal thus occurred when the plant co-consumed with its associated fungi was once described as dispersed through brown bear endozoochory in the Pyrénées.

VI.5 Results

We detected the presence of fungi in almost half (n=68) of the 148 faeces samples analysed by metabarcoding, corresponding to 1,064 OTUs and 9,783,766 reads. Most of the fungi identified were coprophilous contaminants or saprotrophs, producing no fruit bodies (see **Chapter III**).

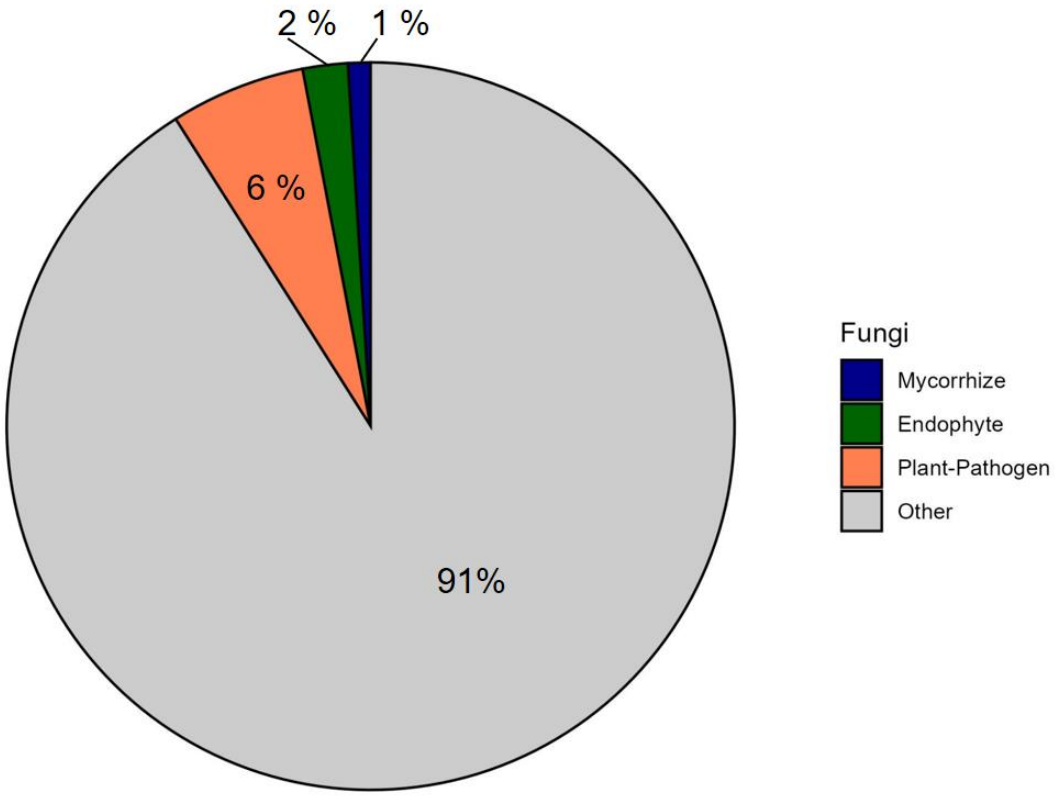

Figure VI.1: Percentage of reads annotated as mycorrhizae, endophytes, and plant-pathogen out of the total number of reads detected with the fungi marker (n=9,783,766).

VI.5.1 Mycorrhizae

We detected four genera of mycorrhizal fungi in 8.8% (n=6) of the faeces samples, corresponding to 0.1% (n=80,781) of the total fungal reads (**Fig. VI.1**). All of them were ectomycorrhizal fungi

(*Boletus*, *Melanogaster*, *Russula* or *Tomentella*) (**Table VI.1**) and although our barcode was designed to capture Mucoromycota. *Boletus* was co-consumed with arbuscular mycorrhizal Apiaceae (not identified at genus level). Among the three occurrences of *Melanogaster*, these fungi were co-consumed with ericoide-mycorrhizal *Calluna* and *Vaccinium*, and arbuscular-mycorrhizal *Cerastium*, *Lathyrus* and *Rubus*. We detected co-consumption of *Russula* with ectomycorrhizal *Quercus*, but also with arbuscular-mycorrhizal *Festuca*. The consumption of *Tomentella* also co-occured with ectomycorrhizal *Quercus* (**Table VI.1**).

Table VI.1: Mycorrhizal fungi genera retrieved in brown bear faeces with the corresponding hosting plants found in the Pyrénées.

Mycorrhiza genera	**#**[1]	**Type**	**Fruiting body**	**Associated plant dispersed in the Pyrénées**	**Plant co-consumed**
Boletus	1	Ectomycorrhiza	Epigeous		NA
Melanogaster	3	Ectomycorrhiza	Hypogeous		NA
Russula	1	Ectomycorrhiza	Epigeous	*Betula* (A,B,C[2]); *Fagus* (A); *Quercus* (A); *Pinaceae* (B); *Salix* (B)	*Quercus*
Tomentella	1	Ectomycorrhiza	Resupinate		*Quercus*

[1]#: Number of samples with the mycorrhizal genus (at least 250 reads to be considered as occurring).
[2] A: Based on Lalleroni et al. 2017; B: Based on Chapter IV; C: Based on Chapter V.

VI.5.2 Endophytes

We retrieved 21 genera of non-mycorrhizal endophytes in 45.6% (n=31) of the faeces samples, corresponding to 2.3% (n=223,735) of the total fungal reads (**Fig. VI.1**), among which 19 endophytes were known to be hosted by plants present in the Pyrénées (**Table VI.2**). Among the hosting plants, there were 15 genera described as previously dispersed through endozoochory by Pyrenean brown bear. Here, we identified four endophyte - plant pairs involved in co-consumption and joint dispersal events. Other plants were co-consumed but not documented as hosting such fungi.

Table VI.2: Non-mycorrhizal endophytic fungi genera retrieved in brown bear faeces and the corresponding hosting plants described in the Pyrénées. (To be continued)

Endophyte genera	**#**[1]	**Plant host found in the Pyrénées**[2]	**Plant dispersed in the Pyrénées**	**Plant co-consumed**
Aspergillus	2	*Aloe; Brassica ;Crocus; Cymodocea; Cynodon; Ipomoea; Juniperus; Melia; Mirabilis; Opuntia; Paris; Scapania; Silybum; Suaeda; Taxus; Viscum; Vitis ;Zea; Ziziphus* [3]	*Juniperus* (B[5])	
Aureobasidium	6	*Acer; Alnus; Artemisia; Brassica; Crataegus; Eucalyptus; Phleum; Pinus; Prunus; Quercus; Teucrium; Trachycarpus; Triticum; Ulex; Vitis*	*Prunus* (A), *Quercus* (A), *Teucrium* (A),	*Quercus* (x1[6])
Chaetomium	2	*Adiantum; Artemisia; Brassica; Cannabis; Crataegus; Cymodocea; Ephedra; Eucalyptus; Fagus; Imperata; Pinus; Potentilla; Prunus; Scapania; Silybum; Ulex; Vitis*	*Fagus* (A), *Prunus* (A)	
Cladosporium	16	*Alnus; Buddleja; Chamaecyparis; Cuscuta; Cymodocea; Eichhornia; Eucalyptus; Festuca; Opuntia; Phaseolus; Populus; Quercus; Silene; Triticum; Vitis*	*Festuca* (B), *Quercus* (A)	*Quercus* (x6), *Festuca* (x6)
Coleophoma	1	*Rhododendron*		
Colletotrichum	1	*Arabidopsis; Artemisia; Betula; Buxus; Fraxinus; Huperzia; Jasminum; Marchantia; Nymphaea; Passiflora; Phaseolus; Rubia; Salsola; Silene; Taxus; Trachycarpus; Triticum; Vaccinium; Vitis; Zea*	*Betula* (A,B,C), *Vaccinium* (A,B,C)	
Coniochaeta	1	*Chamaecyparis; Ulex*		
Cryptococcus	2	*Ammophila; Brassica; Dactylis; Opuntia; Phaseolus; Phragmites; Prunus; Rosa*	*Prunus* (A), *Rosa* (A,B)	
Cytospora	4	*Eucalyptus*; *Pisum; Triticum;*		
Fusarium	1	*Aloe; Artemisia; Arthrocnemum; Beta; Bromus; Buddleja; Centaurea; Celtis; Chamaecyparis; Cirsium; Cupressus; Ephedra; Eryngium; Hyoscyamus; Ipomea; Juniperus; Ligustrum; Limonium; Lygeum; Melia; Ononis; Paris; Phaseolus; Phleum; Pinus; Platanus; Prunus; Ranunculus; Salicornia; Selaginella; Silybum; Sorbus; Sporobolus; Taxus; Teucrium; Trachycarpus; Triticum; Viscum; Viola; Zea*	*Juniperus* (B), *Prunus* (A), *Ranunculus* (A), *Sorbus* (A,B), *Teucrium* (A),	
Menispora	1	*Pseudorchis*		
Microdochium	2	*Triticum*		

Mollisia	4	*Picea; Vaccinium*	*Vaccinium* (A,B,C)	
Penicillium	7	*Artemisia; Aster; Cannabis; Corylus; Eleusine; Eucalyptus; Melia; Nerium; Opuntia; Phaseolus; Phragmites; Pinus; Polygonatum; Puccinellia; Punica; Suaeda; Silybum; Taxus; Ulva*		
Phacidium	1	*Abies; Angelica; Beta; Bromus; Brassica; Chamaecyparis; Chenopodium; Crocus; Cupressus; Cymodocea; Huperzia; Malus; Potentilla; Rhododendron; Ziziphus*	*Abies* (B), *Malus* (B),	
Phoma	1	*Acer; Anemone; Brassica; Centaurea; Celtis; Eupatorium; Eucalyptus; Holcus; Quercus; Silene; Solanum; Taraxcum; Taxus; Trachycarpus; Triticum*	*Holcus* (C), *Quercus* (A)	
Pyrenochaetopsis	1	*Festuca*[4]	*Festuca* (B)	*Festuca* (x1)
Retroconis	1	NA		
Trichoderma	2	*Artemisia; Eucalyptus; Fragaria; Melia; Nymphaea; Paris; Phragmites; Pinus; Populus; Quercus; Vitis*	*Fragaria* (A), *Quercus* (A)	*Quercus* (x2)

[1]#: Number of occurrences.
[2] Plant host based on the review by Rashmi et al. 2023.
[3] Underlined meaning that all of the species of the genera are not native to the Pyrénées.
[4] Based on Panke-Buisse et al. 2020.
[5] A: Based on Lalleroni et al. 2017; B: Based on Chapter IV; C: Based on Chapter V.
[6] Quercus (x1): It means that co-consumption with Quercus occurred only once.

VI.5.3 Pathogens

We detected 44 genera described as plant pathogens in 52.9% (n=36) of the faeces samples, corresponding to 6.4% (n=626,878) of the total fungal reads (**Fig. VI.1**). Among them, 8 were also considered as endophytes (*Cladosporium*, *Coleophoma*, *Colletotrichum*, *Fusarium*, *Microdochium*, *Mollisia*, *Phacidium*, *Phoma*). *Cladosporium* (n=16), *Taphrina* (n=8) and *Ramularia* (n=7) were the only pathogens found in more than five faeces samples.

Table VI.3: Fungal plant-pathogen retrieved in brown bear faeces in the Pyrénées.

Fungal Pathogen	#[1]	**Fungal Pathogen**	#	**Fungal Pathogen**	#
Bryochiton	1	*Itersonilia*	1	*Plectosphaerella*	1
Calophoma	1	*Laetisaria*	1	*Plenodomus*	1
Ceratobasidium	1	*Limonomyces*	1	*Podosphaera*	1
Ceuthospora	1	*Microdochium*	2	*Polyscytalum*	1
Cladosporium	16	*Microstroma*	1	*Protomyces*	1
Clarireedia	3	*Mollisia*	4	*Ramularia*	7
Clonostachys	1	*Mycosphaerella*	1	*Setophoma*	1
Coleophoma	1	*Neoascochyta*	2	*Sphaerulina*	5
Colletotrichum	1	*Oculimacula*	2	*Taphrina*	8
Colpoma	2	*Parastagonospora*	1	*Teratosphaeria*	1
Cytospora	4	*Peniophora*	3	*Typhula*	1
Discosia	1	*Phacidium*	1	*Venturia*	1
Elsinoe	1	*Phaeomoniella*	1	*Vuilleminia*	1
Fusarium	1	*Phoma*	1	*Xenoramularia*	2
Fusicladium	1	*Phyllactinia*	5		

[1]#: Number of occurrences.

VI.6 Discussion

Our study is the first investigation of potential dispersal of symbiotic and pathogen fungi by an Ursid species (Cázares and Trappe, 1994), the brown bear. Based on metabarcoding analyses, some co-occurences suggest a potential consumption and potential dispersal of plant-associated mycorrhizae, non-mycorrhizal endophytes and pathogens, including 18 potential events of joint dispersal with their host plant. Considering the displacement rate and gut retention time of brown bear, such dispersal may occur over long distances (Lalleroni et al. 2017). Furthermore, this study brings new evidence on a very limited knowledge on endophyte and fungal plant-pathogen dispersal through endozoochory. In accordance with our hypothesis, the fungal pathogens and endophytes were quite frequent in Pyrenean brown bear faeces, probably following accidental consumption of leaves, shoots, roots or even following soil ingestion. On the contrary, we found few occurrences of ectomycorrhizae

consumption, which is more related to occasional consumption of sporocarpes (Claridge and Trappe, 2005) that complete the diet (**Chapter III**).

In Pyrenean brown bear faeces, we retrieved four species of ectomycorrhizae but no arbuscular or even ericoid-mycorrhizae associated with the frequently dispersed *Vaccinium* genera (García-Rodríguez et al., 2021a; García-Rodríguez and Selva, 2021). Previous evidence showed that three of the four taxa identified here in brown bear faeces were already retrieved viable in mammal faeces including *Melanogaster* (Nuñez et al., 2013), *Tomentela* (Ashkannejhad and Horton, 2006), *Rusulla* (Castillo-Guevara et al., 2012), whereas there is no evidence for *Boletus*. The dispersal of ectomycorrhizae by brown bear- if this pattern is confirmed from other clues - may have significant ecological implications at the landscape scale for associated tree species (Vašutová et al., 2019) including the dominant oak, beech and fir trees in the Pyrénées. For instance, it has been shown that ectomycorrhizal fungi dispersal by mammals may greatly affect forest development and soil mycoflora (Aguirre et al., 2021; Livne-Luzon et al., 2017; Nuñez et al., 2013; Nuske et al., 2019). The dispersal of the other mycorrhizal types (e.g. arbuscular) through endozoochory has also been documented for other mammals (Paugy et al., 2004; Vernes and Dunn, 2009), even if the type of propagules that is dispersed (mycelia, spores and sclerotia) still need to be detailed (Vašutová et al., 2019). The lack of detection for arbuscular mycorrhizae can be related to the marker, so the use of a more specialized marker could be relevant (WANDA and AML2 (Dumbrell et al., 2011; Lee et al., 2008). For ericoid mycorrhiza, the absence is probably more related to an absence of *Vaccinium* roots.

Among the endophytes retrieved, we found dominant grass-inhabiting genera of temperate ecosystems, including *Cladosporium*, *Penicillium* and *Aureobasidium* (Rashmi et al., 2019). According to other plant hosts and previous studies in agricultural fields, those genera are involved in anti-pathogen activity (Di Francesco et al., 2021; Toghueo and Boyom, 2020; Wang et al., 2013), defense to herbivory (Nicoletti et al., 2024; Toghueo and Boyom, 2020) or plant growth (Di Francesco

et al., 2021; Hamayun et al., 2009; Toghueo and Boyom, 2020). Such findings have also been documented on the other endophytes retrieved (e.g. *Chaetomium* and *Trichoderma* in herbivory resistance (Natsiopoulos et al., 2024; Zhou et al., 2016), respectively). Other endophytes and host plants still need to be identified (Rashmi et al., 2019) and the range of endophyte dispersal may be even greater. In this context, potential dispersal of endophytes mediated by brown bear may influence the structure and dynamics of plant populations and communities.

In the same way, we retrieved numerous plant pathogen fungi in the Pyrenean brown bear faeces and part of them are also described as endophytes. This kind of polyvalent effect on plants may be due to the potential latent pathogenic effect of some endophytes that still represent a small fraction of endophytes (Zabalgogeazcoa, 2008). For instance, *Ramularia* may cause severe leaf-spot disease infesting a wide host of herbaceous plants (Shi and Li, 2024), whereas *Taphrina* is implicated in both herb and tree diseases inducing leaf-spot, galle or deformation (Ownley and Trigiano, 2016). Other plant-pathogen fungi retrieved are also widespread such as *Cytospora* implied in canker disease (Lin et al., 2024) or *Clarireedia* causing dollar spot disease (Salgado-Salazar et al., 2018). The dispersal of plant fungal pathogens mediated by animals from a plant to another plant is quite documented for insects that may transport pathogens externally or internally, but remains almost unknown for mammals (Kumar et al., 2022). Our results represent one of the first study revealing mammal-mediated endozoochory of plant-pathogen. The plant-pathogen dispersal (potentially along plants) could challenge the escape-hypothesis of (Connell, 1971; Janzen, 1970), who propose that plant dispersal allows plants to escape from constraining conditions including the presence of plant-pathogens (e.g. Augspurger, 1983).

Based on the co-consumption of fungi and their hosting plant, we highlighted 16 potential joint-dispersal of endophytes or mycorrhiza with *Festuca* and *Quercus*. These co-occurences remain rare in our dataset and we can only partially confirm our hypothesis, as mycorrhizae are only found in

association with *Quercus* that are rarely dispersed by brown bears in the Pyrénées. Indeed, *Quercus* acorns have been retrieved very rarely intact in brown bear faeces (Lalleroni et al., 2017) and are most of the time destroyed by the animal's mastication (**Chapters IV and V**). Thus, an effective co-dispersal event of *Quercus* is little probable, but the dispersal of their associated mycorrhiza and endophytes may nuance the negative effect of brown bear on *Quercus* dispersal. For instance, the significant positive effect of mycorrhizae on *Quercus* at seedling and adult stages has been long-time established (Southworth, 2013; Trappe, 1962) and such dispersal may be significant. The endophytes co-consumed are also beneficial for oak; for instance *Trichoderma* is implied in pathogen resistance (Oszako et al., 2021; Ruiz-Gómez and Miguel-Rojas, 2021), while *Cladosporium* and *Aureobasidium* effect on oak is not well investigated although evidence suggests an implication in leaf decomposition in fall for the latter (Shirouzu et al., 2009). For *Festuca* as well, the effect of *Cladosporium* is also not well established but based on other plant hosts, it should be quite beneficial for both *Quercus* and *Festuca* (Hamayun et al., 2009; Nicoletti et al., 2024; Yang et al., 2023). Furthermore, the association of *Festuca* and *Pyrenochaetopsis* has been highlighted in drought resistance, which can be crucial under the accelerated climate change (Panke-Buisse et al., 2020). Our results thus suggest that brown bear may be an effective vector of joint dispersal of plant and fungi.

The use of metabarcoding on faeces eDNA leads to the detection of a quite higher diversity of fungi compared to visual methods (Soteras et al., 2017). However, its use faces issues in taxa identification related to the marker used and the reference database. We were aware that fungi detection in the faeces does not necessarily mean propagule (mycelia, spores, sclerotia) dispersal, and so our study is still based on the inference of such dispersal. However, our study represents the first of this kind to investigate potential dispersal and joint dispersal of mycorrhiza, endophytes and pathogens by mammals, in a field that is still mainly unexplored (Vašutová et al., 2019). The next step to confirm such dispersal will be the investigation of effective colonization of such fungi in the faeces deposition site and its contribution to plant germination.

Overall, our study suggests the role of a large mammal, the brown bear, in the dispersal of several fungi, including symbiotic endophytes and mycorrhiza but also pathogens, over long distances based on a long gut retention time and associated long displacement (Lalleroni et al., 2017). Those dispersal events can be of significant relevance for the structure and dynamics of plant populations and communities and our findings contribute to a very limited knowledge especially on animal mediated endophytes and plant pathogen fungi. The investigation of fungi also nuanced the negative effect of brown bear on oak recruitment through seed mastication, thanks to the dispersal of associated beneficial fungi. We encourage future research to investigate plant associated symbiotic and pathogen fungal dispersal and especially to test their effective colonization through a mammal faeces inoculum (ideally using the core of the faeces) (e.g. Correia et al., 2019). Furthermore, the research on animal-mediated fungi not necessarily associated with plants, but of ecological importance, can be very interesting such as saprotroph fungi that are consumed by brown bears for their fruit bodies (**Chapter III**).

Part 4 - Post-release: Activity of brown bear faeces visitors

Experimental design to test the effect of brown bear faeces visitors at Melles (France) in the Pyrénées.

Chapter VII - Dung beetles, but not rodents, contribute to brown bear feces removal, disaggregation, and secondary seed dispersal

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VII.1 Résumé

Contexte : A l'issue d'une dispersion endozoochore primaire, les diaspores se retrouvent dans une fèces, un environnement qui peut être particulièrement hostile pour la germination des graines. Le caractère hostile de cet environnement peut être dû à la presence d'inhibiteurs chimiques, à une forte densité de graines et/ou une structure complexe de la fèces. Cependant, les visiteurs des fèces, incluant des vertébrés (rongeurs intéressés par les graines contenues dans les fèces) et des invertébrés (des bousiers dépendant de la matière fécale pour réaliser leur cycle de vie), peuvent jouer un rôle essentiel dans la dispersion secondaire des graines (DSG) et limiter les contraintes mécaniques des fèces en désagrégeant la matrice fécale.

Méthodes : Nous avons conçu une expérience dans les Pyrénées pour démêler le rôle relatif des vertébrés et des invertébrés dans la désagrégation de fèces d'ours brun (*Ursus arctos*) et la dispersion secondaire de graines de petite et moyenne taille. Pour cela nous avons utilisé 30 fèces fraîches d'ours brun et séparé chacune d'entre elles en trois sous-échantillons permettant soit un accès à aucun visiteur, un accès limité aux invertébrés ou un accès à tous les visiteurs en utilisant respectivement une cage à maille fines, une cage à mailles larges ou aucune cage. Nous avons inséré huit graines de framboise (*Rubus idaeus*) et cinq graines de myrtille (*Vaccinium myrtillus*) colorées dans chaque sous-échantillon pour évaluer la DSG. Parallèlement, nous avons utilisé des pièges photographiques, pour détecter la présence de vertébrés et des pièges à fosse appâtés pour identifier les invertébrés coprophages présents. Après dix jours, nous avons pesé les fèces pour quantifier la perte de matière fécale, compté les graines restantes et évalué la désagrégation des fèces à l'aide de photographies. Nous avons également testé l'effet de la composition des fèces (fruits charnus, glands, herbacées) sur l'attraction des visiteurs.

Résultats : Nous avons observé un effet significatif des invertébrés sur la disparition de la matière fécale, la désagrégation des fèces et la DSG des deux plantes. Les vertébrés n'ont pas visité les fèces

car nous ne les avons pas détecté via les pièges photographiques et n'avons pas observé de différences entre les fèces accessibles aux rongeurs et bousiers et celles accessibles uniquement aux bousiers. A l'inverse, les bousiers ont été capturés dans les pièges à fosse et nous avons observé significativement moins de matière et moins de graines dans les fèces accesibles aux bousiers que dans celles qui ne l'étaient pas. Nous avons également mis en évidence que la composition des fèces de l'ours brun affecte l'attraction des bousiers et leur activité avec notamment moins d'activité dans les fèces composées de glands.

Conclusions : Notre étude dans une zone montagneuse tempérée identifie les bousiers, mais pas les rongeurs, comme des agents clés dans la désagrégation et la dispersion secondaire des graines de petite et moyenne taille. La composition des fèces qui contiennent les graines influencent le devenir des graines en modulant l'activité des bousiers. En libérant des fèces de composition variable, les omnivores comme vecteurs primaires de graines ont un effet encore plus complexe sur le devenir des graines.

Mots clés : Diplochorie, Agent de désaggrégation, Endozoochorie, Invertébrés, *Ursus arctos*, Dispersion efficace des plantes, Taille de graine, Ingéniérie de transport, Vertébrés.

VII.2 Abstract

Seed dispersal by endozoochory is essential to plant dynamics, but once released in the faeces, the seeds face a hostile environment that is not always favourable to germination. Indeed, faeces may contain inhibitors, high seed density and be densely structured. However, faeces visitors such as vertebrates and invertebrates may play an essential role in secondary seed dispersal (SSD) and can alleviate the chemical and physical constraints of the faeces. Yet their relative roles in the dispersal of small and medium-sized seeds are not well documented. In this study, we designed a field experiment in the French Pyrénées mountains to disentangle the relative role of vertebrate and invertebrate on faeces removal, disaggregation and secondary dispersal of small and medium-sized seeds. We thus used 30 brown bear (*Ursus arctos*) fresh faeces and separated each of them into three sub-samples submitted to different treatments allowing total access of any visitor, access restricted to invertebrates and no visitor access respectively. We inserted eight raspberry (*Rubus idaeus)* and five blueberry (*Vaccinium myrtillus)* marked seeds in each sub-sample to assess SSD. In parallel, we used camera and pitfall traps to document the presence of vertebrate and invertebrate visitors, respectively. After ten days we weighted the faecal matter remaining, counted the remaining seeds, and assessed the faeces disaggregation based on visual examination and objective criteria. We observed a significant effect of invertebrates on faeces removal, disaggregation, and secondary dispersal of both seed species. Vertebrates did not visit the faeces. Dung beetles caught in pitfall traps appear as the main secondary seed disperser and disaggregation agents in this area. We also pinpointed that diet composition and structure of brown bear faeces affect dung beetle attraction and activities. Our study in a temperate mountainous area identifies dung beetles as key agents in the disaggregation of large faeces and secondary dispersal of small and medium-sized seeds, with no evidence of rodents. Diet composition and the faecal matter trapping the seeds affect seed fate by modulating dung beetle activity. By releasing variable faecal contents, omnivorous primary seed vectors have an even more complex effect on seed fate than expected.

Keywords: Diplochory; Disaggregation agent; Endozoochory; Invertebrate; Ursus arctos; Seed dispersal effectiveness; Seed size; Transport engineering; Vertebrate.

VII.3 Introduction

Seed dispersal is a key ecological process mediated by a diversity of abiotic and biotic vectors that shape plant distribution and communities. Biotic vectors often enable long-distance and directional dispersal through zoochory (Beckman and Sullivan, 2023; Jordano, 2017; Nathan et al., 2008). Such dispersal enables plants to colonise new environments, to change elevational (Mendes et al., 2025; Naoe et al., 2019, 2016) and latitudinal (Nuñez et al., 2023) range, and to potentially escape unfavourable abiotic or biotic conditions (Beckman and Sullivan, 2023). Vectors including mammals (Baltzinger et al., 2019), frogs (Gould and Valdez, 2024), reptiles (Valido and Olesen, 2019), birds (Lovas-Kiss et al., 2018) and invertebrates (Martins et al., 2006) disperse seeds through epi- (*e.g.* attached on the fur or the hooves) and endozoochory (e.g. consumed and defecated). Unlike epizoochory, endozoochory involves critical phases with repercussions for the seed viability and germinability, either positive or negative. The chewing process already represents an important filter that may alter or even destroy certain seeds, drawing the limit between seed predation and seed dispersal (Janzen, 1971). Once ingested, the seed ends up in the digestive tract. Gut passage can increase germinability by removing the pulp or conversely reduce seed viability. Coevolution between plants and animals selected seed traits favouring their resistance, and adaptation to animal digestive tract (Traveset et al., 2007; Traveset and Verdú, 2002). The journey is not over after digestion because seeds embedded in the faeces have to cope with a harsh (Enders and Vander Wall, 2012; Pauly et al., 2024) but somewhat fertile environment (Traveset et al., 2007).

Frugivores or omnivores faeces may contain a very high seed density, usually from different plant species, leading to competition and potential negative density-dependent or allelopathic effects (Traveset et al., 2007). Furthermore, faeces is a complex matrix with both physical and chemical properties related to the animal diet (Frank et al., 2017; Ramos et al., 2024; Stricklan et al., 2020), which can influence fungi and bacteria development (Meyer and Witmer, 1998) and may reduce

germination potential (Enders and Vander Wall, 2012; Pauly et al., 2024; Valenta and Fedigan, 2009). Indeed, faeces are physically challenging (Mancilla-Leytón et al., 2012; Pauly et al., 2024) and may contain inhibitors (Malo and Suárez, 1995; Ramos et al., 2024; Traveset et al., 2001), affecting germination in the end. Among endozoochorous agents, large mammals appear to release an even more unfavourable faeces environment for seed germination with exacerbated constraints. For instance, (Stricklan et al., 2020) show that small and porous bird poops do not hamper germination in contrast to larger and thicker mammal faeces, which is in agreement with other monospecific studies (Mancilla-Leytón et al., 2012; Miller, 1995; Pauly et al., 2024). However, once seeds germinated, faeces may provide a fertile environment favouring seedlings' growth (Traveset et al., 2007) but see (Miller, 1995; Pauly et al., 2024), though this effect may change among animal species (Ramos et al., 2024) or with intraspecific diet variation (Traveset et al., 2001). In this context, faeces' visitors and disaggregation agents should play a key role in the seed dispersal success by limiting these constraints through disaggregation and secondary seed dispersal (SSD or Diplochory).

Visitors of mammal faeces can remove and disaggregate part of the faeces, reducing seed density within the faeces and secondary disperse part of the seed pool (Lawson et al., 2012; Milotić et al., 2019; Niederhauser and Matlack, 2017; Urrea-Galeano et al., 2019). All of which globally increase seed dispersal effectiveness (Culot et al., 2015; Falcon et al., 2024; Ishikawa, 2011). Faeces disaggregation and SSD agents are usually rodents (Culot et al., 2009; Pan et al., 2016; Vander Wall et al., 2017), dung beetles (Andresen and Urrea-Galeano, 2022) or sometimes ants (Blanco et al., 2011; Böhning-Gaese et al., 1999; Bona et al., 2023). Rodents, attracted by odour of the faeces (Beaune et al., 2012), are interested in the large and numerous seeds contained in mammal faeces that may represent an energetic banquet (Koike et al., 2012; Shakeri et al., 2018). In tropical areas rodents are often considered as seed predators and a threat to seed survival (Nichols et al., 2008) even if some reports involve scatter-hoarding behaviour of viable seeds (Andresen, 2002; Forget and Milleron, 1991; Jansen et al., 2002). In temperate areas, however, rodents are better recognised for their role in

SSD (Enders and Vander Wall, 2012; Koike et al., 2012; Niederhauser and Matlack, 2017; Pan et al., 2016; Shakeri et al., 2018) than for seed predation (but see (Bermejo et al., 1998; Koike et al., 2012; Pan et al., 2016).

Dung beetles are well-known to disaggregate faeces (Milotić et al., 2019) and for their SSD function (Andresen and Urrea-Galeano, 2022; Milotić et al., 2019). They are primarily interested in the faecal matter regardless of the seeds it contains (Andresen and Urrea-Galeano 2022). In fact, several factors can influence visits by dung beetles and SSD as recently reviewed by Andersen and Urrea-Gelano (2022). For instance, the type and texture of faeces may modulate the attraction of dung beetles, due to specific stimuli like volatile organic compounds (Frank et al., 2018, 2017; Santos-Heredia et al., 2010). Therefore, depending on the animal diet and physiology, the faeces may attract particular dung beetle functional groups and in variable abundances (Andresen and Urrea-Galeano, 2022; Enari et al., 2016; Frank et al., 2017; Milotić et al., 2019; Noriega, 2012; Santos-Heredia et al., 2011). In this context, faeces from omnivore such as brown bear may attract a community of dung beetles specific to herbivores and also carnivores (Frank et al., 2017), probably depending on omnivore faeces composition. Variation in the dung beetle community induces different functions and roles for the seed fate (Griffiths et al., 2016; Manning et al., 2016; Milotić et al., 2019) which raises questions about the fate of seeds within the diverse faeces omnivores release. Other factors such as the faecal deposition pattern (Fuzessy et al., 2022) but see (Santos-Heredia et al., 2010), the defecation site (Santos-Heredia et al., 2011) or the amount of faeces (Andresen and Urrea-Galeano, 2022), also modulate the faeces attractivity of dung beetles and thus disaggregation and SSD. In fact, the seeds dispersed are usually smaller or equal to the size of the dung beetle and seed shape or appendages may affect secondary dispersal probability (Andersen et Urrea-Gelano 2022).

However, the relative role of vertebrates and invertebrates in seed fate from mammal faeces has rarely been tested experimentally in sites when or where both are present (Culot et al., 2009; Hulme, 1997;

Pan et al., 2016), especially in temperate areas (Koike et al., 2012). Furthermore, these few previous studies focused on large seeds (Hulme, 1997; Koike et al., 2012; Pan et al., 2016) and their findings cannot be applied to determine the relative contribution of vertebrates and invertebrates to smaller seeds secondary dispersed. Small and medium-sized seeds may interest rodents (Shakeri et al., 2018; Vander Wall et al., 2017) and be easily transferred by dung beetles (Andresen and Urrea-Galeano, 2022; Milotić et al., 2019). We hypothesize faeces visitors can be significant agents on small and medium-sized seed fate by removing part of the faeces, the seed pool or by disaggregating the faecal matrix (H1) and that both type of visitors are implies in such process (H2). As mentioned previously the characteristics of the faeces (*e.g.* amount, deposition site, composition, and release pattern) containing the seeds are critical for their detection and disaggregation. In this sense, omnivores that release faeces composed of meat, plant, insect or mixed items should induce variable seed fate. We hypothesize that for a given omnivore the faeces composition has a determinant effect on its attractivity, disaggregation and SSD by biotic visitors (H3).

To test our first two hypotheses, we designed a realistic experiment (Andresen and Urrea-Galeano, 2022) in a temperate area using faeces of brown bear (*Ursus arctos*, L. 1758). Brown bear is an omnivore that consume plants, insects or meat (Lagalisse et al. 2003) and well-known to disperse seeds of various size from fleshy-fruit bearing plants but also herbaceous plants (García-Rodríguez et al., 2021a; Lalleroni et al., 2017; Pauly et al., 2024) thus making it a relevant biological model for studying these interactions in a temperate area. In our field experiment, we first assessed the relative effect of vertebrates and invertebrates on (i) faeces removal, (ii) faeces disaggregation, and (iii) small and medium-sized seed secondary dispersal. In the same time, we identified the faeces visitors using camera and pitfall traps. Furthermore, we tested the effect of diet composition on visitor attractiveness and activity based on seed secondary dispersed.

VII.4 Materials and Methods

VII.4.1 Study site

Our study was conducted in the Pyrénées mountains (36,600 km²) shared between the South of France Andorra, and the North of Spain, and peaking at 3404 m of altitude. Pyrénées host a wide diversity of plants, including endemics (Ninot et al., 2017), and several potential long-distance seed dispersers among which brown bear, small carnivores (*e.g.* european pine marten *Martes martes*, L. 1758), wild ungulates (*e.g.* Red Deer *Cervus elaphus,* L. 1758; pyrenean chamois *Rupicarpa pyrenaica*, L. 1758) and domestic ungulates (*e.g.* sheep *Ovis aries* L. 1758). Many dung beetles including endemics (Jay-Robert et al., 2003) are present. More precisely, we conducted our field experiment in Melles (Haute-Garonne, France), in an open and flat semi-natural grassland, at the edge of a forest, at 1400 m of altitude and within the Pyrenean brown bear current distribution range.

VII.4.2 Study population and faeces collection

The brown bear population in the Pyrénées includes at least 83 individuals in 2023 and is therefore classified critically endangered by IUCN. It is growing in numbers, benefitting from previous translocations of 11 Slovenian brown bear individuals (in 1996, 1997, 2006, 2016, and 2018). In 2023 the population range covered about 7100 km² from the East to the West of the Pyrénées (Sentilles et al., 2024). Based on coproscopic investigations, Pyrenean brown bear seasonal diet is composed mainly of forbs and ungulates (mostly scavenged) in spring, berries in summer and hard mast in fall. Other mammals and invertebrates also contribute to its diet (Lagalisse et al. 2003).

We collected very fresh (from the day) wild brown bear faeces in the Pyrénées between 2019 and 2023 using a scat detection dog (Sentilles et al., 2021), following spotting, depredation or at identified

feeding sites. We selected 30 faeces large enough to conduct the experiment, collected in spring; summer; fall, resulting in different diet composition. The composition of each faeces was determined based on visual investigation of undigested remains of the main food items (e.g., seeds and fruits for soft plants, fibrous parts for plants, exoskeleton for insects, hair and bones for vertebrates). The pool of faeces thus included eight faeces composed mostly of fragmented hard mast; seven composed of soft mast and 12 composed of vegetative parts of plants. One was composed of vertebrate material, one of invertebrates and the last one of honey wax. There were no 'large seeds' detected in the faeces used (e.g. cherry or apple seeds). Faeces were stored at -20°C before the experiment.

VII.4.3 Experimental design

Our experiment was conducted during the late summer 2024 at the beginning of September in an open area at the edge of the forest. We defrosted and split each of the 30 faeces samples into three 100g sub-samples (i.e. 90 sub-samples). For each faeces, we distributed the three subsamples into three treatments: total access (no cage), access restricted to invertebrates (*i.e.* invertebrate access, thanks to a wide-mesh cage, mesh =1.3 cm) and no access (fine-mesh cage, mesh =0.1 cm), respectively (see **Fig. VII.1**).

Figure VII.1: Illustration of the treatments carried out on the faeces, allowing access of vertebrates and invertebrates ("Total access", with no cage), access only of invertebrates ("Invertebrate access",

wide-mesh cage, mesh=1.3 cm) and no access of above-ground visitors ("No access", fine-mesh cage, mesh=0.1 cm). Pictures were taken by Grégoire Pauly and the silhouettes were obtained freely from Canva.

To test SSD and ensure the same number of seeds per treatment we inserted homogeneously eight *Rubus idaeus* (L. 1753) seeds (medium size, 6.00x3.00 mm, Cappers et al., 2006) and five *Vaccinium myrtillus* (L. 1753) seeds (small size, 1.50x0.25 mm, Cappers et al., 2006) per sub-sample, in line with (Milotić et al., 2019). Seeds were thus inserted inside each sub-sample (n=90) for a total of 720 and 450 seeds respectively. To avoid importing non-pyrenean seeds, they were extracted from Pyrenean brown bear faeces, not used in this specific experiment. All seeds were coloured neon yellow, using a forestry paint that contains no noxious or irritating products, waterproof, temporary, and UV-resistant to facilitate recovery and extraction at the end of the experiment.

The 90 faeces were thus randomly deposited directly on grass separated by 50 cm from each other in nine rows of 10 sub-samples. For each faeces sample, the three subsamples was associated with the three treatments. Each cage was firmly anchored in the ground to prevent passage between the ground and the base of the cage. No ground screen was installed.

We assessed the visiting small vertebrates using three camera traps located at two corners of the experimental design, and at a height of 40 cm, the third one covering another part of the experiment. Vertebrate identification on pictures was done by the authors. We assessed visiting insects, using three black circular, pitfall trap filled with water and one drop of washing-up. We placed a mesh roof onto which we deposited at the centre a non-accessible but odorant brown bear faeces composed of fleshy fruits that was not used in the experiment. The pitfall traps were set a few metres from the experiment and for the same duration as the experiment. Once the faeces were brought back to the laboratory, if any insects were found in the faeces they were identified. Identification was done by one of the author, expert on coprophagous and coprophilous insects.

The experiment and traps were left during 10 days from 10th to 19th of September 2024 with regular checks to ensure that the experiment was running properly. We installed an electric cattle fence around the experiment and the traps (12x10 m) to prevent potential disturbance by roaming megafauna and a rain gauge to monitor precipitation. We took a picture of each sub-sample at the beginning and the end of the experiment directly on the field.

In parallel to the experiment, we set aside ~20g of each of the brown bear faeces used for the experiment (n=30), as a "ratio control". We dried these ratio-control in an oven (60°C) until no more weight loss was observed to estimate their final dry mass. This allowed us to calculate the ratio between fresh and dry mass for each sample and thus estimate the initial dry mass of the fresh 100 g sub-sample (**Table VII.1**).

Table VII.1: Ratio of matter loss from fresh to dry faeces estimated from each faeces samples.

ID	Diet	Ratio of fresh to dry faeces (%)	ID	Diet	Ratio of fresh to dry faeces (%)
1	Hard mast	32	16	Soft Mast	25
2	Hard mast	20	17	Soft Mast	28
3	Vegetative parts	11	18	Soft Mast	38
4	Vegetative parts	11	19	Vegetative parts	19
5	Vegetative parts	22	20	Oak	25
6	Vegetative parts	20	21	Herbs	20
7	Meat	25	22	Soft Mast	18
8	Vegetative parts	9	23	Soft Mast	18
9	Vegetative parts	11	24	Hard mast	30
10	Vegetative parts	17	25	Vegetative parts	10
11	Vegetative parts	16	26	Hard mast	36
12	Soft Mast	20	27	Hard mast	18
13	Soft Mast	23	28	Vegetative parts	30
14	Honey was	50	29	Hard mast	27
15	Invertebrates	40	30	Hard mast	33

VII.4.4 Faeces measurements

At the end of the experiment, each sub-sample was collected, dried in an oven (60°C) in the same way as for the ratio control, and then weighed to determine the final dry matter. We determined the faecal removal by subtracting final from initial dry matter. In each sub-sample we also counted the number of remaining coloured *R. idaeus* and *V. myrtillus* seeds using mortar to break up dry fragments, a binocular magnifier to collect seeds, and deploying similar searching time per sub-sample of the same diet composition to estimate secondary seed dispersal (SSD). SSD is the number of seeds that were not recovered at the end of the experiment for each plant species tested.

Based on the final picture of each sub-sample (n=90) we assess the disaggregation of faeces based on objective and innovative criteria (and never used before) (**Fig. VII.2**). "Intact" single faecal unit with no obvious traces of invertebrate or vertebrate activity. "Disturbed" can be a single faecal unit with the presence of dung invertebrate/vertebrate activity (*e.g.* small holes) on part of the faeces. Alternatively, it can also show a few more or less connected secondary faecal units. "Very disturbed" can be a single unit with the presence of dung invertebrate/vertebrate activity on several parts of the faeces. Alternatively, there may be several more or less connected secondary faecal units (**Fig. VII.2**). The disaggregation status was assessed by wildlife specialists (n=3) and colleagues from our research laboratories (n=9) in single blind based on a picture without information of the treatment. For a given picture, the most frequent assessment among observers was kept, and in the event of a tie, a consultation between authors was held to make a final decision.

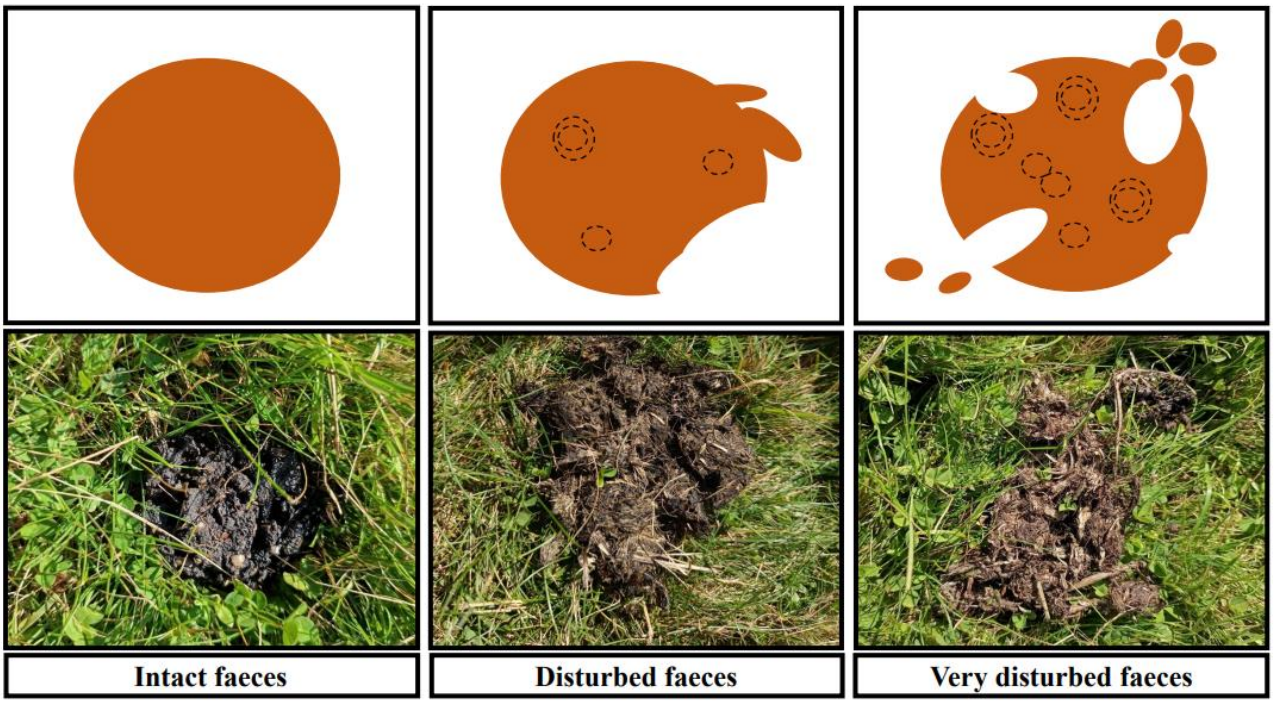

Figure VII.2: Schematic illustration and picture of faeces according to the disaggregation assessment defined here by Pauly et al. "Intact" faeces show no clear evidence of visits by invertebrates or vertebrates. "Disturbed" faeces show evidence of visits (holes, fragments). "Very disturbed" faeces show numerous evidence of visits. Pictures were taken by Grégoire Pauly.

To assess the effect of the main diet composition of faeces on visits we used cumulative numbers of seeds retrieved in treatments with access of visitors (Total access and access restricted to invertebrates).

VII.4.5 Data analysis

To test the relative effect of vertebrate and invertebrate visitors on faeces removal we performed a Gamma General Linear Mixed Model (GLMM), dealing with positive values, using sub-sample final dry mass as the response variable, treatment as the explanatory variable, sample ID as a random factor and sub-sample initial dry mass as a co-variate.

To test the relative effect of vertebrates and invertebrates on small- and medium-sized seed removal we performed a Gamma GLMM, dealing with positive values, using the number of seeds per sub-sample as response variable, treatment as explanatory variable and sample ID as a random factor. We ran a model for each plant species (*R. idaeus* and *V. myrtillus*). If for a species all the seeds were removed from at least one sub-sample (*i.e.* n=0), then a Poisson GLMM was performed to analyse the seed removal for this species, dealing with counted data and zero values.

To test the effect of treatment on the faecal sub-sample disaggregation we performed a $\chi 2$ test of independence per pair of treatment (*e.g.* $\chi 2$ test on faeces with total access vs faeces with no access treatment). To compare the information obtained with the faeces removal values and the disaggregation score, we carried out a Spearman correlation test.

To test the effect of diet composition on visits, we ran separate analyses for *R. idaeus* and *V. myrtillus* and only tested faeces with diet composition that at least occurred twice: hard mast (n=8), soft mast (n=7), and vegetative plant parts (n=12) as treatments. We discarded the other types of faeces with a single occurrence (honey, meat, and insects). We performed a Gamma General Linear Model (GLM), dealing with positive values, on the number of seeds with faeces diet composition as explanatory factor.

All the analyses were carried out in R studio (v. 4.3.3) using the lme4 package (v 1.1-35.5) (Bates et al., 2015) for GLM and GLMM. To obtain the marginal and conditional R^2 of our models we used the MuMIn package (v. 1.48.4) and the trigamma method (Barton, 2024). The visualisations were carried out using Microsoft Office Professional Plus 2016 (Figures 1-2) and the ggplot2 package (v. 3.5.1) (Wickham, 2011) with R studio (Figures 3-5), with keeping in mind colour blind people. The silhouettes of Dung Beetles and Rodents was freely obtained from Canva.

VII.5 Results

VII.5.1 Faeces removal

There was a significant effect of the treatment on faeces material removal (Gamma GLMM, marginal R^2= 0.79, conditional R^2=0.88, see Appendix VII.S1 for details). Faeces transfer was significantly higher in the sub-samples with total access of all visitors (m=7.3g, sd=4.7) than in the sub-samples with no access (m=5.2g, sd=3.6) (p=0.0002, df=inf, z.ratio = 3.995) and significantly higher in the sub-samples with invertebrate access only (m=6.8g, sd=4.9) than in the sub-samples with no access (p=0.0422, df=inf, z.ratio =2.410). We found no significant difference between sub-samples with total access of all visitors and sub-samples with invertebrate access only (p=0.250, df=inf, z.ratio=1.590) (**Fig. VII.3**).

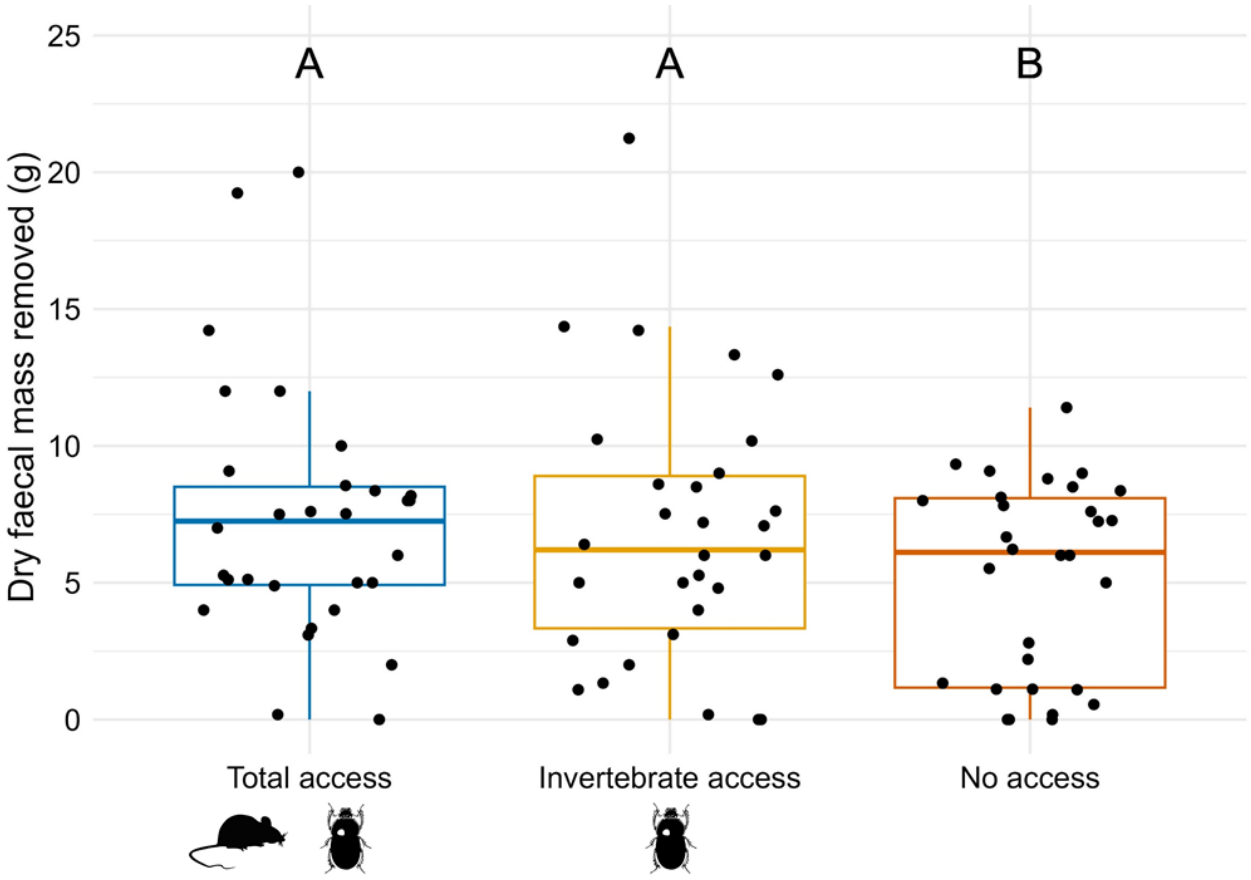

Figure VII.3: Boxplot (midline=median, box limits=quartiles, whiskers=maximum and minimum without outliers) of the dry faecal mass removed (measured as initial dry mass - final dry mass, symbolised by the points) from the sub-samples after ten days in each treatment. Each treatment allowed access of vertebrates and invertebrates ("Total access", color: #0072B2), invertebrates only ("Invertebrate access", color: #E69F00) and no visitors from the surface ("No access", color: #D55E00). The letters represent significant differences among treatments based on a GLMM Gamma. The silhouettes were obtained freely from Canva.

VII.5.2 Secondary seed dispersal

Seed extraction could not be carried out on the faeces composed of honey due to the formation of an unbreakable paste after oven drying. We observed a significant difference in the number of *Rubus idaeus* seeds retrieved among treatments (Gamma GLMM, marginal R^2= 0.16, conditional R^2=0.31, see Appendix VII.S1 for details). Significantly fewer *R. idaeus* seeds were found at the end of the experiment in sub-samples with total access of all visitors (m=6.5, sd=1.9) than in sub-samples with

no access (m=7.9, sd=0.3) (p=0.0059, df=inf, z ratio= -3.081), and in sub-samples with invertebrate access only (m=6.3, sd=1.9) than with no access (p=0.0016, df=inf, z ratio = -3.454). There was no significant difference in sub-samples with total access of all visitors and sub-samples with invertebrate access only (p=0.9235, df=inf, z ratio = 0.380) (**Fig. VII.4**). We observed a significant difference in the number of *V. myrtillus* seeds retrieved among treatments (Poisson GLM, marginal R^2 = 0.11, see Appendix VII.S1 for details). Significantly fewer *V. myrtillus* seeds were found at the end of the experiment in sub-samples with invertebrate access only (m=2.7, sd=1.5) than sub-samples with no access (m=4.4, sd=0.6) (p= 0.0020, df=inf, z ratio = - 3.389). We observed no significant difference between sub-samples with total access of all visitors (m=3.3, sd=1.1) and sub-samples with invertebrate access only (p=0.3610, df=inf, z ratio= 1.362), and a marginal difference between sub-samples with no access and sub-samples with total access of all visitors (p=0.0963, df=inf, z ratio = -2.069) (**Fig. VII.4**).

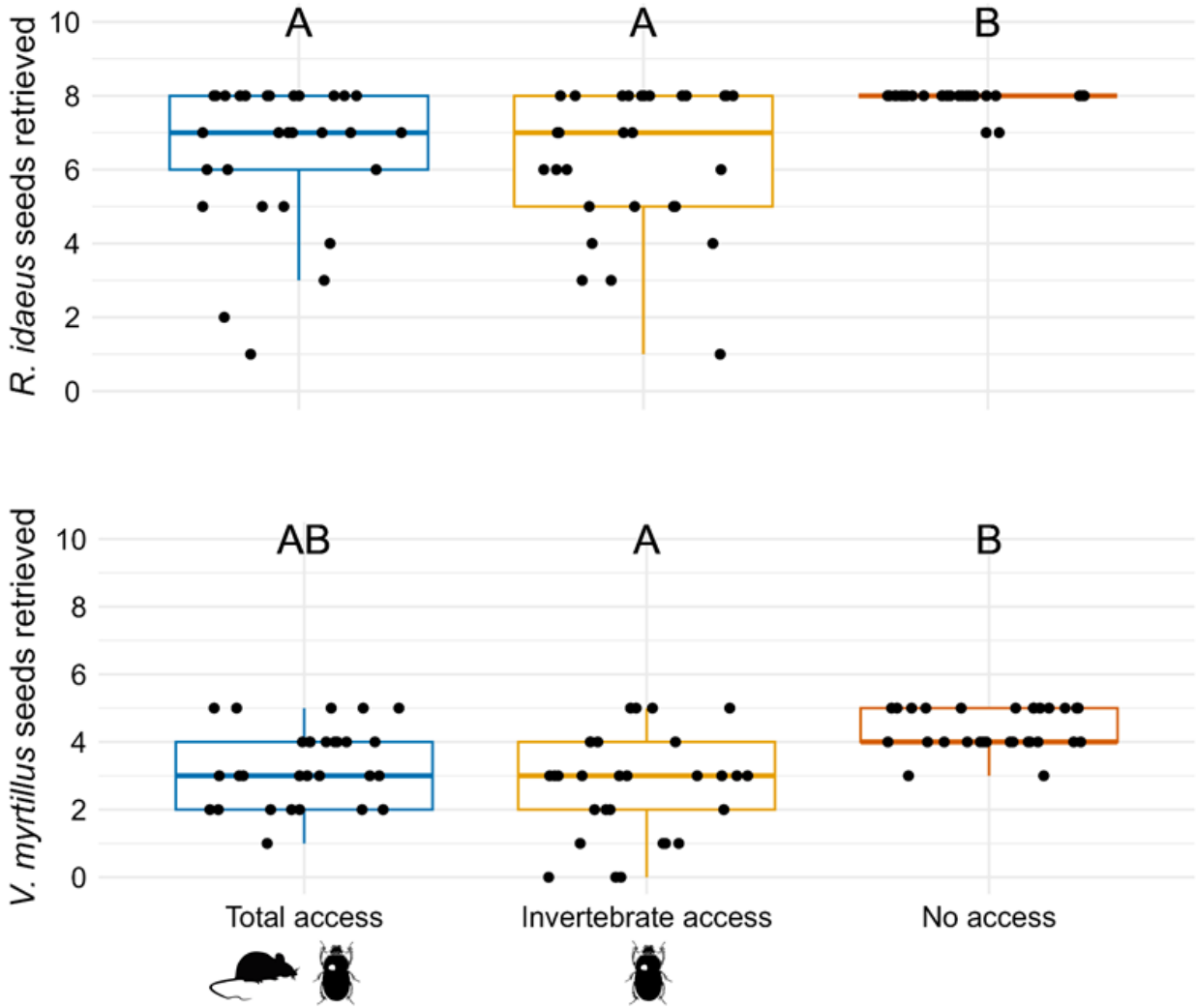

Figure VII.4: Boxplot (midline=median, box limits=quartiles, whiskers=maximum and minimum without outliers) of the number (points) of *Rubus idaeus* (initially n=8) and *Vaccinium myrtillus* (initially n=5) retrieved from faeces sub-samples in each treatment. Each treatment allowed access of vertebrates and invertebrates ("Total access", color: #0072B2), invertebrates only ("Invertebrate access", color: #E69F00) and no visitors from the surface ("No access", color: #D55E00). The letters related to the number of *R. idaeus* represent significant differences among treatments based on a GLMM Gamma. The letters related to the number of *V. myrtillus* represent significant differences among treatments based on a GLM Poisson. The silhouettes were obtained freely from Canva.

VII.5.3 Disaggregation assessment

The disaggregation assessment was done on the 90 sub-samples in blind by 12 people including the authors. Faeces sub-samples with total access of all visitors and sub-samples with access restricted to

invertebrates were assessed as "intact" with 7/30 and 7/30 occurrences each. Faeces sub-samples with no access were assessed as "intact" in 15/30 occurrences (**Table VII.2**). We observed a significant difference in disaggregation between sub-samples with no access and sub-samples with total access of all visitors ($\chi 2$ test, $\chi 2$= 9.3, df=2, p=0.010) and between sub-samples with invertebrate access only and sub-samples with no access ($\chi 2$ test, $\chi 2$= 7.5, df=2, p=0.023). We found no significant difference between sub-samples with no access and sub-samples with invertebrate access only ($\chi 2$ test, $\chi 2$= 0.4, df=2, p=0.826). We found a weak correlation (Spearman correlation, 0.12) between disaggregation score and value of faeces removal.

Table VII.2: Faeces disaggregation assessment of the 90 sub-samples performed by wildlife experts and scientists according to access of faeces to vertebrate and invertebrate visitors (Total access), invertebrates only (Invertebrate access), and no above-ground visitors (No access). Each cell contains the number of sub-samples for a given stage a disturbance and percentage (%) for each type of access.

State of faeces	Total access	Invertebrate access	No access
Intact	7 (23%)	7 (23%)	15 (50%)
Disturbed	14 (47%)	16 (53%)	14 (47%)
Very disturbed	9 (30%)	7 (23%)	1 (3%)

VII.5.4 Effect of diet composition

The main food composition of the faeces had an effect on *R. idaeus* removal (Poisson GLM R^2=0.15, see Appendix VII.S1 for details) with significantly more seeds retrieved in faeces composed of hard mast (m=15.1, sd= 0.8) than composed of vegetative parts (m=12.0, sd=3.1) (p=0.04, t-value = -2.181). There was no significant difference in *R. idaeus* removal between faeces composed of hard mast and faeces composed of soft mast (m=12.7, sd=3.9), as well as between faeces composed of soft mast and vegetative parts (**Fig. VII.5**). We observed no significant differences (see Appendix VII.S1 for details) in *V. myrtillus* removal among faeces composed of hard mast (m=7.0, sd=1.9), soft mast (m=6.6, sd=1.5), and vegetative parts (m=6.7, sd=3.0) (**Fig. VII.5**). In the faeces composed mostly

of meat we retrieved 6/16 *R. idaeus* and 4/10 *V. myrtillus* seeds, while in the faeces composed of insects we retrieved 11/16 *R. idaeus* and 6/10 *V. myrtillus* seeds. We were not able to count seeds in the faeces composed of honey.

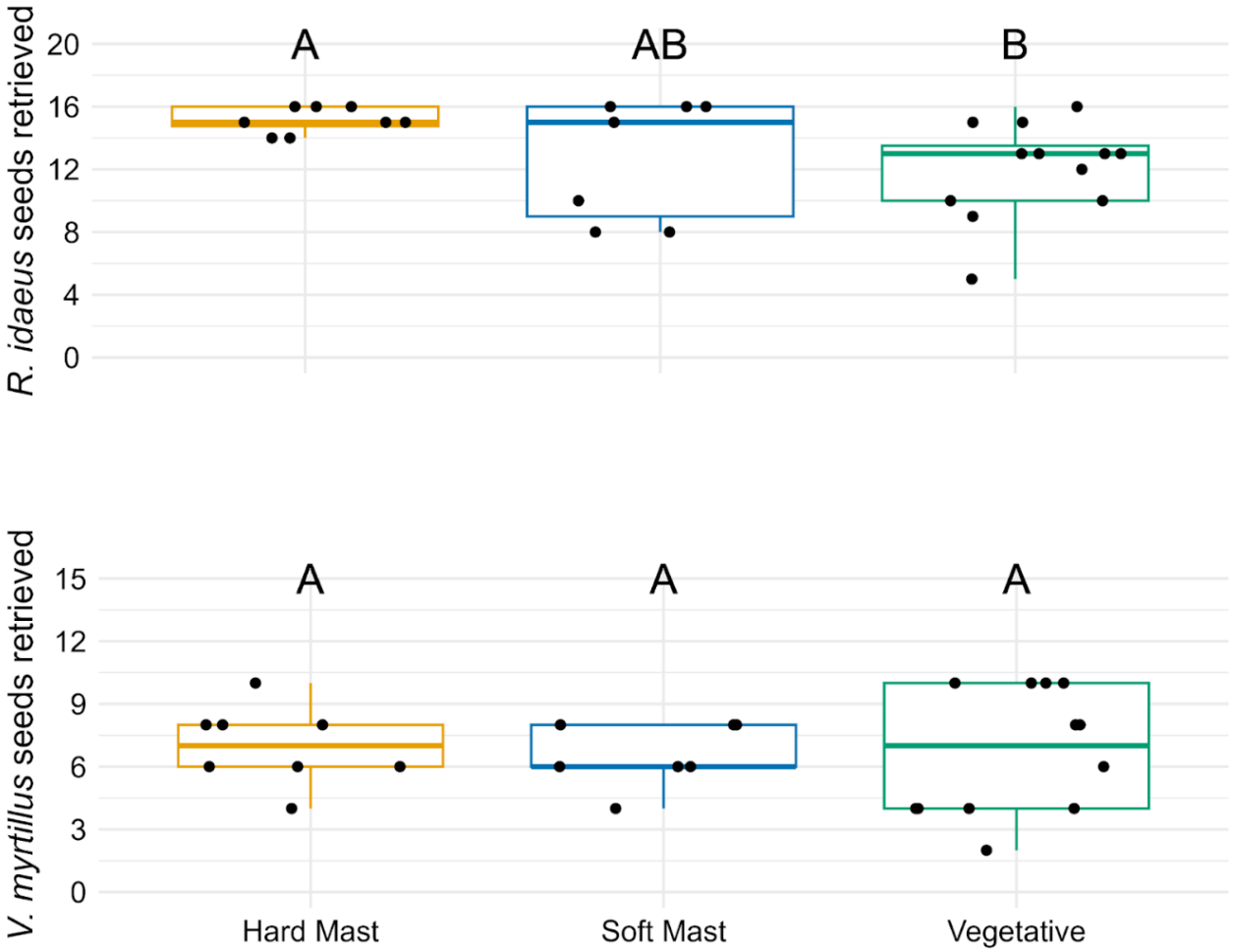

Figure VII.5: Boxplot (midline=median, box limits=quartiles, whiskers=maximum and minimum without outliers) of the number (points) of *Rubus idaeus* and *Vaccinium myrtillus* seeds counted in faeces accessible to visitors (faeces with total access or access restricted to invertebrates) according to the main diet composition: Hard Mast (#E69F00), Soft Mast (#0072B2) or Vegetative parts (#009E73). The letters in graphics represent the significant difference among main food composition from a GLM Gamma.

VII.5.5 Visitors community

No vertebrate visitors were detected with the camera traps during the experiment. The camera traps were frequently triggered during dung beetle flights. Based on pitfall traps and insects retrieved in faeces eight taxa of invertebrates were identified including three dung beetles: two *Anoplotrupes stercorosus* (Scriba 1791); one *Trypocopris pyrenaeus* (Charpentier 1825); four females of *Onthophagus* gr. *ovatus* (Latreille 1802). We also identified ground beetles (one *Calathus luctuosus*, Latreille 1804; one *Amara lunicollis*, Schiødte 1837), earwigs (six *Forficula auricularia*, L. 1758) and honey bees (nine *Apis mellifera*, L. 1758). The *Ontophagus* gr. *ovatus* was retrieved in faeces after the end of experiment.

No disturbance of the experiment from humans or ungulates was reported. There was only one day of rain (11/09/2024) with 14 mm measured with the rain gauge.

VII.6 Discussion

Our experiment in Pyrénées based on brown bear faeces reveals the crucial role that visitors play as disaggregation agents (faeces removal and disaggregation) and secondary seed disperser of small- and medium-sized seeds, and how it is affected by the diet composition. Such activities are essential processes for limiting the constraints exerted by the faeces matrix on seeds and improving their germination (Enders and Vander Wall, 2012; Pauly et al., 2024; Ramos et al., 2024). We observed significantly less faeces material and seeds removed in faeces with a fine-mesh cage, which prevented any visit from above ground visitors, congruent with (Koike et al., 2012) and our hypothesis H1. Based on few seeds inserted per sub-sample, we observed a significant activity of SSD by visitors in only ten days, in agreement with (Milotić et al., 2019) on dung beetles SSD in Europe. It has been reported that such activity of faeces visitor increases the seed dispersal effectiveness of primary seed disperser with more seedlings observed (Culot et al., 2015; Falcon et al., 2024; Ishikawa, 2011). The

disaggregation assessment, as objective as possible, shows that faeces accessible to visitors are more disaggregated than faeces with no above ground visitors, strengthening our other results and congruent with our hypothesis H1. However, part of the variation could also be due to handling bias or to our inability to collect the complete faeces content and seeds even if we did this with high degree of precaution. The loss of faeces material or seeds in sub-samples with no access of above-ground visitors, and the similar percentage of disturbed faeces between the three access treatments, can be due to abiotic factors, bacteria decomposition, soil biotic agents (Koike et al. 2012) or to faeces handling at the beginning or the end of the experiment. Furthermore and contrary to our hypothesis H2, our study in temperate ecosystems reveals that invertebrates are the predominant SSD and disaggregation agents as we observed no vertebrates with camera traps and no difference between treatments with or without access of vertebrates (*i.e.* faeces with no cage or with wide-mesh cage) in faeces removal, seed removal and disaggregation assessment. Based on those findings, for constraining brown bear faeces (Pauly et al. 2024) that may contain numerous seeds with strong competition among them (García-Rodríguez et al. 2022), such activity by Dung Beetles might be crucial in the role of brown bear in seed dispersal (García-Rodríguez et al. 2021).

The invertebrates identified included three dung beetle species and a few other species (ground beetles, bees, and earwigs) while other potential agents such as maggots were not observed, probably due to the time of the year (Sladecek et al., 2017). Dung beetles were the most numerous coprophagous group collected. The low abundance of insects collected may be explained by the attractiveness of brown bear faeces (Frank et al., 2017) or by our monitoring to collect them. However, this suggest that Dung Beetles, which also frequently triggered camera traps, were the main invertebrate group of faeces removal, disaggregation and SSD in this study, which are organisms usually implied in such processes (Andresen and Urrea-Galeano, 2022). The seeds were probably secondary dispersed horizontally or vertically and buried in the soil seed bank (Andresen and Urrea-Galeano, 2022). Our results support previous findings on the effect of dung beetles in reducing seed

aggregation within faeces (Milotić et al., 2019; Santos-Heredia et al., 2010; Urrea-Galeano et al., 2019). Studies in tropical areas show also that such dispersal induce a decrease of seedling aggregation but also contrasting effects on the establishment of these seedlings, which depend on other biotic factors (Lawson et al., 2012; Urrea-Galeano et al., 2019). The short duration of our study also reveals that SSD and disaggregation can occur very quickly following faeces release.

In this study, we also pinpointed that the composition of brown bear faeces has a significant effect on visitor activity, here dung beetles, which is congruent with our hypothesis H3. Indeed, faeces composed mostly of hard mast were significantly less visited than faeces composed of soft mast or vegetative parts, and we observed important seed removal in the single faeces composed of meat. This difference is probably due to the texture or the nutrients in the faeces (Andresen and Urrea-Galeano, 2022; Frank et al., 2017) or may be related to the experimental design we used. The effect of faeces composition on dung beetle' community and activity have been noticed previously within frugivore monkey species (Santos-Heredia et al., 2011) or among animal species with different diet (Enari et al., 2016; Frank et al., 2017). In this sense, seed fate may also depends on the faecal matrix in which seeds are embedded. For omnivores like the brown bear, faeces composition are more variable than for a frugivore, suggesting that the spectrum of effects of the faecal matrix on Dung Beetles community attraction (Frank et al. 2017) and the seed fate may be even wider. The effect of faeces composition should be relevant for most of the omnivores involved in seed dispersal (*e.g*. Suids ((Massei and Genov, 2004) or Mustelids (Otani, 2002; Tochigi et al., 2022)), with potential positive implication for dung beetle diversity.

Rodents, usual secondary seed dispersers (Culot et al., 2009; Pan et al., 2016; Vander Wall et al., 2017), did not seem to be attracted by the small- and medium- sized seeds used in our experiment or by hard mast fragments, thus providing no effect on faeces disaggregation or SSD. It contrasts with other studies showing that rodents are important faeces visitors and secondary seed dispersers (Enders

and Vander Wall, 2012; Koike et al., 2012; Pan et al., 2016; Shakeri et al., 2018). Although rodents can be attracted by medium-size seeds (Shakeri et al., 2018; Vander Wall et al., 2017), studies that unveiled such SSD activity focused on larger seeds such as *Prunus* sp. (L. 1753), *Cornus* sp. (L. 1758), *Taxus* sp. (L. 1753), or *Rhamnus* sp. (L. 1753) (Enders and Vander Wall, 2012; Koike et al., 2012; Pan et al., 2016; Shakeri et al., 2018). The faeces may only be attractive to rodents when large seeds are present and visible, and small or medium-sized seeds are only consumed from fruit or when they are available on the ground. The small number of seeds included may also explain the lack of attractiveness to rodents, although we did not observe any activity on faeces initially composed of soft mast (*R. idaeus*, *V. myrtillus*). The site of our experiment (open area at the edge of a forest) may also explain these results, as the rodent community in temperate areas can be more species-rich inside forest (Shakeri et al., 2018). Another explanation can be the proximity of a hiking trail which was potentially limiting rodent activity (Lee et al., 2019). However, brown bear can also transport large seeds (García-Rodríguez et al., 2021a; Lalleroni et al., 2017) and may interest rodents (Shakeri et al., 2018).

Other vertebrates present in the Pyrénées, such as birds, can handle faeces (*e.g. Pyrrhocorax pyrrhocorax*, *Upupa epops* or *Milvus milvus*) (Niederhauser and Matlack, 2017; Young, 2015). For instance, *Upupa epops* can flip dry cow faeces to collect insects beneath (Skead, 1950) whereas some birds such as *Eremophila alpestris* can break open the faeces (Bent, 1942). In fact, other animals (*e.g.* mammals, amphibians, squamates or other invertebrates) may interact with faeces (Young, 2015). Interaction and disturbance by those dung beetle predators may have important effects on the faecal matrix and seed germination (Enders and Vander Wall, 2012; Pauly et al., 2024). Consequently, we argue that similarly to a carrion (Anderson, 2019; Bajerlein et al., 2011), a faeces may represent a trophic successional environment with coprophagous insects and then their predators (Koskela and Hanski, 1977), all potentially playing a role in the faeces decomposition and the fate of the small- and medium-sized seeds in brown bear faeces.

Our field study is the first to test experimentally the relative role of vertebrates and invertebrates on the secondary dispersal of medium and small-sized seeds. To confirm our results, other similar realistic studies should be carried out in temperate or tropical areas. Furthermore, monitoring the fate of displaced seeds would also provide valuable information on the dynamics of small and medium-sized seeds, as well as helping to better characterize the effect of SSD on the seed dispersal effectiveness of brown bear or other species. It has been studied on larger seed removal by both type of visitors (Koike et al., 2012) or in other studies on dung beetles SSD (Lawson et al., 2012; Urrea-Galeano et al., 2019). Our disaggregation assessment seems to complement the measurement of faeces removal and represents a first quantification attempt, but the development of even more objective indicators to determine faeces disaggregation (*e.g.* based on picture with same angle, distance and light) is welcome if we want to better assess this overlooked but crucial aspect (Pauly et al. 2024).

Overall, our study in temperate areas highlighted the role of dung beetles in small and medium-sized seeds removal and faeces disaggregation whereas vertebrates did not forage such faeces (*i.e.* lacking larger seeds). However, other vertebrates, especially predators of coprophagous insects may play a role in faeces disaggregation. Therefore, future research is encouraged to consider the trophic succession in faeces to quantify the role of each visitor in faecal disaggregation and SSD. Furthermore we proved that the composition diversity of omnivore faeces affected visitor activity and thus SSD. In this sense, the role of omnivore in seed dispersal appears even more complex than previously thought and further consideration should be given to the faecal matrix composition enveloping seeds.

VII.7 Acknowledgments

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Part 5 - General discussion, conclusion and perspectives

Pyrenean landscape

Chapter VIII - Brown bear: an omnivorous diet that benefits the ecosystems

My Phd thesis work contributed to a well diverse, significant and historical knowledge on brown bear ecology by providing new and innovative evidence on its diet through metabarcoding, its role in plant (angiosperms, gymnosperms, mosses and ferns; effect of faecal matrix) and fungi (mycorrhizae, endophytes and pathogens) dispersal, all included in a myriad of interactions turning brown bear as a potential keystone species.

VIII.1 Implications of the findings

This PhD thesis provided new evidence to the role of brown bear on plant communities through several mechanisms. First, we demonstrated that brown bear can transport a quite diverse cortege of plants including fleshy- and dry-fruited plants, mosses and ferns, confirming that we must look beyond dispersal syndromes. In addition, we also demonstrated the potential transport of many different fungi symbionts with positive (growth, defense) or negative (pathogen) effects on plants that may be significant in shaping plant community assemblage. In the context of the global changes, the role of highly mobile endozoochorous agents as brown bear appears crucial. Indeed, brown bear may induce uphill dispersal (Mendes et al., 2025; Naoe et al., 2019), favor forest regeneration of degraded habitats (Wunderle, 1997) or following forest fire (Costa et al., 2025). In such a context, the symbiotic

fungi are also vulnerable to habitat fragmentation (Sapsford et al., 2020). Hence, in the Pyrénées, brown bear can mitigate such negative effects. Furthermore, faeces must be disaggregated to favor germination, and this can be performed by dung beetles while also providing secondary seed dispersal. However, dung beetles are also highly sensitive to global change (Sánchez-Bayo and Wyckhuys, 2019), and all of these interactions remain fragile.

In the light of its very diverse diet described here in the Pyrénées (**Chapter III**), many different interactions can also occur as demonstrated in our review (**Chapter II**). The predation or scavenging of wild ungulates may have significant effects on prey, plant, co-predator, co-scavenger communities. Similarly, ant consumption may have significant effect on plants. Furthermore, according to several studies on the transport of invertebrate (Green and Figuerola, 2005; Navarro-Ramos et al., 2022; Vanschoenwinkel et al., 2008), it is also highly probable that brown bear can transport invertebrate propagule through intentional or accidental consumption. The well diverse diet and transport engineering described here in the Pyrénées fit well with the potential keystone status of brown bear.

The conservation of brown bears is therefore not just a matter of protecting one single species, but rather a whole set of interactions with many different organisms. Recent research showed that the loss of interactions may be particularly detrimental for the ecosystem functioning (Valiente-Banuet et al., 2015). In the context of global changes, shifts of the abiotic and biotic conditions may cause significant loss of suitable habitat for brown bear, that may cascade on its trophic and non-trophic interactions (Lucas et al., 2025). However, not all population of brown bear are equal in the face of these global changes, and south-eastern populations appear particularly vulnerable (Lucas et al., 2025).

My Phd work also illustrates the need to investigate (when possible) interactions in a wider and most complete way as possible. For instance, here we went beyond the typical endozoochorous syndrome

and usual angiosperm investigation in plant dispersal. Furthermore, we challenged endozoochory inferences, notably based on germination experiments from intact faeces. This holds true with fungi dispersal investigation and metabarcoding-based diet. These methods are not exhaustive, but they provided additional evidence and paved the way for many new avenues of research. One of the specificities of this PhD thesis was also the parsimonious use of the precious biological material. Indeed, the non-invasive collection of fresh brown bear faeces from a small population (here optimised thanks to the use of scat-detection dogs, Sentilles et al., 2021) was particularly challenging, energy- and time-intensive. This is why most of the faeces were used in two or three experiments, manipulations or chapters, using different portions each time. In this sense, we invite future research to consider the optimised use and valorisation of biological material and collection.

VIII.2 Brown bear in the Pyrénées

One of the objectives of this thesis (part of the OFB-DRAS-SEE EcoSyBear project) was to highlight the key interspecific interactions of brown bear in the Pyrenean ecosystems. The investigation of brown bear benefit was also to temper the socio-political debates surrounding its presence and conservation in the Pyrenees, often linked to its livestock depredatory behaviour, setting aside the key ecological roles and ecosystem services potentially provided by this keystone species (Ouvrier et al., 2025). Here, we first demonstrated that domestic ungulates represent a very small part of its diet (only 6% of faeces containing ewes), which is mostly plant based but commonly included fungi, arthropods and more occasionally meat (wild and domestic). Concerning wild ungulates consumed by brown bear, such predation may have significant effect on ungulate recruitment or their behaviour (**Chapter II**). In other words, brown bear may regulate wild ungulate populations and potentially reduce their associated effects on vegetation through herbivory. We provided the first description of the Pyrenean brown bear diet since the late 90's studies, which is particularly important for the stakeholders involved in brown bear conservation or coexistence in the Pyrénées. Furthermore, its

role in plant dispersal has been more detailed and widely described compared to the previous report (Lalleroni et al., 2017). In the context of global change, its role in plant dispersal, in particular on the Pyrenean emblematic *Vaccinium* spp., is of patrimonial importance for the Pyrenean ecosystem. Brown bear may more largely contribute to the Pyrenean plant community through the dispersal of a diverse flora, and associated mycoflora that favors plant growth, especially of trees and thus contributes to preserving the vulnerable Pyrenean ecosystem.

VIII.3 Perspectives and future research

This PhD thesis work shed light on new interactions, while opening doors to new questions and avenues to explore highlighted below:

- The keystone status of omnivorous ursids and more generally of omnivore animal species still needs to be explored through meta-analyses or directly in the field by quantifying their effects on different ecosystem components. Such approaches could provide more evidence to the crucial role that omnivores play on the structure and functioning of ecosystems

- Here, we detailed in a very new way the diet of brown bears according to age, sex, ecological periods through the use of faecal eDNA metabarcoding and a multi-taxonomic approach. Such an approach should be used on other species to describe their diet, identify cryptic food items such as fungi and to highlight inter- and intra-population diet variability. Furthermore the use of more specific markers to identify mosses, ferns or endomycorrhizae could be particularly relevant (Taberlet et al., 2018). However, the metabarcoding approach faces several issues, and principally the ability to distinguish taxa related to the marker used and the reference database. Furthermore, and even if approaches based on the number of reads exist (e.g. Jaroszewicz et al., 2023), a confident proxy of the volume of each item within the faeces is

still missing. In this sense, it might be relevant to combine the innovative use of metabarcoding with visual coproscopic methods to describe the diet of animals in the most complete way possible both in qualitative and quantitative terms.

- We also highlighted the importance of considering each endozoochorous filter for the inference of plant dispersal, especially the faecal matrix. In this sense, this Phd thesis also encourages future research on the effect of the faecal matrix according to the animal involved. Furthermore, a better understanding and investigation of secondary dispersal or faeces disaggregation on seed dispersal success is welcome (e.g. Ishikawa, 2011).

- Finally, we shed light on the potential dispersal of symbiotic fungi and plants by brown bears using metabarcoding of faecal eDNA. This study and the level of inference reached is a first step into the understanding of such fungi dispersal. Future research should focus on the use of faeces as a fungal inoculum in a sterile environment in order to quantify the colonisation of such fungi, as recenlty done for mycorrhizae (Correia et al., 2019). Furthermore, for endozoochorous agents, investigating dispersal of non-fleshy-fruited plants remains crucial to properly investigate the role of animals in plant dynamics.

To conclude, while brown bear is an omnivorous animal involved in many processes, there is still a lot to investigate. Concerning the contribution of mammals to plant dynamics, their role appears much more important if we consider their implication in each plant life form and their associated fungi dispersal

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Appendices

Appendix II.S1

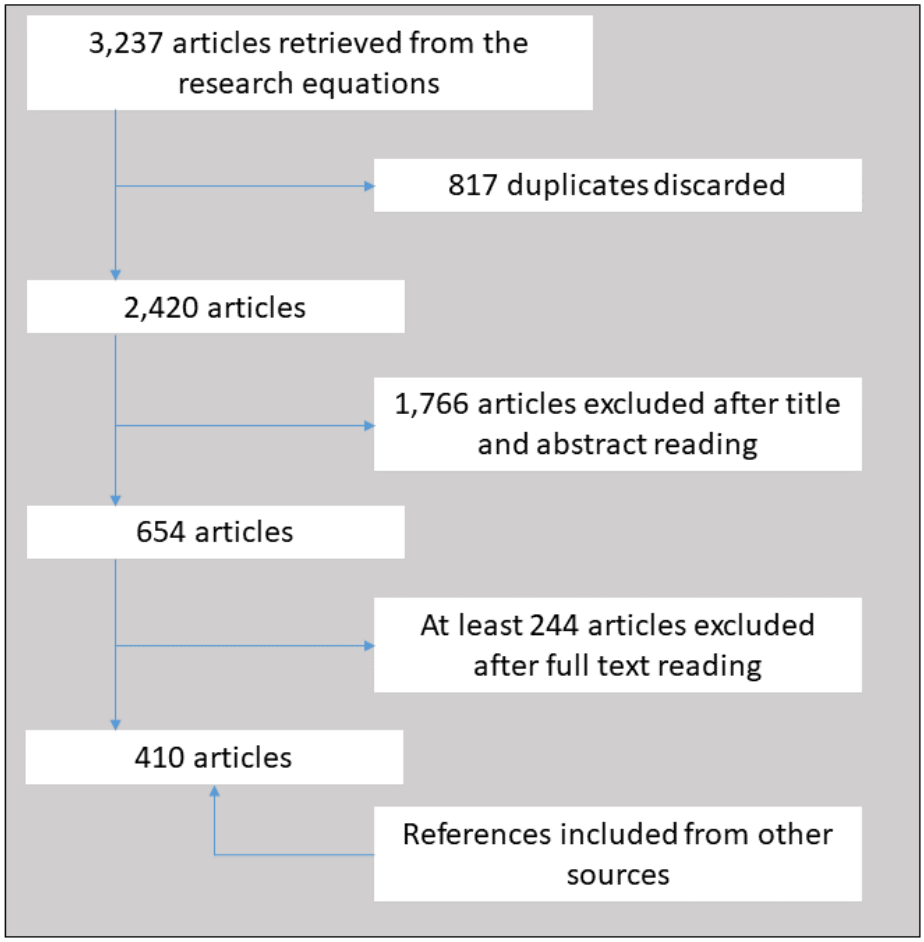

Figure II.S1.1: Flow chart of article selection on Ursid trophic and non-trophic interactions.

Appendix II.S2

Table II.S2.1: Number of articles collected according to country and omnivore bear species

Country	*Hma*[1]	*Tor*[2]	*Mur*[3]	*Uth*[4]	*Uar*[5]	*Uam*[6]
Belarus					2	
Bolivia		4[7]				
Bosnia and Herzegovina					1	
Canada					26	39
China				1	1	
Colombia		2				
Croatia					8	
Ecuador		7				
Estonia					1	
France					4	
Greece					1	
India	1		7	3	1	
Indonesia	6					
Iran					2	
Italy					3	
Japan				32	10	
Malaysia	1					
Nepal			2			
Norway					10	
Pakistan				2		
Peru		4				
Poland					8	
Russia				3	6	
Slovakia					1	
Slovenia					5	
Spain					4	
Sweden					19	
Taiwan				1		
Thailand	2			3		
Turkey					1	
UK					1	
USA					108	119
Venezuela						
Without_site	1				19	13
Mexico						2

[1]Helarctos malayanus, [2]Tremarctos ornatus, [3]Melursus ursinus, [4]Ursus thibetanus, [5]Ursus arctos, [6]Ursus americanus,

[7]Number of studies

Appendix II.S3

Section II.S3.1: List of references related to Ursus thibetanus interaction map (Figure II.5).

Ab – Diet – Stable isotopes –										
Aa – Diet – Frequency of occurrence –										
References	**Country**	**Data**								
		Herbs	**Soft mast**	**Hard mast**	**Tree parts**	**Fungi**	**Invertebrates**	**Small mammals**	**Ungulate**	**Other animal**
1) Ali et al., 2017	Pakistan	1.9%	17,0%	9.4%			5.7%		3.8%	5.7%
2) Basnett et al., 2021	India	62%	10%	23%						
3) Hashimoto & Anrui, 2013	Japan	80,8%	1.4%	17.7%			6.3%	2.0%	1.4%	
4) Hashimoto, 2002	Japan	44.7-53,9%	31.0-42.7%	28.1-53.7%	0-1.1%		28.1-35.3%		0-2%	0.9-2%
5) Huygens et al., 2003	Japan	24%	16%	74%			12%		2%	
6) Hwang et al., 2002	Taiwan	0%	4%	77%			1%		11%	
7) Koike et al., 2013	Japan	24-34%	31%	11-17%			9-16%		1-37%	
8) Koike, 2010	Japan	16,9-44,2%	9.2-44.2%	15.3-53.8%		0,0 - 3,8%	11,5 -18,9%		0-1,0%	
9) Koike, Morimoto, Goto, et al., 2012	Japan	45%					54%			1%
10) Naganuma et al., 2022	Japan		47%	49%			25%		22%	6%
11) Reid et al., 1991	China	50-56%	27-51%	0-31%			0-10%		0-12%	
12) Takahashi & Takahashi, 2022	Japan	0-48%	74-100%	0-1%			22-30%			0-5%
13) Torii, 1989	Japan	34%	30%	46%	55.7%		28%		0%	
14) Yadav et al., 2019	India	21%	47%	35%			47%		0%	

B- Terrestrial vertebrate – Landscape of fear preys –

C – Terrestrial vertebrate – Landscape of fear carnivores –

Da – Terrestrial vertebrate – Neonate ungulate predation –

Db – Terrestrial vertebrate – Adult ungulate predation –

E – Terrestrial vertebrate – Ungulate by kleptoparasitisme –

F – Terrestrial vertebrate – Effect of kleptoparasitism –

Ga – Terrestrial vertebrate – Carrion use –		
Reference	**Country**	**% of carrion use**
1) Inagaki et al., 2020	Japan	74%

Gb – Terrestrial vertebrate – Effect on scavenger community –	
Reference	**Country**
1) Inagaki et al., 2022	Japan
2) Inagaki et al., 2023	Japan

H – Terrestrial vertebrates – Competition with predators –

I – Aquatic vertebrate – Anadromous fish predation –

J – Aquatic vertebrate – Anadromous fish recruitment –

K – Aquatic vertebrates – Carcass flesh remains –

L – Aquatic vertebrates – Scavenger –

M – Aquatic vertebrates – Soil fertilization –

N – Aquatic vertebrates – Effect on Riparian community –

O – Plant component – Epizoochory –		
Reference	**Country**	**Families dispersed**
1) Kitamura & Terashima, 2020	Japan	Polygonaceae ; Poaceae ; Fabaceae ; Amaranthaceae

P – Plant component – Endozoochory –		
Reference	**Country**	**Families dispersed**

1) Koike et al., 2011	Japan	Moraceae ;Rosaceae ;Rhamnaceae ;Cannabaceae Cornaceae ;Lauraceae ;Actinidiaceae ;Aquifoliaceae Adoxaceae ;Lardizablaceae ; Vitaceae ; Schisandraceae ; Ebenaceae
2) Koike, Kasai, et al., 2008	Japan	Rosaceae
3) Koike, Morimoto, et al., 2008	Japan	Rosaceae; Rhamnaceae; Cornaceae Actinidiaceae; Lardizabalaceae; Vitaceae; Ebenaceae Schisandraceae
4) Naoe et al., 2016	Japan	Rosaceae
5) Naoe et al., 2019	Japan	Actinidiaceae
6) Sathyakumar & Viswanath, 2003	India	Symplocaceae
7) Takahashi et al., 2008	Japan	Moraceae ; Rosaceae ; Cornaceae ; Magnoliaceae ; Lardizabalaceae ; Schisandraceae ; Actinidiaceae
8) Tochigi et al., 2022	Japan	Vitaceae ; Schisandaraceae ; Rosaceae ; Ebenaceae ; Cornaceae ; Rhamnaceae ; Lardizablaceae ; Actinidiaceae

Q – Plant component – Secondary seed users –	
Reference	**Country**
1) Koike, Morimoto, Kozakai, et al., 2012	Japan

R – Plant component - Soil disturbance –

S – Plant component – Tree damages associated to omnivory –	
Reference	**Country**
1) Kitamura & Ohnishi, 2011	Japan
2) Kobashikawa & Koike, 2016	Japan
3) Mori et al., 2020	Japan
4) Seryodkin, Zakharenko, et al., 2017	Japan
5) Ullah et al., 2021	Pakistan
6) Watanabe, 1980	Japan
7) Yamada & Fujioka, 2010	Japan
8) Yamazaki, 2003	Japan

T – Plant component – Tree damages unassociated to omnivory –	
Reference	**Country**
1) Ogawa et al., 2020	Japan

U – Plant component – Tree damages – Tree fitness –

V – Plant component – Tree damages – Canopy Gaps –	
Reference	**Country**
1) Basnett et al., 2021	India
2) Huygens et al., 2003	Japan
3) Hwang et al., 2002	Taiwan
4) Ngoprasert et al., 2011	Thailand
5) Steinmetz et al., 2011	Thailand
6) Takahashi & Takahashi, 2013	Japan

W – Soil disturbance – Effect on plant community –

X – Tree damages – Effect on Deadwood associated community –

Y – Tree gaps – Understory associated community –	
Reference	**Country**
1) Takahashi et al., 2015	Japan

Z – Fungi component – Fungi dispersal –

Section II.S3.2: List of references related to Ursus arctos interaction map (Figure II.3).

Aa – Diet – Frequency of occurrence –											
References	**Country**	**Frequency of occurrence in the diet**									
		Herbs	**Mosses**	**Soft mast**	**Hard mast**	**Tree parts**	**Fungi**	**Invertebrates**	**Small mammals**	**Ungulates**	**Other animals**
1) Berducou et al., 1982	France	11-12%		35-39%	2-10%			7-9%	0-1%	3-10%	0%
2) Cicnjak et al., 1987	Croatia	28%		40%	33%	4%		21%	3%	1%	
3) Clevenger et al., 1992	Spain	64%		22%	39%			9%		20%	
4) Dahle et al., 1998	Norway/Sweden	36%		35%	0%		8%	62%		5.2%	
5) De Barba et al., 2014	Italy	46%		20%	3%			18%	4%	1%	
6) Elgmork & Kaasa, 1992	Norway	48%	66%	80%	93%	14%		46%	14%		
7) Frackowiak, 1997	Poland	32%		6%	27%			11%			
8) Garcia-Rodriguez et al., 2021	Poland	18%		56%	11%			13%		6%	
9) Gau et al., 2002	Canada	50%		37%					19%	67%	
10) Große et al., 2003	Slovenia							37%			
11) Gunther et al., 2014	United States of America (USA)	59%		5%	15%		2%	16%		8%	
12) Hamer & Herrero, 1987	Canada							49%			
13) Lagalisse et al., 2003	France	59%		9%	12%			37%	7%	27%	
14) Mace & Jonkel, 1986	USA	35-73%		31-46%	>0-15%			18-47%	3-11%	6-11%	
15) MacHutchon & Wellwood, 2003	Canada	74%		45%	0%			6%	4%	6%	
16) Mattson et al., 2002	USA						1%				
17) McLellan & Hovey, 1995	Canada	50%						16%	3%	11%	
18) Mealey, 1980	USA	65%		4%	6%			9%	10%	11%	
19) Naves et al., 2006	Spain	25%		47%	44%		>0%	15%		4%	
20) Nawaz et al., 2019	Pakistan	93%	2%	0%	0%			7%	19%	7%	
21) Niedzialkowska et al., 2019	Review									0-28%	
22) Ogurtsov, 2018	Russia	98%		52%	6%			6%			1%
23) Pereira et al., 2021	Croatia	58%		27%	4%		8%				

24) Persson et al., 2001	Norway	24%		57%		26%	4%	39%		54%	
25) Rathore et al., 2014	India	58%		2%	0%		2%	9%			
26) Rigg & Gorman, 2005	Poland/Slovakia	42%		21%	4%	2%		13%	1%	5%	
27) Stenset et al., 2016	Sweden	50%		71%	0%		10%	59%			
28) Sidorovich, 2006	Belarus	74%		40%				58%	5%	8%	1%
29) Sidorovich et al., 2000	Belarus	41%						70%	1%	8%	
30) Vlachos et al., 2000	Greece	17%		22%	11%			3%		0%	
31) Vulla et al., 2009	Estonia	65%		18%			0%	54%			
32) Zunino & Herrero, 1972	Italy	87%						13%			

Ab – Diet – Stable isotopes –		
References	**Country**	**Percentage of fishes in the diet**
1) Belant et al., 2006	USA	53%
2) Edwards et al., 2011	Canada	0-61%
3) Fortin et al., 2007	USA	66%
4) Hilderbrand et al., 1996	USA	60%
5) Jacoby et al., 1999	USA	0-50%
6) Adams et al., 2017	Canada	62%
7) Matsubayashi et al., 2015	Japan	0-8%
8) Milakovic & Parker, 2013	Canada	0%
9) Mowat & Heard, 2006	USA/Canada	0-82%
10) Van Daele et al., 2013	USA	0-100%

B – Terrestrial vertebrate component – Landscape of fear prey –	
References	**Country**
1) Berger et al., 2001	USA
2) Childress & Lung, 2003	USA
3) Clinchy et al., 2016	United Kingdom
4) Noell, 2013	Sweden
5) Rivrud et al., 2018	USA
6) Sivertsen, 2017	Sweden
7) White & Berger, 2001	Sweden
8) White et al., 2001	USA
9) But see Proffitt et al., 2014	USA, Alaska
10) But see Sivertsen et al., 2016	Sweden
11) But see Young & McCabe, 1997	USA

C – Terrestrial vertebrate component – Landscape of fear carnivores –

References	Country
1) Milleret et al., 2018	Sweden
2) Monson et al., 2022	USA
3) Ordiz et al., 2015	Sweden/Norway
4) Ordiz, Milleret, et al., 2020	Sweden/Norway
5) Sanz-Pérez et al., 2018	Sweden/Norway
6) But see Ordiz, Uzal, et al., 2020	Sweden/Norway

Da – Terrestrial vertebrate component – Neonate ungulate predation –		
References	**Country**	**% of mortality induced**
1) Adams et al., 1995	USA	49%
2) Arthur & Del Vecchio, 2017	USA	58%
3) Ballard et al., 1981	USA	79%
4) Ballard et al., 1990	USA	65%
5) Ballard & Miller, 1990	USA	75%
6) Ballard et al., 1991	USA	73%
7) Barber-Meyer et al., 2008	USA	29-34%
8) Bertram & Vivion, 2002	USA	21-24%
9) Boertje et al., 1987	USA	63%
10) Franzmann & Schwartz, 1986	USA	5%
11) Franzmann et al., 1980	USA	59%
12) Gasaway et al., 1992	USA	65%
13) Griffin et al., 2011	USA	5%
14) Keech et al., 2011	USA	12-28%
15) Larsen, Douglas G et al., 1989	Canada	54%
16) Osborne et al., 1991	USA	5%
17) Singer et al., 1997	USA	17-22%
18) Swenson et al., 2007	Sweden	61-78%
19) Valkenburg et al., 2004	USA	31%

Db – Terrestrial vertebrate component – Adult ungulate predation –		
References	**Country**	**% of mortality induced**
1) Arthur & Del Vecchio, 2017	USA	61%
2) Ballard et al., 1991	USA	24%
3) Boertje et al., 1987	USA	35%
4) Dahle et al., 2013	Sweden	1%
5) Keech et al., 2011	USA	0%
6) Larsen, Douglas G et al., 1989	Canada	30%

7) Reynolds et al., 2002	USA	19-39%

E – Terrestrial vertebrate component – Ungulate by kleptoparasitisme –		
Reference	**Country**	**% of stolen prey**
1) Krofel & Jerina, 2016	Croatia, Slovenia	8-74%
2) Krofel & Kos, 2010	Croatia, Slovenia	27%
3) Krofel et al., 2012	Croatia, Slovenia	32%
4) Krofel et al., 2019	Croatia, Slovenia	33%
5) Mattisson et al., 2011	Sweden	2%
6) Milleret, 2011	Sweden	44%
7) Murphy et al., 1998	USA	15-35%
8) Ordiz, Milleret, et al., 2020	Sweden, Norway	50-60%

F – Terrestrial vertebrate component – Effect of kleptoparasitism -		
References	**Country**	**% of kill rate increase**
Krofel & Kos, 2010	Croatia, Slovenia	16%
Krofel et al., 2012	Croatia, Slovenia	23%
Tallian et al., 2017	Sweden, Norway	0%

Ga – Terrestrial vertebrate component – Carrion use –

Gb – Terrestrial vertebrate component – Effect of scavenger community –	
References	Country
1) Allen et al., 2021 - Review of 12 articles	/

H – Terrestrial vertebrates component – Competition with predators –	
References	Country
1) Tallian et al., 2017	Sweden/Norway/USA
2) Tallian et al., 2022	Sweden/Norway/USA

I – Aquatic vertebrate component – Anadromous fish predation –		
References	**Country**	**% of mortality induced**
1) Andersson & Reynolds, 2017	Canada	0-63%
2) Andersson & Reynolds, 2018	Canada	2-22%
3) Carlson et al., 2007	USA	30-90%
4) Carlson et al., 2009	USA	30-49%
5) Cunningham et al., 2013	USA	12-97%
6) Gard, 1971	USA	79%

7) Gende et al., 2004a	USA	64%
8) Gende et al., 2004b	USA	47%
9) Koshino et al., 2013	Japan	29%
10) Lin et al., 2016	USA	4-80%
11) Lincoln et al., 2020	USA	1-98%
12) Peirce et al., 2013	USA	99%
13) Quinn & Buck, 2001	USA	11-73%
14) Quinn & Kinnison, 1999	USA	2-100%
15) Quinn et al., 2003	USA	12-58%
16) Quinn et al., 2014	USA	20-90%
17) Quinn et al., 2017	USA	12-77%
18) Quinn, Hendry, et al., 2001	USA	4-59%
19) Quinn, Wetzel, et al., 2001	USA	6-91%
20) Ruggerone et al., 2000	USA	16-92%
21) Winder et al., 2005	USA	2-100%

J – Aquatic vertebrate component – Anadromous fish recruitment –		
References	**Country**	**% of unspawned fish killed**
1) Gard, 1971	USA	8%
2) Gende et al., 2004b	USA	25%
3) Peirce et al., 2013	USA	58%
4) Quinn & Buck, 2001	USA	1.2%
5) Quinn, Hendry, et al., 2001	USA	4%
6) Ruggerone et al., 2000	USA	9-10%

K – Aquatic vertebrates component – Carcass flesh remains –		
References	**Country**	**% of flesh available**
1) Lincoln & Quinn, 2019	USA	0-<100%
2) Gende et al., 2001	USA	44-99%
3) Gende et al., 2004b	USA	25-44%
4) Quinn et al., 2009	USA	22-24%
5) Winder et al., 2005	USA	20%

L – Aquatic vertebrates component – Scavenger –	
References	**Country**
1) Cederholm et al., 2001	/
2) Chaloner et al., 2002	USA
3) Francis et al., 2006	USA

4) Gende & Quinn, 2004	USA
5) Gende et al., 2004b	USA
6) Hocking & Reimchen, 2006	Canada
7) Hocking & Reimchen, 2009	Canada
8) Johnston et al., 2004	USA
9) Lincoln et al., 2021	USA
10) Meehan et al., 2005	USA
11) Quinn & Buck, 2000	USA
12) Schindler et al., 2013	USA

M – Aquatic vertebrates component – Soil fertilization –	
References	**Country**
1) Francis et al., 2006	USA
2) Hilderbrand et al., 2004	/
3) Gende et al., 2002	/
4) Gende et al., 2007	USA
5) Gende et al., 2004b	USA
6) Harding et al., 2019	Canada
7) Helfield & Naiman, 2006	USA
8) Hilderbrand, Hanley, et al., 1999	USA
9) Holtgrieve et al., 2009	USA
10) Naiman et al., 2002	/
11) Quinn et al., 2009	USA

N – Aquatic vertebrates component – Effect on Riparian community –	
References	**Country**
1) Christie & Reimchen, 2008	Canada
2) Harding et al., 2019	Canada
3) Hocking & Reimchen, 2009	Canada
4) Hocking et al., 2009	Canada
5) Helfield & Naiman, 2002	USA
6) Kieran et al., 2021	Canada
7) Koshino et al., 2013	Japan
8) Levi et al., 2020	/
9) Lisi & Schindler, 2011	USA
10) Nagasaka et al., 2006	Japan
11) Quinn et al., 2018	USA

O – Plant component – Epizoochory –

P – Plant component – Endozoochory –		
References	**Country**	**Families dispersed**
1) Applegate et al., 1979	USA	Apiaceae
2) Garcia-Rodriguez & Selva, 2021	Poland	Ericaceae
3) García-Rodríguez et al., 2021	Poland	Rosaceae ; Rhamaceae ; Adoxaceae ; Caprifoliaceae ;
4) Harrer & Levi, 2018	USA	Araliaceae
5) Karimi et al., 2018	Iran	Brassicaceae; Berberidaceae; Rosaceae; Chenopodiaceae; Asteraceae; Convolvulaceae ; Cyperaceae; Rubiaceae; Malvaceae; Fabaceae; Poaceae; Polygonaceae; Portulaceae; Rhamnaceae; Crassulaceae; Caryophilaceae; Valerianaceae ; Scrophulariaceae
6) Karimi et al., 2020	Iran	Poaceae; Brassicaceae; Berberidaceae ; Rosaceae; Chenopodiaceae; Asteraceae; Convolvulaceae; Cornaceae; Cyperaceae; Rubiaceae; Caprifoliaceae; Malvaceae; Fabaceae; Polygonaceae; Portulaceae; Rhamnaceae; Crassulaceae; Valerianaceae; Scrophulariaceae
7) Lalleroni et al., 2017	France	Amaryllidaceae; Aquifoliaceae ; Betulaceae ; Ericaceae ; Fagaceae; Fabaceae; Juncaceae ; Lamiaceae; Onagraceae ; Oxalidaceae ; Plantaginaceae; Poaceae ; Polygonaceae; Potamogetonaceae; Ranunculaceae; Rosaceae
8) Nowak & Crone, 2012	USA	Elaeagnaceae; Rosaceae; Ericaceae
9) Patten, 1993	USA	Ericaceae; Rosaceae
10) Shakeri et al., 2018	USA	Araliaceae; Ericaceae; Elaegnaceae; Caprifoliaceae; Cornaceae; Liliaceae; Rosaceae; Grossullariaceae
11) Steyaert et al., 2019	Sweden	Ericaceae
12) Tavşanoğlu et al., 2021	Turkey	Amaryllidaceae; Aquifoliaceae; Betulaceae; Caprifoliaceae; Cornaceae; Ericaceae; Fagaceae; Juglandaceae; Pinaceae; Poaceae; Rosaceae
13) Traveset & Willson, 1997	Canada	Rosaceae; Caprifoliaceae; Saxifragaceae; Liliaceae; Araliaceae; Ericaceae
14) Traveset et al., 2001	USA	Ericaceae; Rosaceae
15) Willson & Gende, 2004	USA	Ericaceae; Araliaceae; Rosaceae; Grossulariaceae;Liliaceae

Q – Plant component – Secondary seed users –	
References	**Country**
1) Bermejo et al., 1998	USA

2) Shakeri et al., 2018	USA

R – Plant component - Soil disturbance –	
References	**Country**
1) Aichun et al., 2006	China
2) Barker et al., 2015	Canada
3) Butler, 1992	USA
4) Carl, 1971	USA
5) Doak & Loso, 2003	USA
6) Elgmork & Unander, 1998	Norway
7) Hall & Lamont, 2003	Canada
8) Hamer & Herrero, 1987	Canada
9) Linnell et al., 2000	Europe
10) Mattson & Reinhart, 1997	USA
11) Mattson, 2004	USA
12) Mealey, 1980	USA
13) Swenson et al., 1999	Sweden
14) Tardiff & Stanford, 1998	USA
15) Tomita & Hiura, 2020	Japan
16) Tomita & Hiura, 2021	Japan
17) Tomita & Hiura, 2022	Japan
18) Tomita & Hiura, 2023	Japan
19) Tomita, 2021	Japan

S – Plant component – Tree damages associated –	
References	**Country**
1) Krapinec, Majnaric, et al., 2011	Croatia
2) Krapinec, Majnarič, et al., 2011	Croatia
3) Kunovac et al., 2008	Bosnia-Herzegovina
4) Seryodkin, Zakharenko, et al., 2017	Russia
5) Zysk-Gorczynska & Jakubiec, 2014	Poland
6) Zysk-Gorczynska & Jakubiec, 2018	Poland

T – Plant component – Tree damages unassociated –	
References	**Country**
1) Bowersock et al., 2022	USA
2) Clapham et al., 2012	Canada

3) Clapham et al., 2013	Canada
4) Green & Mattson, 2003	USA
5) Sato et al., 2014	Japan

U – Plant component – Tree damages – Tree fitness –	
References	**Country**
1) Seryodkin, Zakharenko, et al., 2017	Russia

V – Plant component - Tree damages – Canopy gaps –

W – Soil disturbance – Effect on plant community –	
References	**Country**
1) Doak & Loso, 2003	USA
2) Tardiff & Stanford, 1998	USA
3) Tomita & Hiura, 2022	Japan
4) Tomita & Hiura, 2023	Japan

X – Tree damages – Deadwood associated community –	
References	**Country**
1) Zysk-Gorczynska & Jakubiec, 2014	Poland

Y – Tree gaps – Understory associated community –

Z – Fungi component – Fungi dispersal –

Section II.S3.3: List of references related to Ursus americanus interaction map (Figure II.8).

Aa – Diet – Frequency of occurrence –											
References	**Country**	**Data**									
		Herbs	**Mosses**	**Soft mast**	**Hard mast**	**Tree parts**	**Fungi**	**Invertebrates**	**Small mammals**	**Ungulate**	**Other animal**
1) Beeman & Pelton, 1980	United states of America (USA)	6%		18%	9%			29%			
2) Benson & Chamberlain, 2006	USA	12%		45%	36%			52%	3%	7%	
3) Bull et al., 2001	USA	39%		34-36%	0%	65-82%	Traces	67-73%	24%		
4) Dobey et al., 2005	USA	3-7%	Traces	33-42%	Traces-14%			1-4%	Traces	Traces	
5) Garland et al., 2016	USA	25%		86%	80%			25%		3%	
6) Graber & White, 1983	USA	71%		18%	9%			33%	7%	3%	
7) Greenleaf et al., 2009	USA	44%		57%	14%			28%			
8) Juárez-Casillas & Varas, 2013	Mexico							16%			
9) Lundgren et al., 2022	USA	86%		14%	0%	5%		90%	5%		
10) McLaren et al., 2021	USA	97%	23%					16%		3%	2%
11) Montague, 2014	USA	24,2%		51%	46%			42%	10%	39%	
12) Noyce et al., 1997	USA							50-84%			
13) Popp et al., 2018	Canada							0%	2%	11%	
14) Romain et al., 2013	USA	93-95%		46-63%	3-14%			82-97%	3-11%	0-3%	0-7%
15) Roof, 1997	USA										
16) Murphy et al., 2017	USA	34,6%		53%	36%			52%			2%
17) Stubblefield, 1993	USA	39%		14%	12%	4%		9%		8%	
18) Ulrey, 2008	USA	28%		61%	43%			53%	2%	2%	2%

Ab – Diet – Stable isotopes –		
References	**Country**	**Percentage of fishes in the diet**
1) Adams et al., 2017	Canada	6%
2) Belant et al., 2006	USA	0-25%
3) Fortin et al., 2007	USA	8%
4) Jacoby et al., 1999	USA	0-53%

5) Schwartz et al., 2014	USA	0%
6) Service et al., 2019	Canada	1-93%

B – Terrestrial vertebrate component – Landscape of fear preys –	
References	**Country**
1) Bastille-Rousseau et al., 2016	Canada
2) Berger et al., 2001	USA
3) Latham et al., 2011	Canada
4) Morris, 2005	Canada
5) Patterson et al., 2016	Canada
6) Seamans et al., 2016	USA
7) But see Chamaillé-Jammes et al., 2014	Canada

C – Terrestrial vertebrate component – Landscape of fear carnivores –	
References	**Country**
1) Allen, Elbroch, et al., 2021	USA
2) Allen, Elbroch, Wilmers, et al., 2014	USA
3) Engebretsen et al., 2021	USA
4) But see Ballard et al., 2003	Book
5) But see Tattersall et al., 2020	Canada

Da – Terrestrial vertebrate component – Neonate ungulate predation –		
References	**Country**	**% of mortality induced on total mortality**
1) Ballard et al., 1990	USA	11%
2) Ballard et al., 1991	USA	3%
3) Ballard et al., 1999	USA	23%
4) Ballard, 1992	USA	4-100%
5) Barber-Meyer et al., 2008	USA	16-21%
6) Bastille-Rousseau et al., 2016	USA	34-46%
7) Bertram & Vivion, 2002	USA	24-28%
8) Boertje et al., 1987	USA	4%
9) Carstensen et al., 2009	USA	29-36%
10) DeVivo et al., 2011, p. 201	USA	0%
11) Eacker et al., 2016	USA	15%
12) Franzmann & Schwartz, 1986	USA	61-75%
13) Franzmann et al., 1980	USA	59-60%
14) Gasaway et al., 1992	USA/Canada	3%

15) Griffin et al., 2011	USA	29%
16) Kautz et al., 2019	USA	20%
17) Keech et al., 2011	USA	14-34%
18) Kunkel & Mech, 1994	USA	49%
19) Lambert et al., 2006	Canada	57%
20) Larsen et al., 1989	Canada	5%
21) Lewis et al., 2017	Canada	5-29%
22) Mahoney et al., 2016	Canada	46-59%
23) Mathews & Porter, 1988	USA	23%
24) Obermoller et al., 2019	USA	20%
25) Osborne et al., 1991	USA	50-54%
26) Patterson et al., 2013	Canada	22%
27) Peterson et al., 2018	USA	17-22%
28) Schwartz & Franzmann, 1989	USA	70%
29) Shuman et al., 2017	USA	33%
30) Singer et al., 1997	USA	2-6%
31) Smith & Anderson, 1996	USA	20-67%
32) Smith, 1983	USA	13%
33) Tatman et al., 2018	USA	30-47%
34) Wolf et al., 2021	USA	32%
35) Zager & Beecham, 2006	USA	4-100%

Db – Terrestrial vertebrate component – Adult ungulate predation –		
References	**Country**	**% of mortality induced on total mortality**
1) Boertje et al., 1987	USA	0%
2) Gasaway et al., 1992	USA	0%
3) Keech et al., 2011	USA	0-3%
4) Larsen et al., 1989	Canada	0%
5) Smith, 1983	USA	0%
6) Ballard, 1994	/	0-5%

E – Terrestrial vertebrate component – Ungulate by kleptoparasitisme –		
References	**Country**	**% of stolen prey**
1) Allen, Elbroch, et al., 2021	USA	72%
2) Clark et al., 2014	USA	25%
3) Elbroch et al., 2015	USA	48-77%

4) Engebretsen et al., 2021	USA	44%
5) Murphy et al., 1998	USA	0-14%

F - Terrestrial component component – Effect of kleptoparasitism –		
References	Country	% of predator kill rate increase
1) Allen, Elbroch, et al., 2021	USA	24%
2) Clark et al., 2014	USA	31%
3) Elbroch et al., 2015	USA	48%

Ga – Terrestrial vertebrate – Carrion use –

Gb – Terrestrial vertebrate component – Effect of scavenger community –	
1) Allen et al., 2015	USA
2) Allen, Elbroch, Casady, et al., 2014	USA
3) Allen, Elbroch, Wilmers, et al., 2014	USA
4) Allen, Wittmer, et al., 2021	/

H – Terrestrial vertebrates component – Competition with predators –

I – Aquatic vertebrate component – Anadromous fish predation –		
References	**Country**	**% of mortality induced on total mortality**
Andersson & Reynolds, 2017	Canada	0-63%
Harding et al., 2019	Canada	0-23%
Hocking & Reimchen, 2006	Canada	4-48%
Quinn et al., 2001	USA	4-59%
Reimchen, 1994	Canada	81%
Reimchen, 2000	Canada	58-92%

J – Aquatic vertebrate component – Anadromous fish recruitment –		
References	**Country**	**% of unspawned fish killed**
Reimchen, 1994	Canada	29%
Reimchen, 2000	Canada	20-30%

K – Aquatic vertebrates component – Carcass flesh remains –

References	Country	% of flesh available per carcase
Frame, 1974	USA	0-100%
Hocking & Reimchen, 2006	Canada	<5%-100%
Reimchen, 1994	Canada	6-100%
Reimchen, 2017	Canada	2-98%

L – Aquatic vertebrates component – Scavenger –	
References	**Country**
5) Collins & Baxter, 2014	USA
6) Frame, 1974	USA
7) Hocking & Reimchen, 2006	Canada
8) Hocking et al., 2009	Canada
9) Reimchen, 1994	Canada
10) Reimchen, 2017	Canada

M – Aquatic vertebrates component – Soil fertilization –	
References	**Country**
1) Francis et al., 2006	USA
2) Gende et al., 2004b	USA

N – Aquatic vertebrates component – Effect on Riparian community–	
References	**Country**
1) Chaloner et al., 2002	USA
2) Christie & Reimchen, 2008	Canada
3) Gende et al., 2002	/
4) Hocking & Reimchen, 2009	Canada
5) Levi et al., 2020	/
6) Reimchen & Fox, 2013	Canada
7) Reimchen et al., 2003	Canada
8) Reimchen, 2000	Canada
9) Reimchen, 2017	Canada

O – Plant component – Epizoochory –		
References	**Country**	**Families dispersed**
1) Kulbaba, 2004	/	Renunculaceae , Asteraceae , Rosaceae, Fabaceae , Boraginaceae, Apiaceae,

P – Plant component – Endozoochory –		
References	**Country**	**Families dispersed**
1) Auger et al., 2002	USA	Rosaceae ; Berberidaceae ; Anacardiaceae
2) Borchert & Tyler, 2010	USA	Rosaceae
3) Enders & Vander Wall, 2012	USA	Rosaceae ; Cornaceae ; Rhamnaceae
4) Harrer & Levi, 2018	USA	Araliaceae
5) Maehr, 1984	USA	Arecaceae ; Lauraceae ; Anacardiaceae ;
6) Nowak & Crone, 2012	USA	Elaeagnaceae ; Rosaceae ; Ericaceae
7) Rogers & Applegate, 1983	USA	Rosaceae ; Araliaceae ; Ericaceae ; Cornaceae
8) Traveset & Willson, 1997	USA	Rosaceae ; Adoxaceae ; Grossulariacées ; Liliacées ; Araliaceae ; Ericaceae

Q – Plant component – Secondary seed users –	
References	**Country**
1) Enders & Vander Wall, 2012	USA

R – Plant component – Soil disturbance –	
References	**Country**
1) Baldwin & Bender, 2008	USA
2) Beecham et al., 1983	USA
3) Cipollini & Cipollini, 2011	USA
4) Grinath et al., 2015	USA
5) Hayes & Pelton, 1994	USA
6) Johnson & Pelton, 1981	USA
7) Kendall, 1983	USA
8) Lindzey & Meslow, 1976	USA
9) Lundgren et al., 2022	USA
10) Mattson & Reinhart, 1997	USA
11) Schafer et al., 2018	USA
12) Tietje & Ruff, 1980	Canada
13) Weaver & Pelton, 1994	USA

S – Plant component – Tree damages associated to omnivory –	
References	**Country**
1) Collins et al., 2002	USA
2) Dagley et al., 2018	USA
3) Kanaskie et al., 2001	USA
4) Kimball et al., 1998	USA
5) Kimball, Nolte, et al., 1998	USA

6) Kimball, Turnblom, et al., 1998	USA
7) Kline et al., 2018	USA
8) Lowell et al., 2010	USA
9) Mendia et al., 2019	USA
10) Miller et al., 2007	USA
11) Noble & Meslow, 1998	USA
12) Russell et al., 2001	USA
13) Shane Tedder, 2012	USA
14) Stewart et al., 1999	USA
15) Stewart et al., 2002	USA
16) Taylor et al., 2019	USA
17) Ziegltrum, 2004	USA

T – Plant component – Tree damages unassociated to omnivory –	
References	**Country**
1) Bowersock et al., 2022	USA
2) Burst & Pelton, 1983	USA
3) Taylor et al., 2015	USA

U – Plant component – Tree damages – Tree fitness –	
References	**Country**
1) Collins et al., 2002	USA
2) Dagley et al., 2018	USA
3) Kanaskie et al., 2001	USA
4) Mendia et al., 2019	USA
5) Miller et al., 2007	USA
6) Taylor et al., 2019	USA
7) Ziegltrum & Nolte, 2001	USA

V – Plant component – Tree damages – Canopy gaps –

W – Soil disturbance – Effect on plant community –	
References	**Country**
1) Grinath et al., 2015	USA
2) Grinath, 2018	USA

X – Tree damages – Deadwood associated community –	
References	**Country**

1) Mendia et al., 2019	USA
2) Shane Tedder, 2012	USA
3) Ziegltrum & Nolte, 2001	USA

Y – Tree gaps – Understory associated community –

Z – Fungi component – Fungi dispersal –	
References	**Country**
1) Cázares & Trappe, 1994	USA

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Appendix III.S1

III.S1.1 DNA extraction, amplification and sequencing

DNA extraction and metabarcoding analyses were all performed by us at the Molecular Biology and Microbiology Technical facility of the Molecular Biology and Bioinformatics Department of the Centre de Recherche sur la Biodiversité et l'Environnement (CRBE) research laboratory. Molecular analyses were performed in 148 bear faecal samples, 80 samples analysed in 2022 and 68 additional samples in 2023 using plant and fungi markers, whereas for vertebrates and arthropods markers all samples were analysed in 2023. DNA extraction was performed using NucleoSpin Soil kit (Macherey Nagel) adapted protocol as described by Taberlet et al., (2012b), starting from a large amount of material, 15 g of feces were suspended in 30 mL of phosphate buffer. Extraction negative controls were performed to monitor contamination during DNA extractions.

We used the Sper02, Fung02, Vert01 and Arth01 markers to amplify plants, fungi, vertebrates and arthropods (**Table S.III.1**). The 20 µL PCR consisted of 2X Master Mix AmpliTaq Gold (Fisher), 0,008X Bovine Serum Albumine, 0.25 µM forward primer and 0.25 µM reverse primer and 2 µL DNA extract. For Vert01 and Arth01, we had to add respectively 2.5 µM of human blocker and 2.5 µM of mammals blocker (**Table S.III.1**). The PCR profile had an initial denaturation step of 10 min at 95 °C, followed by a few cycles of 30 seconds at 95 °C, 30 seconds at the annealing temperature, 1 min at 72°C and a final 7 min elongation at 72°C. The annealing temperature and number of cycles were different between primers (**Table S.III.1**). Three PCR replicates were performed for all samples. Four negative controls of extraction and PCR were included every 92 samples to monitor contamination during PCR preparation. We also included four positive controls of DNA samples. Libraries were performed with TruSeq DNA Nano kit (Illumina) following the manufacturer's instructions. The sequencing was performed on a NovaSeq 6000 of Illumina in 2 x 250 bp.

Table III.S1.2: DNA extraction and amplification procedure.

	Sper01	**Fung02**	**Vert01**	**Arth01**
Prey taxon	Plants	Fungi	Vertebrates	Arthropods
DNA region	trnL	ITS1 nuclear	12S mtDNA	16S mtDNA
Forward primer	GGGCAATCCTGAGCCAA	GGAAGTAAAAGTCGTAACAAGG	TTAGATACCCCACTATGC	CCAACATCGAGGTCRYAA
Reverse primer	CCATTGAGTCTCTGCACCTATC	CAAGAGATCCCGTTGYTGAAAGTK	TAGAACAGGCTCCTCTAG	ARTTACYNTAGGGATAACAG
Block primer	n.a.	n.a.	Human blocker: CTATGCTTAGCCCTAAACCTCAACAGTTAAATCAACAAACTGCT-C3	Mammals blocker: CCTAGGGATAACAGCGCAATCCTATT-C3
PCR **Initial denaturation** **Nb cycles** **Denaturation** **Annealing** **Elongation** **Final elongation**	 95°C – 10 min 40 cycles: 95°C – 30 sec 52°C – 30 sec 72°C – 1 min 72°C – 7 min	 95°C – 10 min 45 cycles: 95°C – 30 sec 55°C – 30 sec 72°C – 1 min 72°C – 7 min	 95°C – 10 min 55 cycles: 95°C – 30 sec 55°C – 30 sec 72°C – 1 min 72°C – 7 min	 95°C – 10 min 55 cycles: 95°C – 30 sec 55°C – 30 sec 72°C – 1 min 72°C – 7 min

III.S1.2 Bioinformatics

Sequence analysis was performed using the *OBITools v1.2.11* (Boyer et al., 2016) and the *sumaclust* (Mercier et al., 2013) softwares, through a modified version of the *Snakemake v7.20.0* (Mölder et al., 2021) pipeline of Benoiston (2022) (a taxonomic annotation rule was added). Forward and reverse reads were aligned with the *illuminapairedend* command. Alignments with a score below 40 were filtered out. Sequences were then assigned to samples using the *ngsfilter* command, allowing 0 and 2 errors on the tags and primers respectively. Identical sequences were merged with the *obiuniq* command. Next, low quality sequences were filtered out, i.e. sequences with less than 1 read in the whole dataset, sequences containing ambiguous bases or that are shorter than expected (< 15 bp for the arthropod marker, < 60 bp for the fungal marker, < 10 bp for the plant marker, and < 50 bp for the vertebrate marker). The remaining sequences were clustered into Molecular Operational Taxonomic Units (MOTUs) with *sumaclust* using a similarity threshold of 97%. The most abundant

sequence of each MOTU was considered as its representative sequence and its abundance corresponded to the sum of the abundance of its members. Taxonomic annotation was performed with the *ecotag* program of the *OBITools*, using a subset of the *Genbank* database (release 259) extracted with the *ecoPCR* program (Bellemain et al., 2010; Ficetola et al., 2010). Maximum number of mismatches allowed per primer was three; the minimum-maximum length of the *in silico* amplified DNA fragment, excluding primers was 10-230 bp for plants, 55-930 bp for fungi, 40-145 bp for vertebrates and 15-110 bp for arthropods. The *'metabaR'* package (Zinger et al., 2021) of R (v.4.4.2) was used to minimize PCR/sequencing errors, contaminant sequences, tag-jumps and dysfunctional PCRs. MOTUs with maximum abundance in negative controls were considered as contaminants, and those with a similarity below 90% to the reference sequence were considered degraded sequences or chimeras and discarded. MOTUs not belonging to the targeted clade were excluded. Noise from tag-jumps was reduced by removing a MOTU in a given PCR product if its relative abundance was less than 0.03% of the total MOTU abundance in the entire dataset. PCR replicates with sequencing depth below specific thresholds (< 1,000 for the Vert01 and Sper01 datasets, < 500 for the Arth01 and Fung02 datasets), and those with poor reproducibility were removed. The final MOTU table was produced by summing the reads from PCR replicates originating from the same sample. Based on high Good's coverage (>0.96) for plant and fungi markers in both runs, we were able to combine results from the two metabarcoding runs.

To refine the annotation obtained with *ecotag*, we performed a Blast search using online NCBI resources on all the MOTUs with at least 250 reads not annotated at least at gender level. We chose the annotation (gender or family level) when there was a taxa with the best E value, percent of identity, and query cover, but also based on their occurrence using local databases. We used FLORAPYR (https://atlasflorapyrenaea.eu) for plants, and INPN (inpn.mnhn.fr) and the Pyrenees National Park Atlas (biodiversite.pyrenees-parcnational.fr) for insects and vertebrates. For fungi, we did not use any database due to the absence of a detailed local database.

Based on the fungi identified at genera and family rank, we functionally annotated the growth form and ecology of each taxa using the *FungalTraits* database (Põlme et al., 2020). Fungi that were reported on dung, or as dung-saprophyte, at least for part of their life cycle were removed. Yeast forming fungi, fungi only present in soils as mycelial form, and aquatic chytridiomycota were removed. For the remaining fungi, each genus was checked manually to ensure only fungi producing a reproductive structure that may be edible were kept in our diet analyses (we removed 59% of MOTUs, 60% of reads, **Table S.III.2**). For the vertebrate marker, we removed Ursidae and Hominidae annotations (representing 79% of MOTUs and 96% of reads, **Table S.III.2**) as they clearly represented host DNA contamination or human DNA contamination during the samples manipulation.

Table III.S1.2: Number of reads and MOTUs per marker and occurrence per samples at the end of the bioinformatic procedure.

			DNA metabarcoding markers			
			Arth01	Fung02	Sper01	Vert01
Both runs	Post-datasets merging	# reads	223, 405	9, 783, 766	16, 257, 389	17, 122, 996
		# motus	688	1, 064	12, 089	733
		# samples[1]	29	68	115	100
	Post-taxo filtering	# reads	223, 405	3,941,144	16, 257, 389	644, 770
		# motus	688	437	12, 089	155
		# samples	29	53	115	96

[1]Number of samples with at least one read.

III.S1.3 List of references

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Appendix VI.S1

VI.S1.1 DNA extraction, amplification and sequencing

DNA extraction and metabarcoding analyses were all performed by us at the Molecular Biology and Microbiology Technical facility of the Molecular Biology and Bioinformatics Department of the Centre de Recherche sur la Biodiversité et l'Environnement (CRBE) research laboratory in Toulouse (France). Molecular analyses were performed in 148 bear faecal samples, 80 samples analysed in 2022 and 68 additional samples in 2023 using plant and fungi markers, whereas for vertebrates and arthropods markers all samples were analysed in 2023. DNA extraction was performed using NucleoSpin Soil kit (Macherey Nagel) adapted protocol as described by Taberlet et al. (2012b). Starting from a large amount of material, 15 g of faeces were suspended in 30 mL of phosphate buffer. Extraction negative controls were performed to monitor contamination during DNA extractions.

We used the Sper02 and Fung02 markers to amplify plants and fungi, respectively (**Table VI.S1.1**). The 20 µL PCR consisted of 2X Master Mix AmpliTaq Gold (Fisher), 0,008X Bovine Serum Albumine, 0.25 µM forward primer and 0.25 µM reverse primer and 2 µL DNA extract. The PCR profile had an initial denaturation step of 10 min at 95°C, followed by a few cycles of 30 seconds at 95 °C, 30 seconds at the annealing temperature, 1 min at 72°C and a final 7 min elongation at 72°C. The annealing temperature and number of cycles were different between primers (**Table VI.S1.1**). Three PCR replicates were performed for all samples. Four negative controls of extraction and PCR were included every 92 samples to monitor contamination during PCR preparation. We also included four positive controls of DNA samples. Libraries were performed with TruSeq DNA Nano kit (Illumina) following the manufacturer's instructions. The sequencing was performed on a NovaSeq 6000 of Illumina in 2 x 250 bp.

VI.S1.2 Bioinformatics

Sequence analysis was performed using the *OBITools v1.2.1.1* 1 (Boyer et al., 2016) and the *sumaclus*t (Mercier et al., 2013) softwares, through a modified version of the *Snakemake v7.20.*0 (Mölder et al., 2021) pipeline of Benoiston (2022) (a taxonomic annotation rule was added). Forward and reverse reads were aligned with the *illuminapairedend* command. Alignments with a score below 40 were filtered out. Sequences were then assigned to samples using the *ngsfilter* command, allowing 0 and 2 errors on the tags and primers respectively. Identical sequences were merged with the *obiuniq* command. Next, low quality sequences were filtered out: i.e. sequences with less than 1 read in the whole dataset, sequences containing ambiguous bases or that were shorter than expected (< 10 bp for the plant marker and < 60 bp for the fungal marker) were excluded. The remaining sequences were clustered into Molecular Operational Taxonomic Units (MOTUs) with *sumaclust* using a similarity threshold of 97%. The most abundant sequence of each MOTU was considered as its representative sequence and its abundance corresponded to the sum of the abundance of its members. Taxonomic annotation was performed with the *ecotag* program of the *OBITools*, using a subset of the *Genbank* database (release 259) extracted with the *ecoPCR* program (Bellemain et al., 2010; Ficetola et al., 2010). The maximum number of mismatches allowed per primer was three; the minimum-maximum length of the *in silico* amplified DNA fragment, excluding primers was 10-230 bp for plants and 55-930 bp for fungi. The *'metabaR'* package (Zinger et al., 2021) of R (v.4.4.2) was used to minimize PCR/sequencing errors, contaminant sequences, tag-jumps and dysfunctional PCRs. MOTUs with maximum abundance in negative controls were considered as contaminants, and those with a similarity below 90% to the reference sequence were considered degraded sequences or chimeras and discarded. MOTUs not belonging to the targeted clade were excluded. Noise from tag-jumps was reduced by removing a MOTU in a given PCR product if its relative abundance was less than 0.03% of the total MOTU abundance in the entire dataset. PCR replicates with sequencing depth below specific thresholds (< 1,000 for Sper01 datasets and < 500 for the Fung02 datasets), and those with

poor reproducibility were removed. The final MOTU table was produced by summing the reads from PCR replicates originating from the same sample. Based on high Good's coverage (>0.96) for plant and fungal markers in both runs, we were able to combine results from the two metabarcoding runs.

To refine the annotation obtained with *ecotag*, we performed a Blast search using online NCBI resources on all the MOTUs with at least 250 reads not annotated at least at gender level. We chose the annotation (gender or family level) when there was a taxa with the best E value, percent of identity, and query cover, but also based on their occurrence using local databases for plants (https://atlasflorapyrenaea.eu).

Based on the fungi identified at genera and family rank, we functionally annotated the growth form and ecology of each taxa using the *FungalTraits* database (Põlme et al., 2020).

Table VI.S1.1: Characteristics and protocol used for plant (Sper01) and fungal (Fung02) markers.

	Sper01	**Fung02**
Prey taxon	Plants	Fungi
DNA region	trnL	ITS1 nuclear
Forward primer	GGGCAATCCTGAGCCAA	GGAAGTAAAAGTCGTAACAAGG
Reverse primer	CCATTGAGTCTCTGCACCTATC	CAAGAGATCCCGTTGYTGAAAGTK
Block primer	n.a.	n.a.
PCR *Initial denaturation* *Nb cycles* *Denaturation* *Annealing* *Elongation* *Final elongation*	 95°C – 10 min 40 cycles: 95°C – 30 sec 52°C – 30 sec 72°C – 1 min 72°C – 7 min	 95°C – 10 min 45 cycles: 95°C – 30 sec 55°C – 30 sec 72°C – 1 min 72°C – 7 min

VI.S1.3 List of references

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Appendix VII.S1

Table VII.I.S1: Statistical results from GLMM performed on dry faecal mass removal and seed removal (small and medium) according to treatments, and on seed removal (both) according to the diet.

GLMM Gamma Formula: Mass final ~ Treatment + Mass initial + (1|Sample)				
	Estimate	Standard Error	t value	*p value*
Intercept (Total access)	1.653395	0.126037	13.118	*<2e-16*
Invertebrate access	0.059668	0.037532	1.590	*0.112*
No access	0.150064	0.037563	3.995	*6.47e-05*
Mass final	0.042785	0.004939	8.662	*< 2e-16*
GLMM Gamma Formula: *Rubus* seeds ~ Treatment + (1|Sample)				
	Estimate	Standard Error	t value	*p value*
Intercept (Total access)	1.84221	0.06518	28.262	*<2e-16*
Invertebrate access	-0.02822	0.07425	0.380	*0.70392*
No access	0.22996	0.07465	3.081	*0.00207*
GLM Poisson Formula: *Vaccinium* seeds ~ Treatment + (1|Sample)				
	Estimate	Standard Error	z value	*p value*
Intercept (Total access)	1.1971	0.1021	11.729	*<2e-16*
Invertebrate access	-0.2076	0.1524	-1.362	*0.1732*
No access	0.2798	0.1352	2.069	*0.0385*
GLM Gamma Formula: *Rubus* seeds ~ Diet				
	Estimate	Standard Error	t value	*p value*
Intercept (Hard mast)	2.71635	0.08218	33.053	*<2e-16*
Soft mast	-0.17362	0.12030	-1.443	*0.1619*
Vegetative parts	-0.23144	0.10610	-2.181	*0.0392*
GLM Gamma Formula: *Vaccinium* seeds ~ Diet				
	Estimate	Standard Error	t value	*p value*

Intercept (Hard mast)	1.94591	0.12557	15.497	*5.33e-14*
Soft mast	-0.06318	0.18381	-0.344	*0.734*
Vegetative parts	-0.04879	0.16211	-0.301	*0.766*
GLM Poisson Formula: Pair differences of *Rubus* seeds ~ Diet				
	Estimate	Standard Error	z value	*p value*
Intercept (Hard mast)	-0.03637	0.19245	-0.189	*0.85*
Soft mast	1.51363	0.21888	6.915	*4.66e-12*
Vegetative parts	1.27606	0.20353	6.270	*3.62e-10*
GLM Poisson Formula: Pair differences of *Vaccinium* seeds ~ Diet				
	Estimate	Standard Error	z value	*p value*
Intercept (Hard mast)	0.7621	0.1291	5.904	*3.56e-09*
Soft mast	-0.2231	0.2108	-1.058	*0.289844*
Vegetative parts	0.4776	0.1451	3.291	*0.000997*

Grégoire **PAULY**

Une étude intégrative du régime de l'Ours Brun (Ursus arctos) dans les Pyrénées et son rôle dans la dispersion des plantes et des champignons.

Résumé: La grande faune est reconnue pour son impact dans les écosystèmes par le biais de leurs interactions trophiques ou non trophiques. Un contexte dans lequel les omnivores sont encore mal connus. Cependant, en consommant un peu de tout, les omnivores peuvent interagir avec divers compartiments de l'écosystème. L'un des omnivores les plus connus et les plus répandus dans le monde est l'ours brun (Ursus arctos). C'est un animal étudié historiquement dont l'examen de la littérature met en lumière son rôle dans la régulation de ses proies (invertébrés, vertébrés), l'altération du comportement des co-prédateurs ou en tant qu'ingénieur de l'écosystème. Cette ingénierie se caractérise par une perturbation du sol, la formation de bois morts ou le transport de matériel biologique tel que des diaspores (spores ou graines), des processus clés dans le fonctionnement de l'écosystème. Dans ce doctorat, on s'est intéressé au dernier processus à savoir la dispersion de diaspores par ingestion (i.e. endozoochorie) par l'ours brun à partir de l'étude de la population des Pyrénées (sud-ouest de l'Europe). Dans un premier temps, on a étudié son régime alimentaire selon le sexe, l'âge et les besoins biologiques de l'ours. Son régime étant inconnu depuis la fin des années 90, cela permet une mise à jour des connaissances cruciale pour cette population en danger critique d'extinction. Dans un second temps, on s'est intéressé à son rôle dans la dispersion des plantes à partir de plusieurs méthodes. Une fois dispersées, on a voulu examiner l'importance des visiteurs de fèces d'ours dans le destin des diaspores. On s'est aussi intéressé à la dispersion de champignons symbiotiques aux plantes (occasionnellement ou accidentellement consommés). Mes recherches ont permis de caractériser un régime de l'ours constitué principalement de plantes (herbes, fruits secs ou charnus) et complété par des arthropodes (fourmis, guêpes), des vertébrés (surtout des ongulés sauvages) et des champignons (truffe notamment). On a décrit ici la plus grande diversité de champignons consommés par un ursidé. Également mes résultats montrent que les femelles sont plus herbivores que les mâles et que le régime évolue selon les besoins biologiques et physiologiques de l'ours. Ici, on à décrit la dispersion de plantes à fruits secs ou charnus et aussi de fougères et de mousses. On souligne aussi l'importance de considérer le processus endozoochore jusqu'à la matricé fécale, pouvant limiter la germination. Dans ce contexte, on à pu démontrer que les bousiers jouent un rôle unique dans la désagrégation des fèces et la dispersion secondaire des diaspores. Concernant la dispersion des champignons symbiotiques aux plantes, on a pu inférer la dispersion potentielle de mycorhizes, d'endophytes et de pathogènes de plantes, contribuant à un domaine très peu étudié. Dans l'ensemble, ma thèse de doctorat a permis d'identifier un régime alimentaire diversifié comme jamais décrit auparavant grâce à l'utilisation du métabarcoding et à l'utilisation de fèces de différents sexes et âges. Elle révèle la dispersion d'une gamme de plantes plus large par les Ursidés qu'on ne le pensait auparavant, et potentiellement un cortège pertinent de champignons symbiotiques, tous pouvant influer la structure et la dynamique des communautés végétales et par suite le fonctionnement et la résilience des écosystèmes pyrénéens face aux changements globaux. Plus largement, les résultats invitent à mener des recherches futures pour étudier cette dispersion chez d'autres animaux, mais aussi pour prendre en compte le mécanisme d'endozoochorie jusqu'à la la matrice fécale. Il reste encore beaucoup à faire, notamment sur la dispersion effective des champignons ou le devenir concret des graines après le passage des bousiers, mais cette thèse de doctorat apporte de nouvelles preuves précieuses pour la recherche historique sur l'écologie de l'ours brun et construit les bases de recherches futures.

Mots clés : Co-dispersion, Endozoochorie, Dispersion secondaire, Ingénieur de l'écosystème, Omnivorie, Ursidae

A comprehensive investigation into the diet of the Brown Bear (Ursus arctos) in the Pyrénées and its role in the dispersal of plants and fungi.

Summary: Large animals are recognised for their impact on ecosystems through their trophic and non-trophic interactions. This is a context in which omnivores are still not fully appreciated. However, by consuming a little of everything, omnivores can interact with various ecosystem compartments. The most well-known and widespread omnivore in the world is the brown bear (Ursus arctos). It is an animal that has been studied historically, and the literature highlights its role in regulating its prey (invertebrates and vertebrates), altering the behaviour of co-predators and acting as an ecosystem engineer. This engineering is characterised by soil disturbance, the formation of dead wood or the transport of biological material such as diaspores (spores or seeds), which are key processes in the functioning of the ecosystem. In this PhD, we investigated the latter process, that is, the dispersal of diaspores through ingestion (i.e. endozoochory) by brown bears, based on a study of the Pyrenean population (south-western Europe). As a first step, we studied its diet in relation to its sex, age and needs. The diet of this critically endangered population has been unknown since the late 90s, so this will provide a crucial update of our knowledge. Secondly, we investigated its role in plant dispersal using several methods. Once dispersed, we wanted to examine the importance of bear faeces visitors in the fate of diaspores. We also investigated the dispersal of plant-symbiotic fungi (occasionally or accidentally consumed). My research enabled the characterisation of a diet mainly composed of plants (grasses, dried or fleshy fruits) supplemented by arthropods (ants, wasps), vertebrates (especially wild ungulates) and fungi (truffles in particular). Here we have described the greatest diversity of fungi consumed by an ursid. My results also show that females are more herbivorous than males and that the diet changes according to the bear's biological and physiological needs. Here we describe the dispersal of plants that produce dry or fleshy fruits, as well as ferns and mosses. We also highlight the importance of considering the endozoochore process up to the faecal matrix, which can limit germination. In this context, it has been shown that dung beetles play a unique role in the disintegration of faeces and the secondary dispersal of diaspores. Concerning the dispersal of symbiotic fungi to plants, we were able to infer the potential dispersal of mycorrhizae, endophytes and plant pathogens, contributing to a little-studied topic. Overall, my PhD thesis identified a diverse diet as never before described through the use of metabarcoding and faeces from different sexes and ages. It reveals the dispersal of a wider range of plants than previously thought in Ursids, and relevant symbiotic fungi, all of which could influence the structure and dynamics of Pyrenean plant communities and consequently the functioning and resilience of Pyrenean ecosystems in the face of global changes. More broadly, the results call for future research to study such dispersal in other animals, but also to take appropriate account of the endozoochory mechanism, including the faecal matrix. Much remains to be done, particularly on the actual dispersal of fungi or the fate of seeds after the passage of dung beetles, yet this PhD thesis provides valuable new evidence to historical research on the ecology of the brown bear and lays the foundations for future research.

Keywords: Endozoochory, Engineering of ecosystems, Joint dispersal, Omnivory, Secondary seed dispersal, Ursidae

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