



# The bear-berry connection: Ecological and management implications of brown bears' food habits in a highly touristic protected area

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## ABSTRACT

Diet studies are essential to understand animal ecology and ecosystem dynamics, especially in the case of large omnivores. These studies are particularly relevant in areas where human disturbance is intense and, thus, species dietary patterns might change due to the easy accessibility of food resources of human origin, which may hinder the ecosystem services these species provide. We assessed the diet of brown bears (*Ursus arctos*) by DNA metabarcoding in Tatra National Park (southern Poland), a highly touristic protected area. Brown bears' diet showed a marked seasonality, a characteristic feature of brown bear populations relying on natural foods. Graminoids represented the main food during spring, while fleshy-fruited plants became more important from mid-summer. Fleshy-fruited plants were present in 56% of faeces and during the entire activity period of bears, revealing that fruits play a pivotal role in the feeding ecology of Tatra brown bears. Two berry species, *Vaccinium myrtillus* and *Rubus idaeus*, were the most frequently detected (in 42% and 20% of faeces, respectively). The large consumption of fleshy-fruited plants, and particularly of berries, suggests that, despite high levels of human disturbance in the area, brown bears still play a key role as seed dispersers. Management strategies focused on an effective waste management, control of berry picking, strict regulations about human activities in specific areas during sensitive periods in the feeding ecology of bears, and the lack of artificial food provisioning are crucial to ensure the seed dispersal processes and associated ecosystem services that bears and other frugivores provide.

## 1. Introduction

Human population is currently increasing in unprecedented numbers, with the environmental conditions worsening worldwide as a consequence of human-driven processes such as resource exploitation, pollution, climate change and their synergistic interactions (Brook et al., 2008). As a consequence, many wildlife species are forced to live in fragmented anthropogenic landscapes (Goudie, 2013). Human disturbance may act as a strong driver of biodiversity change that does not only compromise species persistence but also the ecological interactions in which they are involved and their related ecosystem services (Fontúrbel et al., 2015; Valiente-Banuet et al., 2015). For instance, habitat fragmentation and degradation have effects on animal-mediated seed

dispersal, especially on the diversity of seed dispersers and the frequency of plant-animal interactions (McConkey et al., 2012; Fontúrbel et al., 2015). However, we still know little about how other forms of human disturbance in natural areas such as mountain tourism, the provision of artificial food to wildlife or the extraction of natural foods by humans (e.g. berry picking) may hinder animal-mediated seed dispersal processes.

Understanding animal-mediated ecosystem functions, such as seed dispersal by frugivores, requires a good knowledge of species diet, especially in those with a complex feeding ecology such as large carnivores with an omnivorous diet (Nawaz et al., 2019). Large carnivores have an important conservation value as they play key roles in ecosystems, thus, a better understanding of their feeding ecology is crucial to

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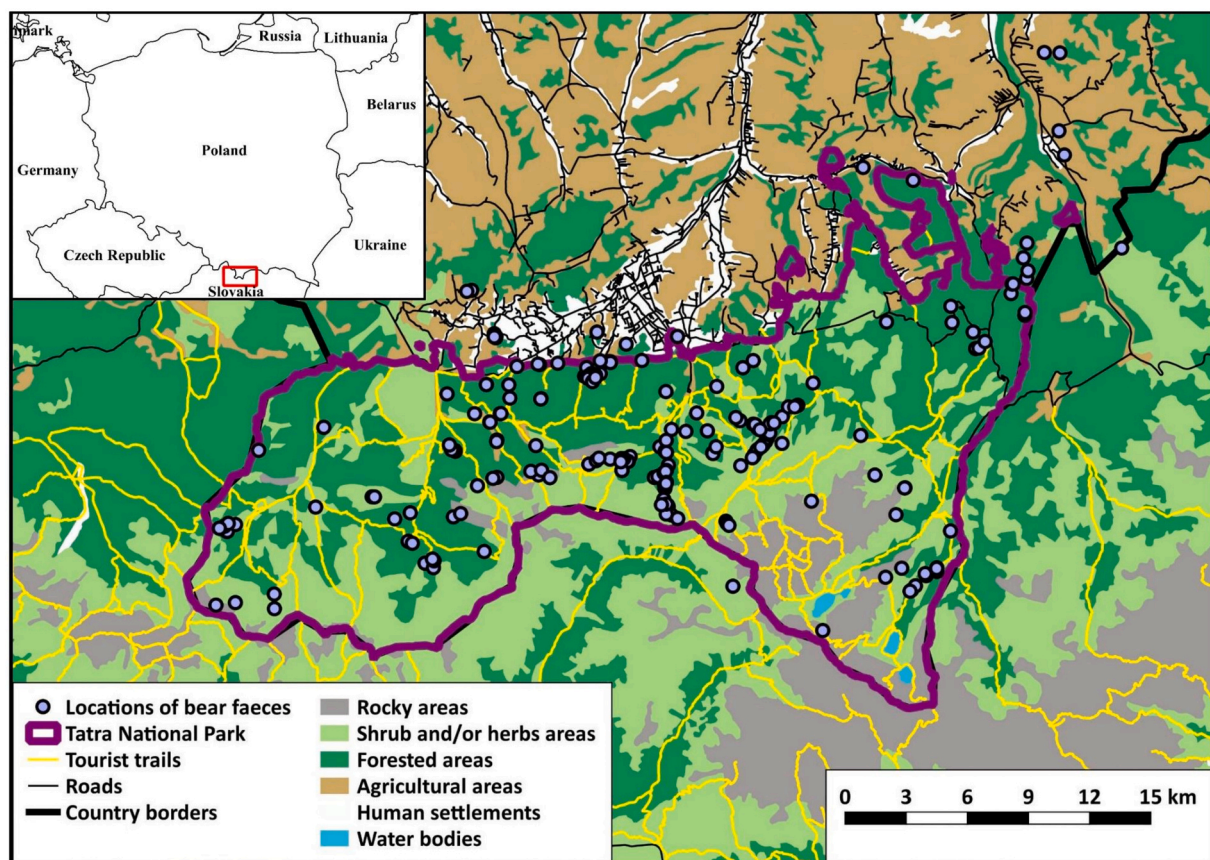
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determine the effects they exert on other trophic levels (Monterroso et al., 2018; Ciucci et al., 2020). Accurate diet analyses are mandatory to enhance our understanding of ecosystem functioning and to implement effective conservation and management actions, particularly in highly humanized ecosystems. However, precise knowledge about the feeding ecology of omnivores and the ecological implications of consumer – resource interactions is still limited due to the difficulties in accurately determining the complex variety of food items consumed (De Barba et al., 2014). To solve this limitation, DNA metabarcoding approaches and high throughput sequencing (HTS hereafter) have been increasingly used as a tool to obtain a more accurate identification of the food items consumed, even for food remains which are too small or too digested to be identified microscopically and from complex diet mixtures (Valentini et al., 2009; De Barba et al., 2014). By using universal primers, this approach allows the simultaneous identification of various DNA sequences of taxa present in dietary samples collected non-invasively in the field (e.g. faecal or regurgitate remains; Pompanon et al., 2012). Metabarcoding techniques have already been successfully applied to diet studies of different groups of mammals such as large carnivores, ungulates or rodents (Elfström et al., 2014; Fløjgaard et al., 2017; Lopes et al., 2020; Nørgaard et al., 2021).

The brown bear *Ursus arctos* (Order: Carnivora, Family: Ursidae) is one of the world's most widely distributed terrestrial mammals and the largest living terrestrial carnivore. As other omnivore species, brown bears are flexible dietary generalists that rapidly adapt to environmental conditions and seasonal differences in food availability (Bojarska and Selva, 2012). During the hyperphagic season prior to hibernation,

brown bears inhabiting boreal, temperate and Mediterranean areas feed intensively on fleshy fruits, whose seeds usually remain undamaged after bear ingestion and can be deposited over long distances. Consequently, this fleshy-fruit-based diet is important not only for bears but also for the seed dispersal and recruitment of the plant species they consume (García-Rodríguez and Selva, In press; García-Rodríguez et al., 2021). Human activities are known to reduce natural resource use and alter spatiotemporal activity patterns in brown bears (Nevin and Gilbert, 2005a; Nevin and Gilbert, 2005b; Rode et al., 2007; Ordiz et al., 2017), and are likely to have consequences for the seed dispersal services provided by this species (Penteriani et al., 2017). However, the impact of human activities on the diet of brown bears and on their role as seed dispersers is still poorly understood. Here we analyzed the dietary patterns of brown bears inhabiting Tatra National Park (southern Poland), a highly populated and touristic alpine area in the Carpathian Mountains holding a high density of brown bears (Konopiński et al., 2019), with a particular focus on their role as seed dispersers. Specifically, we aimed to answer the following questions: 1) Which is the dietary diversity of brown bears in Tatra National Park across the entire activity period of the species? 2) Are fleshy fruits an important food, frequently consumed by brown bears inhabiting the area? and 3) Can brown bears still provide effective seed dispersal services despite high levels of human disturbance? Finally, we discuss the management actions which should be implemented in order to preserve the ecosystem services provided by brown bears in human-modified landscapes.



**Fig. 1.** Map showing the location of the brown bear faeces collected in the Polish side of the Tatra Mountains between 2017 and 2019 for this study ( $n = 246$ ). Tourist trails, paths and roads within Tatra National Park ("Tourist trails"; in yellow), main roads in the vicinity of the study area (i.e. motorways and primary, secondary and tertiary roads; "Roads"; in black) and land use according to Corine Land Cover inventory for 2018, including human settlements and agricultural areas, are also included in the map. Fleshy fruits, especially of *Vaccinium myrtillus* and/or *Rubus idaeus*, are common and widespread in most forested (dark green) and shrub/herb (light green) areas within Tatra National Park. An extended map including also Slovakian Tatra National Park and its surroundings is provided in Fig. A1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

## 2. Material and methods

### 2.1. Study area

The study was conducted in Tatra National Park (Poland) and its vicinity, a 211 km<sup>2</sup> protected area located in the Tatra Mountains, a mountain range belonging to the western part of the Carpathian Mountains in the Poland - Slovakia borderline (Figs. 1, A1). Tatra National Park ranges from 774 to 2499 meters above sea level (m.a.s.l.) and lies entirely in the temperate conifer forests terrestrial biome (Olson et al., 2001). Montane forests (below 1550 m.a.s.l.) occupy around 60% of the total surface of the area and are dominated by *Picea abies*, partly introduced in the original habitat of *Abies alba* and *Fagus sylvatica* during the 19th century. *Pinus mugo* are abundant in subalpine areas (1550–1800 m.a.s.l.). *Vaccinium myrtillus* dominates montane, subalpine and alpine floors (up to 2300 m.a.s.l.). Other shrub species such as *V. vitis-idaea*, *V. gaultherioides* and *Rubus idaeus* can be found at different elevations (Mirek and Piekos-Mirkowa, 1992).

Tatra National Park is one of the most popular tourist destinations in Poland (see pictures in Fig. A2), visited currently by more than 3.5 million tourists annually. The number of visitors peaks in July and August, when up to 40,000 people may enter the park daily (<https://tpn.pl/zwiedzaj/turystyka/statystyka>). Visitors' presence, which from March to November is only allowed during daylight hours, is limited to a network of more than 270 km of touristic trails and associated resting areas, which yields a density of more than 1 km of public paths per km<sup>2</sup> within the protected area (Figs. 1, A1). Berry picking within the national park is only allowed under special permits (e.g. for scientific research), but illegal picking still happens, even on a large scale in some areas (authors' personal observations). No artificial feeding of wildlife is conducted within the national park (Zwijacz-Kozica et al., 2017). However, artificial feeding sites for ungulates are found in surrounding areas, although in small numbers in the Polish territory (authors' personal observation), but in much larger numbers in neighbouring areas in Slovakia (Rigg and Gorman, 2005). Agricultural areas and several human settlements, including Zakopane (ca. 30,000 inhabitants and known as the “winter capital of Poland”), are located on the northern boundary of Tatra National Park (Figs. 1, A1). To the south, the protected area borders its counterpart national park in Slovakia.

The Tatra brown bear population segment is transboundary, with some animals moving regularly between Poland and Slovakia, and it is estimated at 45–79 individuals for Tatra National Park (Konopiński et al., 2019; Bartoń et al., 2019), which suggests one of the highest bear densities in Europe. Brown bears in the area usually hibernate from November to March, have a low to normal feeding activity from den emergence and until the end of the mating season (“hypophagia” hereafter; April–June) and start feeding intensively from July until hibernation (“hyperphagia”; Bartoń et al., 2019; García-Rodríguez et al., 2020). Bear sightings by tourists are frequent in the area and some animals can approach human settlements, especially during the autumn. However, bear attacks to humans are rare and damages to human properties (i.e. livestock, apiaries, agriculture, etc.) are uncommon when compared to other brown bear areas in Europe (Bautista et al., 2017; Bombieri et al., 2019).

### 2.2. Field collection of brown bear faeces

We collected fresh brown bear faeces in Tatra National Park during a two-year period (from July 2017 to July 2019) and comprising the entire activity period of bears in the area (April to November). Based on our research interests, we considered three days as the approximate age for a fresh sample. We estimated the age of each sample based on its smell and shape, considering the weather conditions of the previous days. We followed three different approaches for collection of faeces: 1) during inspections of clusters of 8 GPS-collared bears; 2) during inspections of nine transects (1.5 km length and 3 m width each)

established in different areas of the national park and surveyed once a month from July to October in 2017 and 2018, and 3) during routine conservation and monitoring tasks conducted by Tatra National Park staff. In order to have a representative subsample of the food items contained in each brown bear faecal sample and to minimize external environmental contamination, we opened each sample using disposable and sterile plastic gloves and took two or three small pieces, depending on sample size, from different parts of the inside of the faeces, obtaining a total subsample of about 1 cm<sup>3</sup>. New plastic gloves were used for each sample. We noted the date of collection, the GPS coordinates (latitude and longitude) and the elevation of each collected faecal sample (Table A1). We put each sample in a tube two thirds full with silica gel and stored it at room temperature until processing for DNA metabarcoding.

### 2.3. Diet composition identification

DNA metabarcoding analysis for the identification of the food taxa contained in bear faeces was performed by amplifying and sequencing on a high-throughput sequencing platform short DNA fragments of plants, insects and vertebrates. We used three universal primer pairs to target each of these major groups of bear diet (Sper01, Inse01, Vert01; Taberlet et al., 2018). DNA extraction, PCR amplification and sequencing, sequence data filtering and analysis as well as taxonomic identification were carried out based on published protocols (Taberlet et al., 2012; De Barba et al., 2014). We used PCR negative and positive controls to monitor the performance of DNA amplification and sequencing, and to guide the selection of filtering parameters in the sequence analysis process. Detailed information of all steps, from DNA extraction to data filtering and analysis, is described in Appendix A. Taxa identified as nonnative species in our study area and not considered to have been introduced by human activities were reassigned to a higher taxonomic level present in the study area. After sequence data filtering, we classified each identified taxon as (i) natural food item, if it naturally occurs in the study area, or as (ii) possibly human-related food item, if the item could be related to human activities (i.e. if natural counterparts also occurred in the area).

### 2.4. Data organization and statistical analysis

Brown bear diet was assessed based on the taxonomically assigned DNA sequences obtained after analysis and filtering of the sequence data. Prior to statistical analysis, we classified all the food items detected in brown bear faeces into 10 different food categories nested in three major groups: vertebrates, insects and plants. Vertebrate taxa were subsequently classified as birds or mammals, whereas plants were divided into seven different categories: plant species producing fleshy fruits (e.g. berries, drupes), plant species producing hard mast (e.g. acorns, nuts), tree species with neither fleshy fruits nor hard mast (e.g. *Acer* sp.), plant species with edible roots (e.g. tubers), graminoids (i.e. herbaceous species with grass-like morphology), forbs (i.e. non-graminoid herbaceous species) and cryptogams (i.e. plant species reproducing by spores, without seeds). Similar food categories have been commonly used in previous brown bear diet studies (e.g. Naves et al., 2006; Nawaz et al., 2019).

We assigned each brown bear faecal sample to the month of collection and to the season of feeding activity (hypophagia or hyperphagia). We collected only three samples during early November (before November 11th) and one of them was discarded after sequence quality filtering. Thus, we included the other two samples in October for further analyses (Table A1). We extracted information about the number of unique DNA sequence reads produced and assigned them to each taxon in each faecal sample. Additionally, we calculated the frequency of occurrence of each taxon detected as the number of faeces in which a given food taxon was recorded divided by the total number of faeces. We constructed a brown bear faecal sample × food taxon matrix of



presence/absence of each taxon in each faecal sample. We used this matrix to measure the diversity of Tatra brown bears' diet with two complementary indices: (1) the Hill series number 0 (i.e. the total number of taxa detected in each sample; “ $N_0$ ” hereafter; Hill, 1973) and (2) the Gini-Simpson index ( $\lambda = 1 - \sum p_i^2$ ; the probability that two items randomly taken from a faecal sample belong to different food categories; Simpson, 1949). We calculated these two indexes for each faecal sample

separately.

We used univariate generalized linear models to analyze the effects of seasonality (separately for the feeding season – hypo and hyperphagia- and the month – from April to October) on the scores of the two indexes calculated to measure trophic diversity ( $N_0$  and Gini-Simpson index) and on the presence/absence of each of the ten food categories in each faecal sample. Models related to Gini-Simpson's index and to the

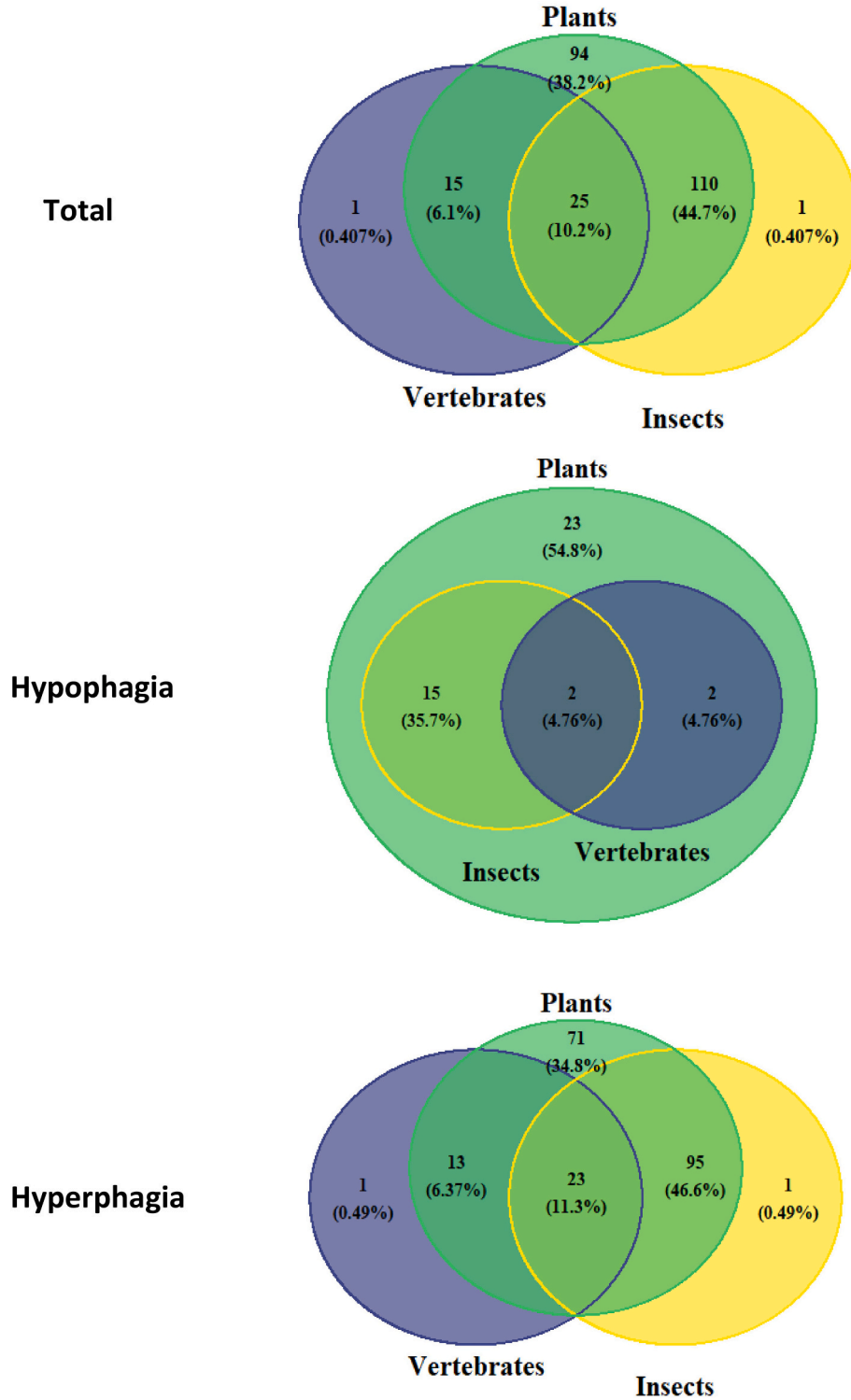


Fig. 2. Venn diagrams showing the number and the percentage (in brackets) of brown bear faeces collected in the Tatra Mountains (Poland) containing food taxa belonging to each of the three major food groups (plants, vertebrates and insects) for the entire activity period of brown bears and for hypophagia (April – June) and hyperphagia (July – November), separately.

presence/absence of food categories were fitted with a binomial distribution, whereas the two models analyzing the influence of the phenology on  $N_0$  index were fitted with a negative binomial distribution to account for overdispersion. We used the R statistical environment (version 3.4.0, R Development Core Team, 2017) to perform all statistical analyses. The map in Fig. 1 was built in QGIS software (v2.14.22). We extracted information about roads and land use from Open Street Map and Corine Land Cover v2018, respectively. The other figures were created using the R packages *ggplot2* (Wickham, 2011), *bipartite* (Dormann et al., 2008) and *VennDiagram* (Chen and Boutros, 2011).

### 3. Results

We collected a total of 253 brown bear faeces in the study area between July 2017 and July 2019. PCR products generated a total of 26,901,502 paired-end sequence reads. We discarded seven samples that yielded no sequence reads after sequence data analysis and filtering. Thus, we used 246 faeces for all further analyses (42 and 204 from hypo and hyperphagia, respectively; Table A1, Fig. 1).

#### 3.1. Diet composition

We detected a total of 285 different molecular operational taxonomic units -MOTUS- (see online supplementary information) corresponding to 173 different taxa identified in brown bear faeces. Among these, 25 taxa were identified as vertebrates (8 avian and 17 mammalian taxa), 48 as insects and 100 as plants (7 of them were assigned to plant species producing fleshy fruits, 2 to plant species producing hard mast, 6 to tree species with neither fleshy fruits nor hard mast, 2 to plant species with edible roots, 14 to graminoids, 55 to forbs and 14 to cryptogams; Table A2). Taxonomic resolution varied among vertebrates, insects and plants, but in the three groups more than 50% of the taxa were assigned at least to genus level (Table A3). We could assign 46% of the detected insect taxa, 44% of vertebrate taxa and 12% of plant taxa to species level

(Table A3).

The number of taxa detected per brown bear faecal sample ranged from one to 19 (mean  $\pm$  standard deviation =  $6.37 \pm 3.47$  taxa; Table A4). As much as 97% and 67% of the faeces contained more than one and five food items, respectively (Table A1). Forty six percent of the taxa were detected exclusively in one faecal sample and 58% of the taxa in less than 1% of the faeces (i.e. only in one or two faeces). Plant material was detected in 99% of the faeces (244 out of 246; Fig. 2). We found insect and vertebrate materials in 55% and 17% of the samples, respectively. Vertebrate, insect and plant materials were present together in 10% of the faeces (Fig. 2).

Apiaceae and Ericaceae were the plant families most commonly detected, being present in 78% and 42% of the bear faeces. Psychodidae and Anisopodidae were the most frequent among insects (found in 13% and 6% of samples, respectively), whereas Cervidae and Canidae were the mammalian families most often detected (7% and 3%, respectively; Fig. A3). Seven genera (six plants and one insect) were detected in more than 10% of the faeces. Among them, two fleshy-fruited plant genera, *Vaccinium* and *Rubus*, were the most frequently detected (in 42% and 20% of faeces, respectively), while *Psychomora* and *Cervus* were the most common insect and vertebrate genera (13% and 6%, respectively; Table 1). At species level, only four plants were detected in more than 10% of the samples. Two fleshy-fruited plant species were the most commonly found: *V. myrtillus* (present in 42% of faeces) and *R. idaeus* (20%), followed by the forb *Stellaria nemorum* (12%) and by the hard mast tree *Fagus sylvatica* (11%). The diptera *Sylvicola fenestralis* and the hymenoptera *Vespula vulgaris* were the insects most commonly found (6% and 5%, respectively) and *Cervus elaphus* the most common vertebrate (6%; Table 1).

Only 14 out of the 173 taxa identified could possibly derive from human activities, which means 8% of the taxa detected. Specifically, seven vertebrate, one insect and six plant taxa could have a possible anthropogenic origin (Tables A2, A5). These food items were detected in 17 faeces (7% of the total). Among these taxa, only five vertebrates,

**Table 1**

Diet composition of brown bears in the Tatra Mountains (Poland) in 2017–2019, indicating the most common species and genera identified in the faeces analyzed ( $n = 246$ ) by DNA metabarcoding techniques. The frequency of occurrence for each food taxon (proportion of faeces with a given taxon) is calculated for the entire activity period of brown bears (April–November), as well as for the hypophagia (April–June) and hyperphagia (July–November) seasons separately. Only taxa detected in more than 3% of the faeces are listed (see Table A2 for the full list).

|                              | Family          | Category      | Frequency of occurrence |            |             |
|------------------------------|-----------------|---------------|-------------------------|------------|-------------|
|                              |                 |               | Total                   | Hypophagia | Hyperphagia |
| <b>Species</b>               |                 |               |                         |            |             |
| <i>Vaccinium myrtillus</i>   | Ericaceae       | Fleshy fruits | 41.9%                   | 9.3%       | 48.5%       |
| <i>Rubus idaeus</i>          | Rosaceae        | Fleshy fruits | 20.3%                   | 23.3%      | 19.6%       |
| <i>Stellaria nemorum</i>     | Caryophyllaceae | Forbs         | 11.8%                   | 16.3%      | 10.8%       |
| <i>Fagus sylvatica</i>       | Fagaceae        | Hard mast     | 11.4%                   | 0          | 13.7%       |
| <i>Sylvicola fenestralis</i> | Anisopodidae    | Insects       | 6.1%                    | 0          | 7.4%        |
| <i>Cervus elaphus</i>        | Cervidae        | Mammals       | 5.7%                    | 0          | 6.9%        |
| <i>Vespula vulgaris</i>      | Vespidae        | Insects       | 5.3%                    | 0          | 6.4%        |
| <i>Vaccinium vitis-idaea</i> | Ericaceae       | Fleshy fruits | 3.7%                    | 4.7%       | 3.4%        |
| <b>Genera</b>                |                 |               |                         |            |             |
| <i>Vaccinium</i>             | Ericaceae       | Fleshy fruits | 42.3%                   | 11.6%      | 48.5%       |
| <i>Rubus</i>                 | Rosaceae        | Fleshy fruits | 20.3%                   | 23.3%      | 19.6%       |
| <i>Luzula</i>                | Juncaceae       | Graminoids    | 17.9%                   | 51.2%      | 10.8%       |
| <i>Urtica</i>                | Urticaceae      | Forbs         | 15.9%                   | 25.6%      | 13.7%       |
| <i>Psychomora</i>            | Psychodidae     | Insects       | 13.0%                   | 2.3%       | 15.2%       |
| <i>Stellaria</i>             | Caryophyllaceae | Forbs         | 11.8%                   | 16.3%      | 10.8%       |
| <i>Fagus</i>                 | Fagaceae        | Hard mast     | 11.4%                   | 0          | 13.7%       |
| <i>Athyrium</i>              | Woodsiaceae     | Cryptogams    | 8.1%                    | 0          | 9.8%        |
| <i>Sylvicola</i>             | Anisopodidae    | Insects       | 6.1%                    | 0          | 7.4%        |
| <i>Cervus</i>                | Cervidae        | Mammals       | 5.7%                    | 0          | 6.9%        |
| <i>Vespula</i>               | Vespidae        | Insects       | 5.3%                    | 0          | 6.4%        |
| <i>Leontodon</i>             | Asteraceae      | Forbs         | 4.9%                    | 0          | 5.9%        |
| <i>Rhipidia</i>              | Limoniidae      | Insects       | 4.5%                    | 0          | 5.4%        |
| <i>Trifolium</i>             | Fabaceae        | Forbs         | 4.1%                    | 4.7%       | 3.9%        |
| <i>Dryopteris</i>            | Dryopteridaceae | Cryptogams    | 3.3%                    | 0          | 3.9%        |
| <i>Prunus</i>                | Rosaceae        | Fleshy fruits | 3.3%                    | 0          | 3.9%        |

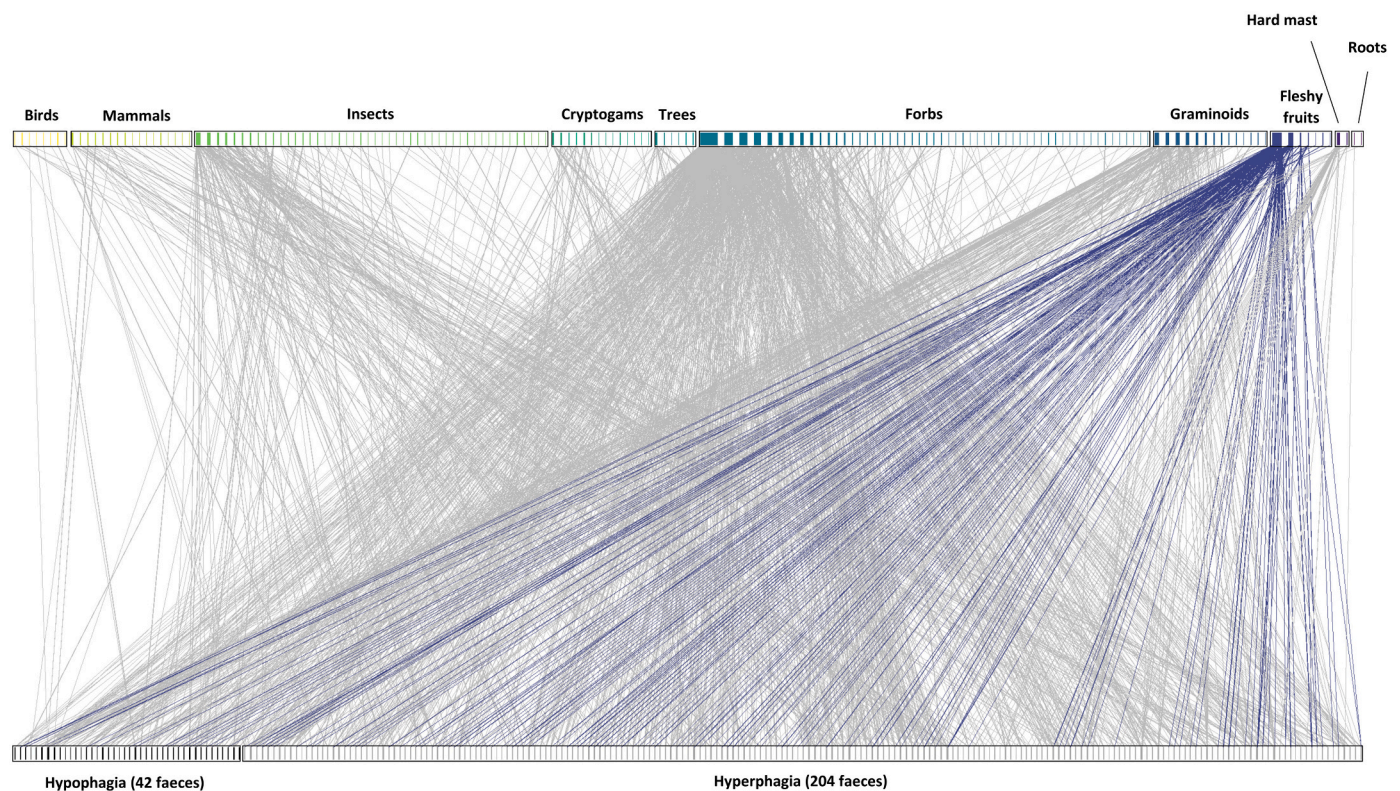
mostly related to livestock activities, were found in more than one bear faeces. Additionally, in three cases, these taxa have a wild counterpart present in the study area and, thus, we could confirm the anthropogenic origin of only two of these five items (*Bos* sp. was found in five samples and *Meleagris gallipavo* in two; Tables A2, A5).

### 3.2. Temporal patterns in brown bear diet

We found both a seasonal and a monthly variation in the diet of Tatra brown bears, with the frequency of occurrence of four out of the ten food categories considered being influenced by the feeding season (hypo and hyperphagia). Similarly, the month of collection also affected the frequency of occurrence of six of these categories (Table A6). Thus, brown bear diet composition showed a strong variation in relation to both the feeding season and the month. When only the feeding season was considered (without taking into account months separately), we found that graminoids were more frequently consumed during hypophagia, whereas insects, cryptogams and fleshy-fruited plant species were more frequently consumed during hyperphagia (Figs. 3, A4, Table A6). When monthly variation in brown bear diet was analyzed, we additionally found that plant species producing hard mast were significantly more frequently consumed towards the end of the bears' activity period (September – October), whereas vertebrates were more common in bear diet just after den emergence (April) and before hibernation (September – October; Fig. A4, Table A6).

### 3.3. Relevance of fleshy-fruited plant species in brown bear diet

Taxa producing fleshy fruits were present in 56% of the faeces and during the entire activity period of brown bears, i.e. from April to November. We registered a peak during August (80%; Figs. 3, A4; Table 2). Native species *V. myrtillus* and *R. idaeus*, present in 42% and 20% of the samples respectively, were the fleshy-fruited plant taxa more frequently consumed. Moreover, *V. myrtillus* was found in faeces collected during the entire activity period of bears, whereas *R. idaeus* was detected in all months except in April (Fig. 3; Table 2). Apart from these two species, five more plant species producing fleshy fruits were consumed by brown bears (Table 2; Table A2). Three of them (*V. vitis-idaea*, *Prunus* sp. and *Ribes* sp.) are also native to the study area. *V. vitis-idaea* was detected in 3.6% of all faeces and was found in faeces collected at the end of the hyperphagia, coinciding with *V. vitis-idaea* fruiting period (September and October), but also in faeces collected just after bear emergence from dens (April and May). *Prunus* sp. was detected in 3.2% of faeces and only in those collected from August to October. *Ribes* sp. was detected only in one faeces collected in July. The other two taxa assigned as fleshy-fruited plant species (the family Actinidiaceae and *Capsicum* sp.) do not naturally occur in the area and, thus, their presence in brown bears' diet is most likely of human origin. These non-native fleshy-fruited taxa were found only in three bear faeces collected at the beginning of bears' activity period (i.e. April; Tables 2, A6).



**Fig. 3.** Bipartite graph linking each brown bear faecal sample and each food taxa identified in the diet of brown bears in the Tatra Mountains (Poland). Bottom bars represent individual brown bear faeces ( $n = 246$ ) and are ordered chronologically based on the date of sample collection (both years merged); bear faeces collected during hypophagia ( $n = 42$ ) and hyperphagia ( $n = 204$ ) are grouped separately and represented in black and grey, respectively. Upper bars represent food taxa detected by DNA metabarcoding techniques ( $n = 173$ ) in brown bear faeces and are organized by the 10 categories considered: 1) birds ( $n = 8$ ), 2) mammals ( $n = 17$ ), 3) insects ( $n = 48$ ), 4) cryptogams ( $n = 14$ ), 5) trees (tree species not producing neither fleshy fruits nor hard mast;  $n = 6$ ), 6) forbs ( $n = 55$ ), 7) graminoids ( $n = 14$ ), 8) fleshy fruits (plant species producing fleshy fruits;  $n = 7$ ), 9) hard mast (tree species producing hard mast;  $n = 2$ ) and 10) roots (plants with edible roots;  $n = 2$ ). All items belonging to the same food category are grouped and represented with a distinct color. Bottom bars width represents the total number of food taxa of each faecal sample, whereas upper bars width represents the number of faecal samples containing each taxon. Purple lines indicate links between brown bear faeces and fleshy-fruited plant species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Table 2**

Frequency of occurrence (proportion of faeces with a given taxon) of fleshy-fruited plant taxa in brown bear faeces collected in the Tatra Mountains (Poland, n = 246). Numbers are given for the entire activity period of brown bears and for each month separately. The number of faeces analyzed each month is provided in brackets. Two samples collected in November were assigned to October.

|                              | Total<br>(246) | April<br>(11) | May<br>(12)  | June<br>(19) | July<br>(36) | August<br>(45) | September<br>(32) | October<br>(91) |
|------------------------------|----------------|---------------|--------------|--------------|--------------|----------------|-------------------|-----------------|
| <i>Vaccinium myrtillus</i>   | 41.9%          | 18.2%         | 8.3%         | 5.3%         | 38.9%        | 73.3%          | 56.3%             | 35.2%           |
| <i>Rubus idaeus</i>          | 20.3%          | 0             | 16.7%        | 42.1%        | 27.8%        | 4.4%           | 15.6%             | 11.0%           |
| <i>Vaccinium vitis-idaea</i> | 3.7%           | 9.1%          | 8.3%         | 0            | 0            | 0              | 3.1%              | 6.6%            |
| <i>Prunus</i> sp.            | 3.3%           | 0             | 0            | 0            | 0            | 4.4%           | 3.1%              | 4.4%            |
| <i>Capsicum</i> sp.          | 0.8%           | 18.2%         | 0            | 0            | 0            | 0              | 0                 | 0               |
| Actinidiaceae                | 0.4%           | 9.1%          | 0            | 0            | 0            | 0              | 0                 | 0               |
| <i>Ribes</i> sp.             | 0.4%           | 0             | 0            | 0            | 2.8%         | 0              | 0                 | 0               |
| <b>Total fleshy fruits</b>   | <b>56.1%</b>   | <b>36.4%</b>  | <b>33.3%</b> | <b>47.4%</b> | <b>58.3%</b> | <b>80.0%</b>   | <b>65.6%</b>      | <b>48.3%</b>    |

## 4. Discussion

### 4.1. Ecological considerations of a berry-based diet in brown bears

Here we have shown that fleshy fruits, and more specifically berries, are among the most frequent food consumed by brown bears inhabiting Tatra National Park. Two fleshy-fruited plant species, *V. myrtillus* and *R. idaeus*, were the most relevant food items for bears in the region, suggesting that, as it also happens in many brown bear populations worldwide, fleshy fruits are pivotal for the species, especially during hyperphagia, when they feed intensively in order to achieve the energetic demands needed to survive the winter (Welch et al., 1997; García-Rodríguez, Albrecht, Szczytkowska et al., 2021). *V. myrtillus* abundance is known to affect brown bears' body size, movement and reproductive success and it is a key feature for habitat selection for Scandinavian brown bears (Hertel et al., 2016; Hertel et al., 2018). Additionally, a recent work on the role of brown bears as seed dispersers across their distribution found that *V. myrtillus* and *R. idaeus* are among the fleshy-fruited plant species that are most commonly consumed by the brown bear across its geographic range (García-Rodríguez, Albrecht, Szczytkowska et al., 2021). Interestingly, we detected consumption of *V. myrtillus* and *V. vitis-idaea* during spring, whereas the fruiting season of these species starts during late summer in the study area. Some fruits, especially of *V. vitis-idaea*, may persist under the snow and they can be available for brown bears and other frugivores the next spring, once the snow has melted. However, for the case of *V. myrtillus*, whose fruits rarely persist in the shrub after heavy snowfalls (authors' personal observation), we believe that brown bears might have fed on other plant parts such as twigs, young shoots or flowers during spring, either intentionally or accidentally when eating other foods. This finding is supported by previous research conducted in Scandinavia where *V. vitis-idaea* fruits were found in up to 34% of brown bear faeces collected during spring, whereas only 4% of these faeces contained *V. myrtillus* fruits (Stenset et al., 2016).

The large consumption of fleshy fruits, reaching up to 80% of their diet in some periods, suggests that brown bears may play an essential role as seed dispersers in Tatra National Park. In line with this, previous research found that brown bears are responsible for the vast majority of dispersal of *V. myrtillus* seeds in the area (García-Rodríguez et al., in press). Together with the huge amounts of berries they consume, other brown bear features are essential to understand the uniqueness of the seed dispersal services provided by the species. For instance, brown bears can defecate several kilometers away from the places where they consumed the fruits and a single bear faeces may contain thousands of undamaged seeds that may germinate (Lalleroni et al., 2017; García-Rodríguez et al., in press). These long-distance seed dispersal events are essential for gene flow and plant population dynamics (Nathan and Muller-Landau, 2000). Additionally, bears usually defecate next to their resting sites, where they dig out soil and create local disturbances on the ground that may enhance germination (Steyaert et al., 2019; García-Rodríguez and Selva, In press). As seedling establishment is usually rare

in clonal species such as *V. myrtillus*, especially within stands of conspecific adults (Eriksson and Fröberg, 1996), these small disturbances created by bears might facilitate seedling recruitment in these species by exposing the defecated seeds to suitable conditions for germination (Steyaert et al., 2019). Research conducted in the study area has found that bilberry germination was associated to all marked brown bear faeces, with up to the 16% of the seedlings surviving for at least one year in the field (García-Rodríguez and Selva, In press). All this combined, and especially considering that other large frugivores that are able to mobilize seeds over long distances are often missing in brown bear areas, suggests that frugivory by brown bears might be essential for the regeneration of fleshy-fruited plants in temperate and boreal ecosystems.

Frugivory by brown bears may be crucial to support the adaptation of fleshy-fruited plant species to global warming, particularly in mountain regions, like the Tatra alpine ecosystem. Climate change is likely to affect the distribution, survivorship and productivity of essential natural foods of brown bears, including *V. myrtillus* and other fleshy-fruited plant species (Rodríguez et al., 2007; Roberts et al., 2014; Penteriani et al., 2019). As fruit maturation in most species occurs later at higher elevations and brown bears can track food availability (Rötzer and Chmielewski, 2001; Deacy et al., 2016), bears might be mobilizing seeds uphill while following the phenology of the fruits they rely on, facilitating the colonization of upper areas by the seeds they disperse. With average temperatures constantly increasing due to climate change and taking into account the negative relationship between temperature and elevation, this uphill movement might be especially important for plants that, as *Vaccinium* species, benefit from being covered by snow during winter. The uphill dispersal of seeds provided by carnivores, including other ursid species such as the Asiatic black bear *U. tibetanus*, has already been suggested as a mechanism to support the adaptation of some fleshy-fruited plant species to global warming (Naoy et al., 2016; González-Varo et al., 2017).

### 4.2. Management considerations of a berry-based diet in brown bears

Our findings suggest that brown bears can still play a crucial role in seed dispersal processes even with high levels of human disturbance. We believe that management actions carried out by the Tatra National Park staff, such as the aversive conditioning to bears approaching human settlements, the proper waste management inside the Park and the strict regulations of berry picking by humans, together with the high productivity in terms of fruit production, are important factors explaining that bears still feed intensively on natural foods, and particularly on fleshy-fruits, in spite of the large amount of visitors and high human disturbance. Additionally, tourists are neither allowed to leave the public paths nor to walk during the night within the national park from March to November, coinciding with the activity period of bears. Thus, human presence in the area can be considered predictable both spatially and temporally. This predictability is known to reduce spatial displacement and minimize nutritional impacts in brown bears

inhabiting areas disturbed by humans (Rode et al., 2007). For instance, total resource use by brown bears in Alaska declined when bears were exposed to 24-hour daily human activity, but not when human presence was limited to daylight, indicating that time regulations may be an effective management strategy to maintain the natural feeding ecology of the species (Rode et al., 2007). All this considered, we believe that the identification and protection of natural feeding areas important for bears should be a priority to make human presence more predictable in such places. This information could be used to implement temporal and spatial restrictions to human activities such as hiking. This strategy has already been suggested in other bear areas in Europe (e.g. the Cantabrian Mountains; Naves et al., 2006). Additionally, this may have positive effects not only for preserving the natural feeding ecology and the seed dispersal services provided by bears and other frugivores but also for minimizing the chances of human-bear encounters, thus, enhancing safety of both bears and humans.

Brown bears in highly disturbed areas can still have a natural diet with an insignificant contribution of human-related foods. Anthropogenic foods, which are known to disrupt temporal dietary patterns and lower the quality of bears' diet (Sergiel et al., 2020), are almost negligible in the diet of bears inhabiting Tatra National Park. This may be at least partially explained by the absence of artificial feeding practices and the scarcity of crops that are potential bear foods (e.g. maize) in the study area, in spite of these practices being common in the neighbouring areas of Slovakia. Our results are clearly in contrast with diet data from the Slovakian side of the Tatra Mountains, where crops, much more widespread there due to milder climatic conditions, represented 30% of the total volume of brown bears' diet and became the most abundant food during autumn (*Avena sativa*, *Zea mais* and *Triticum aestivum*; Rigg and Gorman., 2005), instead of fleshy fruits, as in our study. Artificial feeding practices are known to change dietary patterns in brown bears, especially if provided in large amounts (Kavčič et al., 2015). In this line, bear diet in Tatra National Park had a significantly higher quality and a more seasonal pattern than the diet of bears inhabiting the Bieszczady Mountains, in the eastern part of the Polish Carpathians, where artificial food targeted to ungulates is provided and used year-round by brown bears (Sergiel et al., 2020). In addition to disruptions in the feeding ecology of the species, artificial feeding practices may also reduce movement and long-distance displacements in brown bears (Selva et al., 2017; Penteriani et al., 2021), with the subsequent reduction of the unique and essential seed-dispersal events, particularly long-distance, provided by the species.

We suggest that effective and well-informed management strategies are particularly needed in human-dominated areas to promote the use of natural food resources by brown bears and to enhance the subsequent ecosystem services they provide. However, some considerations should still be highlighted. First, this scenario may be different in areas where brown bears are hunted, as human presence in such areas directly alters habitat selection and forces bears to select less productive areas (Lodberg-Holm et al., 2019), which could affect bears' nutritional requirements and the related ecosystem services provided by the species. Second, little information is available about how berry picking by humans might affect feeding requirements of frugivore species and their subsequent seed dispersal services (Ticktin, 2004; McConkey et al., 2012). Berry picking is a common practice in many brown bear areas (Stryamets et al., 2012) and it might considerably reduce the amounts of fleshy fruits available for wildlife. For instance, berry picking by humans represents as much as 10–15% of the total natural production of *V. myrtillus* and *V. vitis-idaea* in areas of Eastern Finland and Russian Karelia (Belonogova, 1988; Turtiainen et al., 2011). In addition, some countries are nowadays implementing development programs and public measures such as a tax-free income to encourage berry pickers (e.g. Finland; Saastomoiken, 1999). Therefore, there is a need to ensure that these practices do not disrupt seed dispersal processes carried out by bears and other frugivore species, especially considering that the effects of harvest on the productivity of fleshy-fruited plant species may take

years to become apparent (McConkey et al., 2012), which might compromise population dynamics of both fleshy-fruited plants and their associated frugivores in the long term.

## Data availability

Data from this study, including raw reads produced by DNA metabarcoding, and R scripts are available at <https://doi.org/10.6084/m9.figshare.16744126>.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## CRediT authorship contribution statement

AGR, MDB and NS conceived the study and designed the methodology. PT designed the blocking primers to be used with Inse01 marker. AGR and TZK collected the samples in the field. MDB and DR prepared the samples and performed the extraction, amplification and sequencing of DNA material. CL performed bioinformatic analysis and preliminary data filtering, which was subsequently finished by AGR and TZK. AGR performed all statistical analyses and wrote a first draft of the manuscript with significant contributions of MDB and NS. All authors contributed critically to the draft and gave final approval for publication.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109376>.

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