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Are commercial wild-harvested plants just ordinary? Traits, harvesting patterns and conservation implications in France

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ABSTRACT

Wild plant harvesting plays a significant role in daily life, with over 40,000 species having well-documented uses. However, its ecological impacts on wild-harvested plant (WHP) populations are often overlooked. This study provides a comprehensive assessment of commercial wild harvesting in France, exploring the factors that drive this practice and identifying knowledge gaps regarding conservation concerns. We analysed 692 commercially harvested wild plant species in Metropolitan France and Corsica, representing 12 % of the national vascular flora. Our assessment considered their phylogeny, distribution, harvested parts, uses, life forms, Grime's CSR strategies, conservation status, and regulatory measures.

Our findings highlight the taxonomic diversity of WHP, spanning 110 families (60 % of French vascular plant families) and 431 genera (33 % of all genera). Analyses reveal a weak phylogenetic influence on WHP selection, suggesting additional contributing factors to this selection. WHP are geographically widespread, with the highest diversity in the Alps and southern France. Ecologically, they reflect the broad characteristics of French flora in terms of life forms and CSR strategies. These results support the concept of a 'harvesting syndrome' driven mostly by species availability.

WHP can be harvested primarily for medicinal (37 % of WHP species), food (20 %), and craft (14 %) purposes, with destructive methods potentially used in 60 % of cases. Conservation analysis indicates that WHP are generally less at risk than the total flora, with 91 % classified as Least Concern by the IUCN, though more local conservation assessments are needed to address region-specific threats.

1. Introduction

Wild-plant harvesting is a practice that has roots in prehistoric times (Cunningham, 2001). While wild-plant harvesting remains a vital resource for humanity, its socio-economic importance is often overlooked (Borelli et al., 2020). Nowadays this activity plays an essential role in producing medicines, cosmetics, and various other essential products that our society depends on. For example, St. John's Wort (*Hypericum perforatum* L.) is widely harvested for its use in treating depression and anxiety (El Hamdaoui et al., 2022), while gum arabic (*Senegalia senegal* (L.) Britton) is extensively used as a food stabiliser, emulsifier, and thickener in beverages, confectionery, pharmaceuticals, and cosmetics (Prasad et al., 2022). Similarly, wild bilberry (*Vaccinium myrtillus* L.) has recently risen as a superfood, celebrated for its high levels of anthocyanins, antioxidants, and essential nutrients (Martău et al., 2023). A significant portion of the medicinal and aromatic plants traded globally come from wild habitats. According to the World Checklist of Useful Plant Species, over 40,000 species have well-documented uses, though the actual number of species in use is likely much higher (Diazgranados et al., 2020). Additionally, the reported global trade in medicinal plants, now estimated at over US$4.2 billion, has seen substantial growth, increasing by 350 % between 1999 and 2023 (United Nations, 2025). As societies seek more "natural" and "green" products (Pankaj et al., 2024), especially in industrialised countries, the demand for wild plants continues to grow worldwide, raising the question of sustainable harvesting.

While several studies have shown that wild plant harvesting can be sustainable, overharvesting remains a major concern in many cases (de Mello et al., 2020; Papageorgiou et al., 2020; Teixidor-Toneu et al., 2023). Overharvesting is one of the main threats to all species' persistence in the world, alongside other anthropogenic pressures (such as habitat destruction due to agriculture and urban development) (IPBES,

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2019; Maxwell et al., 2016). Examples of plants facing overharvesting are abundant, spanning various countries and applications. For instance, the wild populations of Goldenseal (*Hydrastis canadensis* L.) in the United States and Canada have been severely depleted due to high demand for its roots in traditional Chinese medicine and the dietary supplement industry (Leah and Leaman, 2018). Similarly, the populations of wild-harvested yew tree (*Taxus wallichiana* Zucc.) in Pakistan, prized for its taxol-containing bark used in cancer treatment, face threats from overharvesting (Iqbal et al., 2020). In France, the impact of overharvesting on yellow gentian (*Gentiana lutea* L.) is well-documented. The excessive collection of its roots for medicinal and liqueur-making purposes has raised concerns over its long-term persistence (Association Gentiana lutea, 2023). The growing market interest in valorising wild-harvested plants (WHP) for medicine or food has often outpaced the development of appropriate regulations (Dürbeck and Hüttenhofer, 2015). The effects of such unregulated exploitation are considerable on WHP populations, extending beyond just the plants themselves. For instance, the overharvesting of wild frankincense (*Boswellia* spp.) in Ethiopia has not only reduced tree populations but also degraded the surrounding ecosystem. Excessive resin tapping weakens the trees, diminishing their reproductive capacity and threatening the dryland forests they anchor, which are crucial for preventing desertification and supporting biodiversity (Gidey et al., 2020). Industrial harvesting can also disrupt local networks, undermining traditional livelihoods and cultural practices reliant on plants. For example, the large-scale harvesting of the African cherry (*Prunus africana* (Hook.f.) Kalkman) in Africa for pharmaceuticals displaced traditional practices, eroded local knowledge, and reduced plant availability for community use (Rubegeta et al., 2023). Such impacts underline the urgent need for coordinated action involving governments, local communities, industry stakeholders, and conservation organisations to ensure the sustainable use of WHP. Setting measures such as harvesting quotas, habitat protection, and certification schemes could help balance market demands with ecological viability (Schippmann et al., 2002; Xia et al., 2022).

Due to the great diversity of harvested plants, the first step towards sustainable management of these wild resources is to assess our knowledge of their ecology, as it informs on vulnerability to harvesting. Although many ethnobotanical studies have provided valuable insights into wild-plant harvesting practices (e.g. Gomes et al., 2020; Ssenku et al., 2022; León-Lobos et al., 2022), few have jointly examined the ecological and biological characteristics of plant species alongside their conservation status and the sustainability of harvesting practices. Integrating these aspects into a comprehensive study is key for a more complete understanding of plant vulnerability and the development of sustainable harvesting strategies.

Like herbivory, collecting plant parts alters individual fitness, which can have cascading effects on plant populations. However, the impact on population dynamics varies depending on the species' life-history strategies and the nature of the harvesting practices (Ticktin, 2004; de Mello et al., 2020). Wild-plant harvesting includes a wide diversity of practices, and any plant organs might be subject to harvesting (Cunningham, 2001). While harvesting underground parts is usually lethal (see *Gentiana lutea*, for example), aerial material can alter the growth, survival and reproduction capabilities without directly killing the plant (Zhang et al., 2021). In some cases, slow-growing plants may benefit from increased aboveground biomass production when subjected to moderate grazing (McNaughton, 1983). However, they can experience a sharp decline in individual fitness when overgrazed. Collecting aerial parts may have similar effects, but the threshold at which these practices negatively impact fitness depends on the species' biology and the characteristics of the disturbance (Sinasson and Shackleton, 2023). Therefore, establishing general rules regarding plant responses to harvesting can be challenging. Nevertheless, conservationists have benefited from general ecological frameworks such as Grime's life-history strategies (CSR) to understand how plants respond to various disturbance types (Wonkka et al., 2013). For example, a species exhibiting a stress-tolerant (S) strategy typically has slower growth rates and longer lifespans, making it more susceptible to overharvesting since it requires more time to recover and reproduce after disturbance (Grime, 1977). Linking ecological insights to plant harvesting practices helps understand how the choice of harvested plant parts influences sustainability and impacts plant populations (Castle et al., 2014; Ticktin, 2004). This approach enables scientists to pinpoint WHP species at higher risk due to their ecological ~~traits~~ characteristics and adaptive strategies, guiding the development of sustainable harvesting practices.

In many traditional communities, plant harvesting practices are deeply rooted in the local species pool and the relative abundance of specific taxa (León-Lobos et al., 2022; Oluoch et al., 2023). However, industrial exploitation introduces new dynamics, where the distribution of harvested plants influences exploitation patterns. This can lead to spatial shifts in harvesting when resources in one area are depleted, resulting in habitat-mediated carry-over effects, where the depletion of resources in one location affects the availability of resources in another area, influencing future harvesting practices (Van Allen and Rudolf, 2015). It can also lead to illegal large-scale harvesting, as seen with *Aquilaria* species for agarwood (Yin et al., 2016). Such patterns operate at various scales, from local harvesting to transnational trade networks. Therefore, highlighting the biogeographical structure of WHP across a given territory is key to understanding the socio-economic drivers of harvesting practices. Furthermore, identifying WHP diversity hotspots is essential in managing the wild-harvested plant industry, particularly for setting conservation priorities (Velazco et al., 2022). By pinpointing these critical areas, decision-makers can allocate resources more effectively to mitigate pressures on wild-harvested plant populations (Pironon et al., 2024).

Achieving better assessments for sustainable resource management requires a comprehensive framework that integrates harvesting practices, the sector's socio-economic organisation, and plant populations' vulnerability to intensive harvesting pressures. Unfortunately, such a holistic review is currently lacking on a global scale for WHP despite valuable national syntheses in multiple countries worldwide (e.g. León-Lobos et al., 2022; Mateo-Martín et al., 2023). This creates a considerable gap in our knowledge of WHP conservation status, regardless of their ecological, cultural, and economic roles. The limited assessment of WHP status poses significant challenges in identifying priority species for conservation efforts. According to the International Union for Conservation of Nature (IUCN) Medicinal Plant Specialist Group, only 19 % of the 26,000 species with well-documented medicinal uses have undergone a global conservation status assessment (Timoshyna et al., 2020). This figure contrasts sharply with the assessment rates of other species groups, which approach nearly 100 % for birds or around 90 % for mammals (BirdLife International, 2022; Schipper et al., 2008). 11 % of the aromatic and medicinal plants that have been assessed are threatened with extinction in the wild based on IUCN Red List criteria (Timoshyna et al., 2020). The lack of comprehensive assessments likely means that the extent of the impacts of harvesting on these species is underestimated. This highlights the urgent need for more robust conservation assessments to align regulations with the needs of effective management.

While much attention has been given to WHP in tropical regions due to their high biodiversity and long-standing ethnobotanical traditions, temperate regions such as those in the Palearctic, including Europe, also exhibit extensive wild-harvesting practices that warrant further investigation. France is exceptionally well suited for the harvest of wild plants. Indeed, the country is positioned at the confluence of various climates, including Mediterranean, Alpine, oceanic, and continental; the metropolitan territory boasts approximately 7000 taxa, of which at least 10 % are wild-harvested (Lescure et al., 2015). In 2020, France ranked 5th in WHP exports and 3rd in WHP imports in Europe, establishing plant harvesting as a prominent contributor to the economy (FranceAgriMer, 2020). However, the absence of a comprehensive overview of WHP hinders our understanding of wild-plant harvesting in

France. Existing research, often limited to specific regions or individual species, fails to capture the full scope of the plants harvested and the full implications of these practices. While certain emblematic plants receive attention (see, for example, *Arnica montana* L. (Locqueville et al., 2023), *Artemisia umbelliformis* Lam. (Fontaine et al., 2024)), they represent only part of the diverse array of harvested species. Much of this diversity remains hidden, with untapped harvesting potential and unknown impacts. Our study addresses this gap by providing a broad overview of WHP across metropolitan France, including Corsica.

This paper pursues two main objectives. First, we aim to provide a comprehensive assessment of wild harvesting in France, integrating key aspects such as phylogeny, harvesting practices (including the specific plant parts collected and their intended uses), ecology, and conservation status. Second, we investigate whether certain traits and patterns distinguish commercial WHP from the wider flora, to better understand the drivers of commercial harvesting. In this context, we refer to a "harvesting syndrome" as a set of characteristics and characteristics that make wild plants more likely to be targeted by humans. This is analogous to the domestication syndrome and weedy syndrome, which describe characteristics that make plants better suited for cultivation or survival in disturbed environments.

To attain our objectives, we constructed a comprehensive database that includes detailed information on the distribution, rarity, ecology (e.g. Raunkiaer's life-form, Grime strategy), harvested parts, uses, and legislation for known commercial WHP in France. Additionally, we compared these characteristics to those of the entire French flora (including non-harvested plants) to provide a general ecological and biological context. The results of this analysis form the basis for discussing the conservation challenges linked to exploiting wild resources and proposing guidelines for their sustainable use.

We structured our work around five key research themes. Firstly, we focused on the taxonomic and phylogenetic diversity of commercial WHP in metropolitan France, identifying the core plant families most subject to harvesting. This aimed to highlight taxa that may be particularly vulnerable or economically and culturally important. Secondly, we analysed the uses of commercial WHP, defining the most common applications, their relationship to phylogenetic families, and the plant parts collected. Thirdly, we mapped the distribution of commercial WHP across France to identify diversity hotspots and inform better management strategies. Fourthly, we examined the life-history strategies of these WHP to evaluate harvesting risks linked to species' intrinsic vulnerabilities. Lastly, we assessed the conservation status of commercial WHP, evaluating the proportion reviewed by the IUCN and pointing out conservation gaps by comparing Red List statuses with existing protections and regulations in France.

This study focuses exclusively on commercial wild harvesting due to the limited availability of reliable data on non-commercial gathering. Commercial harvesting also tends to involve larger volumes and poses greater conservation risks. Ganie et al. (2019) noted that while overharvesting for local use often has a small, low-impact scope, illicit trade and large-scale overharvesting have a large scope and high severity. Moreover, species of high commercial value often have a long history of local use, meaning commercial pressures are layered upon existing non-commercial practices (Marouf et al., 2015; Makunga et al., 2008). In France, non-commercial harvesting for personal use is generally local and occasional, with limited large-scale impact, though exceptions exist, such as for wild garlic (*Allium ursinum* L.). We believe that commercially harvested species provide a robust proxy for assessing national sustainability concerns. These species are better documented and more frequently targeted for harvesting. Therefore, studying commercial harvesting allows us to identify species most at risk, representing a "worst-case scenario" of anthropogenic pressures on WHP.

2. Material and methods

2.1. Study area and species

The study area covers metropolitan France and Corsica, totalling 543,940 km^2, and 96 administrative units known as "departments" (i.e. counties) (Appendix A). French plant-harvesting regulations operate at three levels: national, regional, and 'departmental'. National and regional levels define protected species lists, prohibiting their harvest, while departmental regulations set specific quotas and bans tailored to the local context, making departments key units for wild-plant management. From an ecological standpoint, the department scale (median size: 6038 km^2 and mean: 6156 km^2) is also interesting. They are large enough to represent diverse ecosystems and species groups while still small enough to capture local variations in climate and species composition, making them suitable for targeted management. Thus, our analysis aligns with these administrative boundaries. The departments of the Paris region were merged as they are very small (median size 745 km^2 and mean: 1501 km^2) and mostly urban.

The plants we studied come from the list of commercially harvested plants from Lescure et al. (2015), which we limited to vascular plants only (excluding algae, fungi, and lichens for simplicity). While we acknowledge that some subspecies may have ecological or ethnobotanical relevance, our analysis was conducted at the species level to match the resolution of available distribution, use and trait data. After excluding subspecies, this resulted in 692 species: 661 angiosperms, 17 gymnosperms, and 14 ferns (Appendix B). Among these species, 627 are native or likely native, 62 are non-native, and 3 have an uncertain status (Appendix B). This list may not fully reflect recent harvesting trends due to the dynamic nature of plant use and trade. However, it remains the most comprehensive resource available, integrating data from nine nationwide databases.

To ensure consistency across datasets, all species names were standardised using their corresponding identifiers in TaxRef v17, the national taxonomic reference for French biodiversity (Gargominy, 2024). This was applied across all data sources, including uses, distribution, and phylogeny.

2.2. Phylogeny

To study the taxonomic and phylogenetic diversity of commercial WHP, we extracted the list of French vascular flora (~6000 species) from the 2018 French Red List (UICN France et al., 2022). We built a phylogenetic backbone (*V.PhyloMaker2* R package (Jin and Qian, 2022)), based on the default backbone (GBOTB.extended.TPL). From this, we generated a phylogenetic tree covering all French vascular plant families. For each of the 110 families, we calculated the total species count and the percentage of WHP species. The tree was plotted with package *ggtree* in R (R Core Team, 2021; Yu et al., 2017).

To assess the phylogenetic signal for the "harvested" trait, we calculated the D-statistic (Fritz and Purvis, 2010), where $D = 1$ indicates no phylogenetic signal and $D = 0$ indicates a signal consistent with Brownian motion (*caper* R package (Orme et al., 2013)). The significance of D was assessed by permutation tests. We repeated this approach to assess the phylogenetic signal for different uses of WHP.

2.3. Harvested uses and parts

To identify patterns in plant resource utilisation across families, we associated each species with its documented uses. We extracted data from the PFAF website (Plants For A Future, pfaf.org) ("PFAF," 2024) and associated it with Kew's World Checklist of Useful Plant Species (Diazgranados et al., 2020). We also used a 1999 synthesis detailing the uses of WHP plants in the area covered by the Mediterranean Botanical Conservatory area (Chaber and Lieutaghi, unpublished), and unpublished data from the National Botanical Conservatories (CBN, unpublished). We grouped plant uses into five categories: medical/therapeutic, food and beverages, crafts, ornamental plants and cosmetics. Twenty-six species were not associated with any use. Based on the data collected on WHP uses, we studied the potential uses of the 110 families containing wild-harvested plants (Appendices C and D). However, for simplicity, we presented results for the most over-represented families (those containing more harvested species than expected). To identify these families, we conducted a Chi-squared analysis in R, focusing on families with more than 5 species to reduce the impact of small counts. We then selected the families that had significatively more harvested species than expected (standardised residuals >2) and more than 10 harvested species (Appendix E). This process resulted in the selection of 6 families, for which we plotted the percentage of WHP within them and the proportion of species across the three main use categories: medicinal, food, and crafts. The proportion of each use category was calculated as the number of species associated with each use relative to the total species count, noting that a species can have multiple uses.

To document harvested plant parts, we gathered all available data for our study area, including both specific studies and larger-scale databases (Appendices F and G). First, we extracted information from PFAF. We crossed this information with the SICARAPPAM's 2024 selling lists (France's largest WHP cooperative, https://www.sicarappam.com). We also included plant lists from a 2020 report on wild harvesting in the Ardèche department (Muraz and PNR Monts d'Ardèche, 2018). We standardised harvested parts into categories: whole plant, aerial part, underground part, leaves, flowers, fruit, buds, sap, bark, seeds, and shoots. We calculated the proportion of each harvested plant part by dividing the number of species associated with that part by the total number of species. This constitutes the most complete and comprehensive list we could produce for the whole of France.

It must be noted that while the databases used in this section provide insight into potential and documented uses and practices, they do not indicate how widespread these are or where they occur, which should be considered when interpreting the data. All links to the data used for the analysis can be found in the "Data Availability" file.

2.4. Biogeography

To study the biogeography of commercial WHP, we used presence data from two main sources: the OpenObs platform for French vascular flora and the Global Biodiversity Information Facility ("GBIF," 2024). We selected records with a minimum precision of 10 km and from the year 2000 onwards. Through OpenObs, we extracted expert-validated data from French National Botanical Conservatories (CBN, ~18.7 million records), the French National Forestry Office (ONF, ~3.3 thousand records), the French National Geography Institute (IGN, ~2.2 million records), and the French Conservatories of Natural Areas (CEN, ~65 thousand records). We supplemented this with data from GBIF. Data was retrieved using the *rgbif* R package (Chamberlain et al., 2024) excluding records with geospatial inconsistencies (e.g. invalid coordinates, out-of-range coordinates). Given the known issues with the precision and validity of some GBIF records, we further cleaned the GBIF dataset with the *CoordinateCleaner* R package (Zizka et al., 2019) to remove problematic records, running tests for "capitals," "centroids," "equal," "institutions," "outliers," "urban," "seas," and "zeros." This removed 6.7 million of the 28.7 million available records.

Next, we merged the OpenObs and GBIF datasets, amounting to a total of ~43 million records. Using a 20 km by 20 km celled grid (Appendix H), we thinned the data to keep a single observation per species per grid cell (*dismo* R package (Hijmans et al., 2017)), resulting in ~1.9 million records (Appendix I).

We associated each record with its corresponding department to quantify WHP species count, total species count, and total number of records per department. To calculate a proxy of species distribution in each department, we divided the area of cells with records by the department's total area (*exactextractr* R package (Baston, 2023)).

To analyse the biogeographical patterns of WHP, we constructed a hierarchical clustering tree of the departments based on their species composition and distribution. We used Ward's method (*stats* R package (R Core Team, 2021)) on a chi-squared distance matrix calculated from the species abundance data described above (*vegan* R package (Oksanen et al., 2024)).

2.5. Plant biology

To get an overview of commercial WHP survival strategies and adaptations, Raunkiaer's plant life forms were assigned to each WHP species (Raunkiaer, 1934) (Appendix J). Raunkiaer's life forms classify plants into six distinct classes based on the position of their perennating buds relative to the soil surface, reflecting their adaptation to environmental conditions. We used data from the BaseFlor (Julve, 1998), and cross-checked with the Flore de la France méditerranéenne continentale (Tison and de Foucault, 2014) (Appendix K). We calculated the proportion of each life form among WHP species.

To gain insights into WHP responses to stress and disturbance, we computed the Grime CSR (Grime, 1977) strategy for each species, using the StrateFy method developed by Pierce et al. (2016) (Appendices K, L and M). The CSR strategies categorise plant species based on their competitive abilities in ecosystems. This helps to understand how plants respond to pressures and thrive in different ecological settings based on their competitive abilities, stress tolerance, and adaptability to changing environmental conditions. StrateFy provides a score for each of the three CSR strategies: Competitors (C), Stress-tolerators (S), and Ruderals (R). Data was available for 583 of 692 WHP species (84 %). We visualised the distribution of CSR strategies by plotting Grime's triangle (*ggtern* R package (Hamilton, 2024)), a ternary plot that represents the relative dominance of these three primary ecological strategies.

We also calculated life form proportions and plotted Grime's CSR triangle for the entire French vascular flora to identify any unique WHP traits or patterns. Data were available for 178 of 189 plant families (94 %).

2.6. Protections and regulations

To detect potential conservation issues among commercial WHP, we compared WHP species' protection levels and regulations with their national IUCN status. We removed all non-native species from the list then extracted each species' national Red List status, protections (national and regional), and departmental regulations/prefectural decrees from the French National Inventory of Natural Heritage (INPN) "Statuts" database.

We then plotted the number and percentage of WHP species in each IUCN category across protection and regulation levels (national, regional, departmental, and unprotected). A species can be protected in multiple areas at the departmental and regional levels. However, our analysis focused on whether a species is protected or its harvesting is regulated at these levels without considering the number of areas in which it is protected. We compared the results of WHP to those of the entire vascular flora, which enabled us to identify differences in conservation status, regulatory coverage, and protection levels. We performed a Chi-square test to assess whether there were significant differences in the conservation status distribution between harvested and non-harvested species. The standardised residuals (Std Res) from the test were used to identify which categories of conservation status deviated significantly from expected values.

2.7. Data and code availability

*All links to the data used for the analysis can be found in the "Data Availability" file. All analyses were performed with R version 4.4.2 (2024-10-31) (*R Core Team, 2021*). The code used for the analysis can be found at* https://github.com/chloemouillac/Harvesting_syndrome.

3. Results

3.1. Commercial WHP species are scattered across the entire the phylogeny of French vascular plants

WHP can be found in a wide array of taxonomic families. The 692 harvested species (i.e. 12 % of all French vascular plant species) are distributed among 110 vascular plant families, i.e. 60 % of all French vascular plant families, and 431 genera, i.e. 33 % of all French vascular plant genera. The 6 most over-represented families are Lamiaceae, Ranunculaceae, Caprifoliaceae, Ericaceae, Violaceae, and Pinaceae (Fig. 1). Among these families, several largely exceed the average 12 % WHP found in the total flora. Pinaceae, Ericaceae and Lamiaceae have the highest percentages of WHP species (46 %, 34 % and 31 % of total species in each family, respectively) (Fig. 2.a). Asteraceae, though containing the most harvested species among WHP families (99), was not included because these represent only 9 % of the family's total diversity.

At first glance, most WHP species seem to be concentrated in the Lamiids and Campanulids clades. Notably, the Lamiaceae family stands out because it includes many harvested species (53), and a higher percentage (31 %) of its total species are harvested compared to other families. However, phylogenetic analysis reveals a weak signal ($D = 0.78$; $P_{rand} < 0.001$, Appendix N). This indicates that families more frequently harvested than expected by chance tend to cluster within the phylogeny, although not as strongly as would be expected under a Brownian evolution model.

3.2. Commercial WHP families show diverse uses, with medical applications as the primary focus

The phylogenetic signal analyses for different use categories (e.g. medicinal, food, crafts, ornamental, cosmetics) show weak signals, with D values ranging from 0.76 to 0.81 ($P_{rand} < 0.001$, Appendix N). This suggests that plant uses are influenced by evolutionary lineage, but similar uses can arise across more distantly related species too. Commercial WHP can be used for mainly medicinal (37 % of WHP species), food/beverages (20 %) and craft (14 %) purposes (Fig. 2.b). However, many uses are grouped under the "other" category (30 % of WHP species, Appendix F), suggesting a diversity of additional, less common uses that may not fit neatly into the predefined categories. Nearly all (99 %) of the 207 WHP species from the 6 selected families are reported to have potential medicinal applications, and 94 % of all WHP have medicinal applications. Violaceae has the highest proportion of species associated with medicinal (56 % of WHP species) and food uses (28 %). Ranunculaceae and Caprifoliaceae follow in medicinal use (47 % and 44 % of WHP species, respectively) but have limited food-related applications, while Lamiaceae rank high in food use (28 % and 24 % of WHP species, respectively). Pinaceae shows the highest potential use in crafting (25 % of WHP species).

We found that the plant use data was fairly well-distributed across multiple databases, with three main use categories (i.e. medical, food, and crafts) frequently cited across several sources (Appendix G). Notably, no single database documented an entire use category. For medicinal uses, around 80 % overlap between two or more databases, primarily Kew, and Chaber and Lieutaghi. The latter specifically records actual medicinal uses in France dating back to 1999. This multi-source convergence suggests that, while the data is not flawless, this initial compilation of sources offers a reliable overview of the uses of commercial WHP in France.

Leaf harvesting is most common (in 64 % of species), followed by

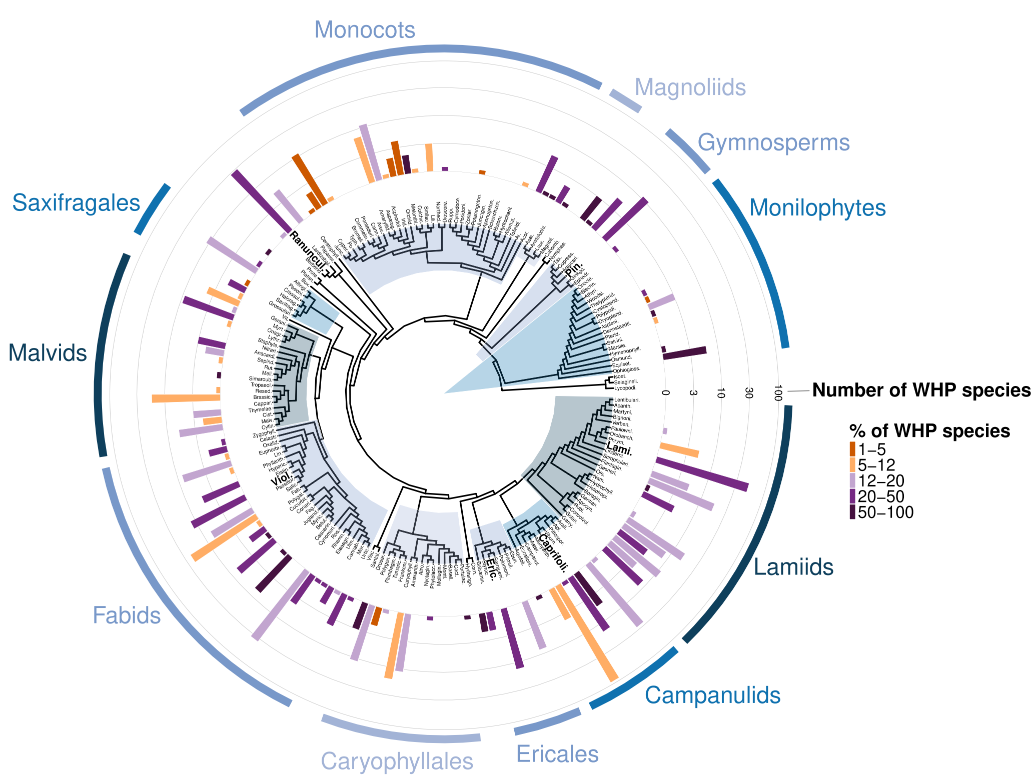

Fig. 1. Phylogenetic distribution of commercial WHP species in metropolitan France's vascular flora.
The height of the bars indicates the number of WHP species among each family in the phylogeny. The colour represents the percentage of WHP species (12 % is the average number of WHP species). The 6 families with significatively more WHP species than expected (and containing more than 10 species) are indicated in bold.

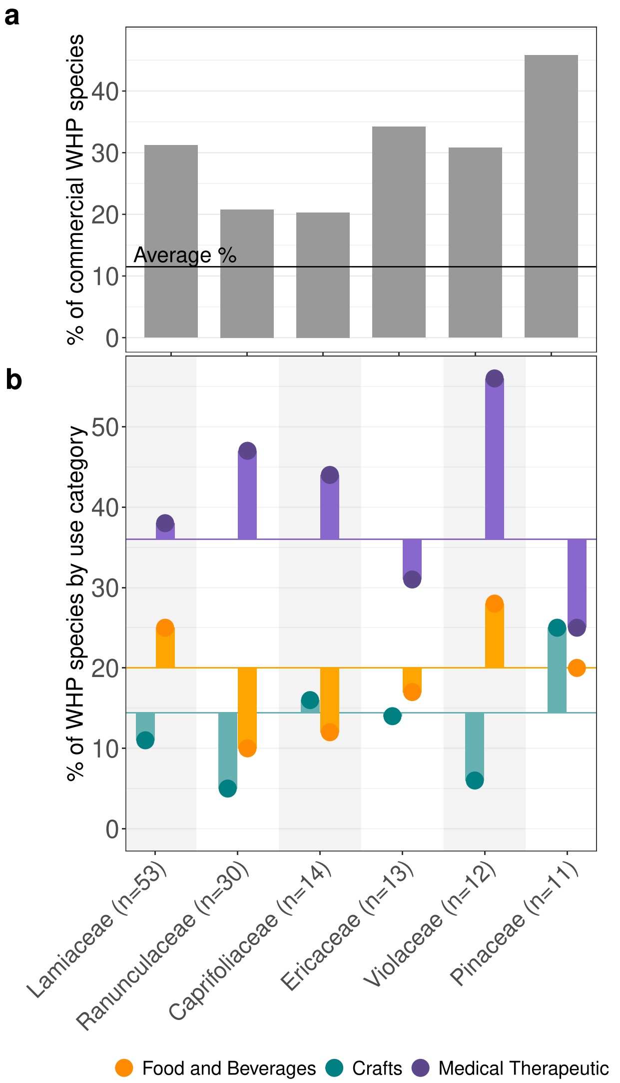

Fig. 2. End-uses of 6 of the most harvested plant families within the French vascular flora.
We selected the 6 families with significatively more harvested species than expected (and over 10 species). They are ordered from the highest to lowest number of WHP species.
a) Percentage of species from each family listed as commercial WHP. The horizontal line indicates the average percentage of WHP species across all 183 families in the French vascular flora.
b) Percentage of WHP species in each family's three main use categories, i.e., food and beverages in orange, crafts in green, and medical and therapeutic in purple. The horizontal lines represent the average percentage of WHP species in each use category for the French vascular flora. The differences from these averages are represented by the vertical bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

whole plants (36 %), underground parts (36 %), flowers (35 %), and aboveground parts (34 %) (Appendix O). Destructive harvesting (whole plant and underground parts) can occur in 60 % of species. Sap is the less commonly harvested part (4 %). Most plant parts are harvested across various use categories, with no single part exclusively used for one purpose (Appendix P).

3.3. Commercial WHP exhibit wide distribution and align with France's biodiversity patterns

Commercial WHP species are found (and potentially harvested) throughout France, with notable differences in diversity between regions. This spatial pattern of diversity aligns with the overall distribution of plant diversity across the country (Fig. 3.a and 3.b). In both WHP and total flora, the Alps exhibit the highest diversity, with rich communities throughout southern France. The Aude département stands out, hosting 595 WHP species, followed by the Alpes-Maritimes with 594 species and the Drôme with 590 species.

Although WHP and total flora share similar spatial patterns, WHP species are more evenly distributed (Fig. 3.a and 3.b). The smaller variation in WHP species numbers between high and low-diversity areas indicates they are generally widespread and common. This observation is further supported by Fig. 3.c, which shows that nearly one-third (28 %) of WHP species are present in all departments (compared to 2 % for total flora), and half occur in 96 % of the departments (compared to 9 % for total flora).

In spite of this wide distribution, WHP species form clear groupings of species with similar biogeographical characteristics (Fig. 3.d). These groups include low to medium mountainous areas (Pyrenees, Massif Central, Vosges and Jura) (1), higher mountainous areas like the Alps (3), the Paris basin (2), Corsica (4) and the Mediterranean region (5). Additional groupings are identified in the Atlantic region, in the Southern part of France (6) and the Northeastern coast (including Brittany and Armorican Massif) (7).

3.4. CSR strategies and life forms of commercial WHP mirror French vascular flora

The distribution of Raunkiaer's life forms among commercial WHP species mirrors that of the entire French flora, with nearly half as hemicryptophytes (46 % of WHP species/46 % of total flora), followed by phanerophytes (17 %/17 %), therophytes (16 %/16 %), geophytes (12 %/12 %, chamaephytes (7 %/7 %), hydrophytes (1 %/1 %), and helophytes (<1 %/<1 %) (Appendix J).

Similarly, WHP species and total flora display almost identical distributions within the Grime triangle with a high density of species in the stress-tolerant (S, 25 % of WHP species/26 % of total flora), ruderal (R, 20 %/23 %), and competitive (CR, 19 %/12 %) areas (Fig. 4, Appendix K). Furthermore, the entire surface of the WHP triangle is covered, highlighting a broad range of ecological strategies.

3.5. Commercial WHP species have lower threat levels than the total French flora

The following results exclude non-native taxa (see Methods). According to the IUCN, 93 % 99.7 % of commercial WHP species have been assessed, compared to 98.2 % of France's total flora. Of the WHP species, 96 % are classified as Least Concern (LC), while around 1.7 % (11 species) are "Threatened" (VU or higher) (Fig. 5). For comparison, 78 % of French vascular flora is considered LC, with 7.6 % (353 species) classified as "Threatened" (VU or above). The standardised residuals from the Chi-square test indicate that harvested species are significantly underrepresented in the "Threatened" categories (Std Resid = −5.14), and overrepresented in the LC and NT categories (Std Resid = +3.50), suggesting that they are at lower risk than the overall French flora. Harvested species are also better evaluated by the IUCN (Std Resid = +2.14).

Approximately 70 % of commercial WHP and total flora species are under no protection or regulation. Among these, one WHP species is classified as "Threatened": *Delphinium montanum* DC., indicating a small conservation gap. Additionally, 10 harvested species from our list are nationally protected and prohibited to harvest. These species include *Drosera rotundifolia* L., *Gratiola officinalis* L., and *Paeonia officinalis* L. (Appendix Q).

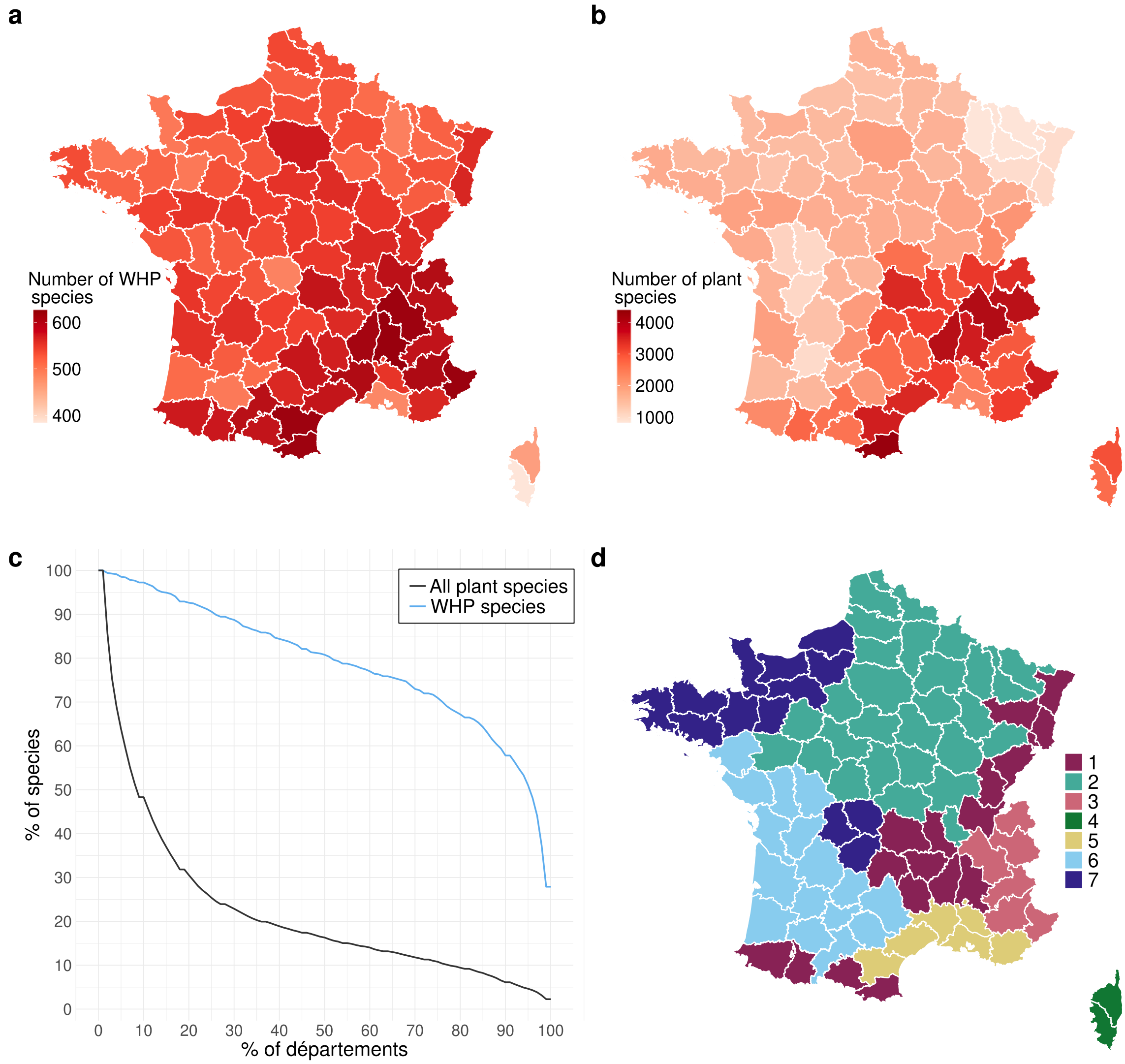

Fig. 3. The distribution of WHP species in metropolitan France and Corsica.
a) Total number of potentially harvested wild species in each French department, based on occurrence data from OpenObs and GBIF. Darker shades of red indicate a higher number of species.
b) Total number of vascular plant species observed in France, based on occurrence data from OpenObs and GBIF. Darker shades of red indicate a higher number of species.
c) Reverse cumulative distribution: the y-axis represents the percentage of species in at least the corresponding percentage of French departments shown on the x-axis.
d) Grouping of metropolitan France's departments into seven clusters based on the similarity of WHP species. Hierarchical clustering was done using the Ward method and chi-squared distance. Each colour represents one of seven clusters of departments sharing similar assemblages of WHP species, based on occurrence data. See Appendix I for the number of records per department. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Managing wild resources is increasingly important in modern society to balance human benefits with biodiversity protection through the sustainable use of species. Achieving this goal begins with assessing current usages and their associated impacts on wild populations. This is especially critical for plants, as knowledge of their use remains sparse. Our study offers the first comprehensive national-level assessment of commercial WHP in France using an integrative framework that combines ecological, phylogenetic, biogeographical, ethnobotanical, and conservation data. This multidimensional approach allows us to uncover patterns and risks that would be overlooked by narrower studies, providing a flexible framework that can be adapted across spatial scales and applied to other contexts internationally. Our results show that commercial WHP species in France cover most taxonomic diversity, encompassing ~60 % of all plant families. WHP can have varied uses, primarily medicinal, and multiple plant parts are harvested across uses without single-part exclusivity. WHP species are generally widespread common species that align with France's known biogeographical areas. Despite limited formal protection, French WHP species face lower conservation risk than non-harvested flora, with better IUCN assessment coverage. Through this section, we discuss the drivers of plant harvesting in France in light of our findings. We then discuss the potential impacts of harvesting on plant populations and conclude with concerns and recommendations for resource management at the national level.

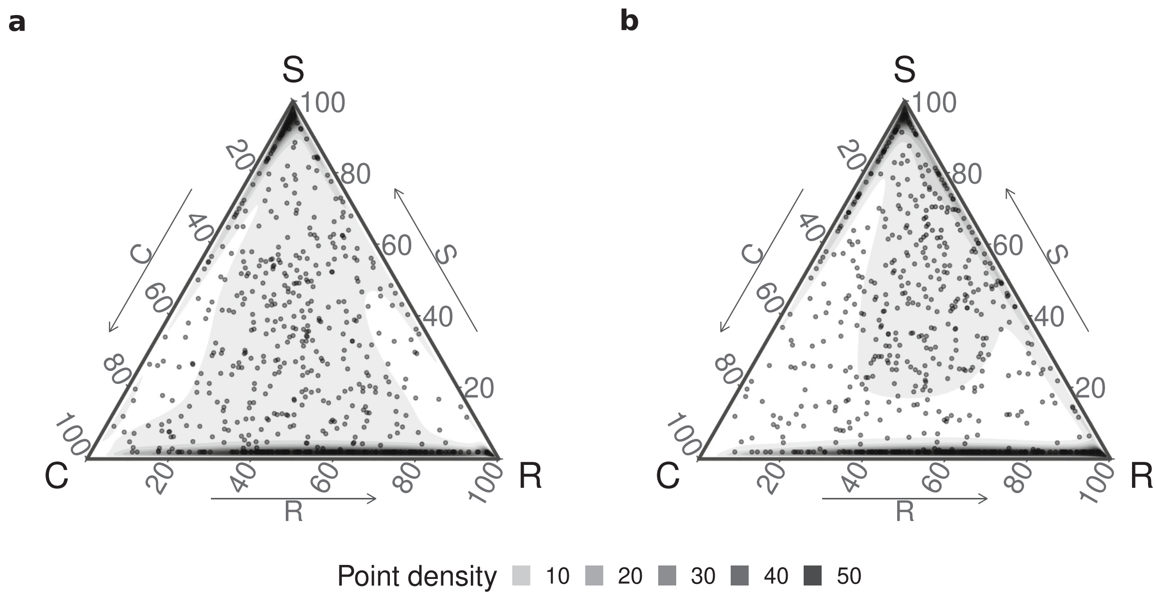

Fig. 4. Visualisation of the distribution of WHP species in the Grime ecological strategy triangle for.
a) French WHP species vs b) all French vascular flora.
C, S, and R correspond to Grime's primary strategies: C - Competitor, S - Stress-tolerant, R - Ruderal.
"Point density" indicates the relative concentration of species in the ternary space; each point represents one species, and darker areas correspond to regions of higher species density.

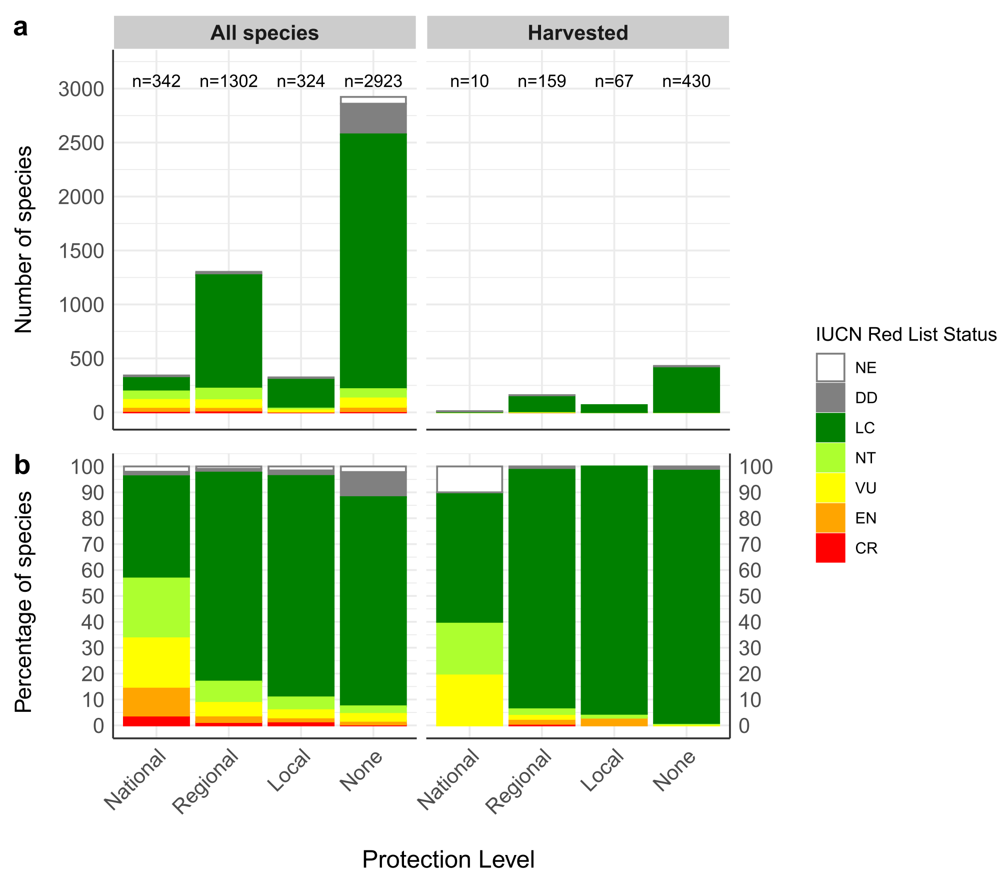

Fig. 5. IUCN status for each protection level in France (all species VS harvested species).
a) Number and b) percentage of species within each IUCN status for each protection level.

4.1. Is there a 'harvesting syndrome' in the French flora?

Understanding the drivers behind plant harvesting can help us determine whether there is a 'harvesting syndrome', i.e. a combination of evolutionary, ecological and biological ~~traits~~ characteristics that would make them particularly susceptible to being harvested.

Ethnobotanical studies reveal that certain families are more frequently harvested than others. In Europe, commonly harvested families include Asteraceae, and Lamiaceae (Licata et al., 2016; Mateo-Martín et al., 2023; Papageorgiou et al., 2020). Fabaceae is often prominent in Africa and Southern America (León-Lobos et al., 2022; Ssenku et al., 2022; Van Wyk, 2020). This pattern suggests WHP may possess evolutionary characteristics that make them particularly amenable to harvesting. Commercial WHP species in France exhibit a remarkable phylogenetic diversity, encompassing 110 families and 431 genera, suggesting varied ecological niches and life strategies. Globally, the literature highlights a similarly vast diversity, with the World Checklist of Useful Plants cataloguing over 40,000 species distributed among 433 families and 6737 genera (Diazgranados et al., 2020). Our analysis reveals a weak phylogenetic signal among WHP, indicating that a plant's evolutionary history influences its likelihood of being harvested, though not strongly. This aligns with other studies done on medicinal plants and supports the non-random hypothesis which suggests that plant selection for medicinal use exhibits taxonomic selectivity due to shared chemical compounds in certain plant families (Gaoue et al., 2021). Nonetheless, the weak signal underscores the role of diverse factors beyond phylogeny in shaping wild-harvesting patterns.

The ecology of WHP species could be one such factor. Harvesters place emphasis on promoting sustainable practices (Papageorgiou et al., 2020; Teixidor-Toneu et al., 2023; Zhao et al., 2023). As a result, a harvesting syndrome may favour species with ecological characteristics that promote resilience to wild harvesting. Fast growth rates generally enhance a plant's capacity to sustain harvesting pressures (Diaz et al., 2004; Ticktin, 2004). In contrast, slower regenerating plants like trees can be more vulnerable to overharvesting, as seen in *Taxus*, *Boswellia*, and *Aquilaria* species (Gidey et al., 2020; Iqbal et al., 2020; Yin et al., 2016). However, our results show that Raunkiaer's life forms and CSR strategies are similarly distributed within WHP species and the total flora. This suggests no clear ecological syndromes based on these broad traits and characteristics, and that resilience to harvesting may not be a primary determinant of WHP selection. However, key correlations (e.g., clonality, growth rate, or specific chemical compounds) may be obscured by the coarse trait resolution and lack of harvesting-intensity data.

Another factor influencing WHP selection is availability, as demonstrated in multiple ethnobotanical studies from Africa (Oluoch et al., 2023), Europe (Papageorgiou et al., 2020), and South America (Gomes et al., 2020). These findings support Phillips and Gentry's apparency theory, which posits that species with wide distributions or greater visibility are more likely to be harvested due to their accessibility (Phillips and Gentry, 1993). We found that commercial WHP species in France are generally widespread and common, with the diversity patterns of WHP matching those of the total flora. WHP harvesting in France aligns closely with the classical biogeographical structure of French flora, such as depicted in the GRECO ecological regions or recent bioregional analysis' (IGN, 2024; Lenormand et al., 2025). Our results indicate no distinct geographic syndrome where certain local floras are preferentially harvested over others. Instead, local plant diversity appears to consistently drive human use, aligning with results on a global scale (Pironon et al., 2024), and suggesting that spatial availability may indeed play a noteworthy role in their selection. Consequently, regions with high plant biodiversity, such as mountains and the Mediterranean belt, serve as key reservoirs of harvested resources.

4.2. Commercial harvesting practices and ecological impacts

In France, commercial WHP can serve various purposes, with medicinal applications being potentially the most dominant, followed by food and craft uses. The dominance of medicinal uses aligns with global patterns reported in the World Checklist of Useful Plant Species (Diazgranados et al., 2020). However, while the checklist indicates that material uses often exceed food uses worldwide, our findings suggest the opposite trend in France. Industrialised countries like France depend less on WHP for everyday materials due to industrial substitutes, while wild plants remain vital for food and medicine, supporting nutrition, tradition, and natural health practices. Global studies often concentrate on medicinal use within specific plant families such as Asteraceae, Fabaceae and Lamiaceae (Cahyaningsih et al., 2021; León-Lobos et al., 2022; Ssenku et al., 2022). In France, Lamiaceae is one of the main harvested families, with applications mainly in medicine and food. However, French medicinal plants appear to be distributed across a broader range of families. For example, Ranunculaceae and Violaceae, which have a high potential for medical use in France, are underrepresented in global reviews of medicinal plants despite their documented uses. Ranunculaceae species, known for their toxic compounds, offer high medical potential but limit their suitability as food sources (Goo, 2022). The possibly important use of Ranunculaceae in France raises the question of whether it is a local pattern or reflects a general bias in global reviews, potentially leading to gaps in conservation priorities and the undervaluation of important species. The data used in this study relies heavily on global databases, which provide potential uses and do not fully capture all local uses of WHP. Due to the limited coverage of French-specific databases, 26 species recorded as commercially harvested by Lescure et al. (2015) lack documented uses in our compilation. This highlights the need for improved data coverage of WHP in France. Additionally, this study primarily captures potential uses of WHP, rather than direct measurements of harvesting intensity or trade volumes. As such, they may not accurately reflect current practices or account for shifts in use over time. For example, growing demand for cosmetics and superfoods has increased pressure on species like *Euphorbia spinosa* L., which is absent from Lescure et al. (2015) but faces known harvesting pressures in southern France due to its use in the cosmetics and perfume industry. This species is referenced in a Corsican prefectural decree (Arrêté n° 2009-166-1 du 15 juin 2009) that restricts harvesting amounts. Moreover, while species listed in Lescure et al. (2015) are known to be used, some are harvested only occasionally or in small quantities, whereas others undergo more regular exploitation.

Harvesting impacts plant populations differently, depending on the part removed and its role in survival. Root harvesting disrupts nutrient uptake and growth, often compromising survival, while leaf or flower harvesting may allow quicker recovery and lower ecological impact (Teixidor-Toneu et al., 2023; Zhao et al., 2023). Furthermore, studies on herbivory suggest that plants may experience compensatory growth, resulting in increased yield after the removal of aboveground biomass (McNaughton, 1983). As such, we expect that most harvested plants are collected for their leaves, while root harvesting is likely uncommon overall and primarily targets widespread, common species. Our results confirm that leaves are the most harvested plant part in France (64 % of WHP species). Though we lack data on actual harvesting intensity and spatial variation in collection pressure, destructive methods can occur in 60 % of species, highlighting that destructive harvesting may not be uncommon. These results are supported by other studies: globally, the proportion of harvested plant parts varies by region, but leaves are commonly used across multiple areas (León-Lobos et al., 2022; Licata et al., 2016; Ssenku et al., 2022), as are roots (Cahyaningsih et al., 2021; León-Lobos et al., 2022; Ssenku et al., 2022). Many studies warn of destructive harvesting risks (e.g. Castle et al., 2014; Leah and Leaman, 2018), driving research into alternative plant parts for valuable compounds, especially in medicine, to reduce impact. Cultivation is also often promoted to reduce harvesting pressure, but evidence shows it may not be a straightforward solution. Barriers like land ownership mean cultivators are often different from wild harvesters (Williams et al., 2014). And cultivation may add to rather than replace wild harvesting if planting material is collected from wild populations. For these reasons, and given the lack of consistent evidence on its effectiveness in reducing pressure on wild populations, we did not include cultivation as a focus in our study. Finally, predicting the impacts of harvesting is also complicated by regional and temporal variations in practice, ranging from local food production to international pharmaceutical industries, which often involve very different volumes of harvested plants (Ticktin, 2004). Another challenge for predicting the impacts of harvesting is the influence of market trends on unregulated WHP resources, where sudden spikes in consumer demand can drive overexploitation, often outpacing regulatory responses (e.g. *Rhodiola rosea* L. harvested in the Alps and Pyrenees, which faces rising demand for anti-aging creams). Many WHP exist in a regulatory grey area, with uncertain availability, harvesting intensity, and ecological impacts. This makes it difficult to anticipate and mitigate overexploitation.

Plant responses to harvesting also vary by life form and ecological strategy. Hemicryptophytes recover efficiently due to their protected growth points, while therophytes focus on rapid reproduction and phanerophytes (trees and shrubs) recover more slowly due to structural complexity (Diaz et al., 2004; Ticktin, 2004). Our results indicate that hemicryptophytes make up the largest proportion of WHP and total flora, constituting nearly a majority of species. This suggests that the French flora may have certain characteristics that allow it to better cope with harvesting pressures, though these ~~traits~~ do not guarantee resilience.

4.3. Conservation implications and the need for localised management strategies

Inconsistencies between harvesting regulations and practices that we observed in our analysis raise serious questions about the effectiveness and enforcement of regulatory frameworks. For example, 10 species in our study were classified as nationally protected, making them off-limits for harvest, transport, sale, or possession. However, their presence on our list of harvested species indicates that they continue to be commercially exploited despite legal bans. This may be partly explained by limited awareness of multi-level regulations and, more critically, by weak enforcement. Information on national, regional, and departmental bans are defined separately and can be difficult to access or interpret, which likely hinders compliance. In France, regional-level protections can also create challenges for enforcement: a species may be harvested legally in one region but cannot be transported or sold in another where it is protected.

The IUCN Red List offers a valuable global perspective on species conservation, and our findings suggest that many commercial WHP species are relatively resilient at the national scale, with only 11 species (1.7 %) classified as threatened. This figure is notably lower than those reported in other studies. For instance, a 2023 study in Spain found 8 % of medicinal plants were threatened (Mateo-Martín et al., 2023), while a 2020 global assessment revealed 11 % of medicinal plants as threatened (among 19 % assessed) (Timoshyna et al., 2020), and a 2022 survey in China identified 58 % as threatened (Zhangjian et al., 2022). These studies include both commercial and non-commercial species, whereas our analysis focuses specifically on commercially harvested WHP. Although there likely is a substantial overlap between the two groups, non-commercial species may be exposed to different pressures, and direct comparisons should be made with caution. Nevertheless, our results indicate that commercial WHP in France are less threatened than the total French flora and may also be less at risk than the worldwide WHP flora. However, this should not be interpreted as a lack of need for conservation efforts. Nation-wide IUCN evaluations do not capture the localised pressures WHP may face (Possingham et al., 2002). As a result, even species listed as "Least Concern" nationally may face local challenges, including habitat degradation and overharvesting. Therefore, conservation attention remains necessary to protect these species and their contributions to local communities and ecosystems. Species may show latent vulnerability, with rapid declines possible if pressures rise or conservation stops. For example, *Arnica montana* L. has declined locally in the Vosges due to overharvesting and habitat change and climate change. Stakeholders have introduced regulated harvesting and habitat management (mowing, grazing) to support population resilience. This underscores the need for continued conservation and management efforts, even when populations seem stable. Furthermore, many non-threatened species play essential roles in biodiversity maintenance, such as pollination and soil health (Balvanera et al., 2014), or hold significant cultural value in traditional practices (Van Wyk, 2020; Zhao et al., 2023). As such, conservation efforts should go beyond large scale IUCN classifications to ensure that even non-threatened species are adequately protected at local scales to maintain their ecological and cultural roles.

4.4. Conclusions and perspectives

This study represents a novel contribution to both national and international research on WHP. Unlike most previous work conducted in France, which has tended to focus on individual species, our approach provides a broader perspective across a diverse range of commercially harvested taxa. Internationally, few studies have examined the entire WHP flora of a country through an integrated lens that combines phylogenetic structure, plant uses and practices, ecological characteristics, and conservation. This approach reveals the richness and importance of an often-overlooked group of species, many of which play a significant role in daily life, and brings to light pressing conservation concerns that are likely to be shared beyond the French context.

We found that harvesters tend to favour the most available plants and that WHP are more phylogenetically clustered than expected by chance, supporting the concept of a harvesting syndrome. Since closely related species may share similar characteristics, this can influence WHP selection. Future research should integrate trait-specific data, such as chemical composition and secondary metabolites, to better understand the mechanisms driving selection. Examining chemical profiles could reveal links to taste, toxicity, nutritional value, or medicinal properties (Chikezie et al., 2015), potentially strengthening observed phylogenetic patterns. Additionally, WHP selection is likely influenced by various other factors such as cultural significance or local knowledge (Gomes et al., 2020; Oluoch et al., 2023), which may differ depending on plant use. While most studies focus on medicinal plants, food plants may be chosen based on entirely different criteria. For food plants, factors such as accessibility, seasonal availability, taste, and nutritional value may play a more important role. In contrast, the selection of medicinal plants could be driven more by their therapeutic properties, perceived efficacy, and roles in traditional healing practices. Investigating these socio-economic and cultural drivers would provide a more comprehensive understanding of WHP selection. Although this study concentrated on commercial harvesting, similar patterns are likely to occur in non-commercial contexts. Yet, comparative studies across these groups would be necessary to help determine whether the characteristics identified here apply broadly, offering a fuller understanding of wild plant selection.

From a conservation perspective, a striking finding is that some species currently subject to legal protection are still being harvested, including for commercial use. This highlights a gap between regulatory frameworks and on-the-ground practice, reflecting challenges in conservation policy. A more detailed understanding of how rules are communicated, perceived, and enforced would be valuable for addressing these shortcomings. Furthermore, our results indicate that many species, regardless of their resilience, are subject to destructive harvesting methods, highlighting the need for stricter monitoring of vulnerable taxa. However, even seemingly low-risk harvesting, such as repeated removal of leaves or reproductive organs, can reduce plant fitness over time, potentially leading to population declines (Cunningham, 2001; Schippmann et al., 2002; Ticktin, 2004). Further research into how different types of organ harvesting affect species with varying characteristics would help identify practices that support the long-term resilience of wild plant populations.

Finally, this work has highlighted that addressing the challenges associated with wild plant harvesting requires more comprehensive and up-to-date data on actual harvesting practices, particularly regarding locations and volumes. Coordinated management strategies must also consider cross-regional regulatory complexities (Gaston et al., 2008). Future research should prioritise field-based studies, including trader interviews, market analysis and participatory monitoring, to track harvesting trends and better assess associated risks. One of the greatest challenges is the difficulty of anticipating rapid shifts in market demand, which can lead to sudden and unsustainable pressure on vulnerable species. In response, localised conservation tools are essential to address harvesting pressures, including community-based conservation approaches incorporating local stakeholder knowledge into adaptive management strategies. By combining community priorities with scientific knowledge, we can help sustain biodiversity, cultural practices, and the long-term viability of WHP populations.

CRediT authorship contribution statement

Chloé Mouillac: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Aurélien Besnard:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Guillaume Papuga:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Guillaume Papuga reports financial support was provided by French Biodiversity Office. If there are other authors, they 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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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111480.

Data availability

The authors have compiled a Data Availability file containing all the links to the data used in the study.

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