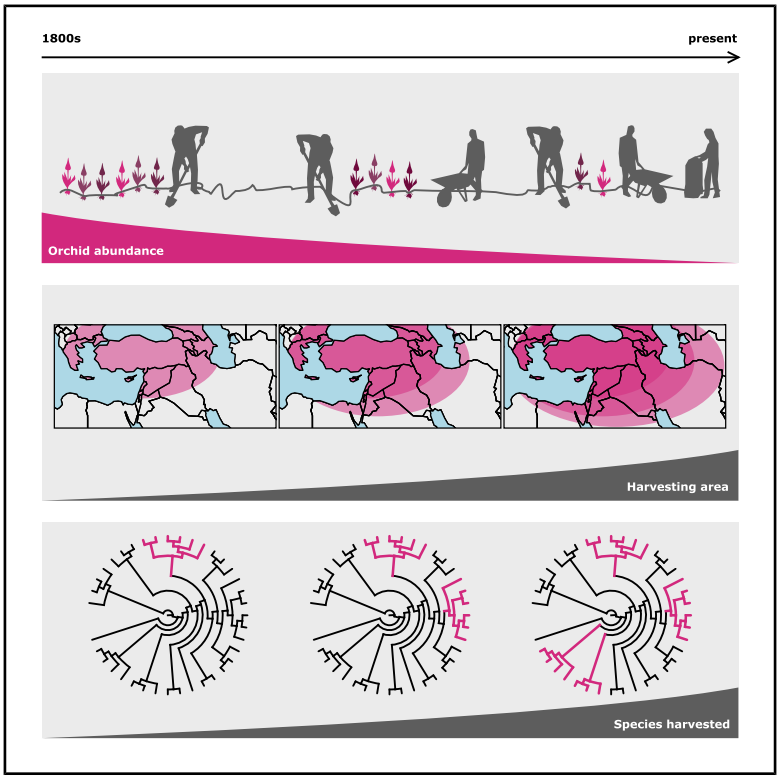
Article

Current Biology

Molecular evidence reveals unsustainable harvest of wild orchids

Graphical abstract



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In brief

Using historical collections of orchid tubers, Veltman et al. demonstrate the growing species diversity of "salep," a traditional product from the eastern Mediterranean. This diversity is associated with intensifying trade, leading to diminished yields and the exploitation of new harvesting areas and seasons, with negative consequences for local orchid populations.

Highlights

- Diversity of orchid species used for salep has grown sharply in the last 200 years
- Compositional turnover is driven by seasonal and geographic expansion of harvesting
- Downward trends in tuber size and weight point to the effects of overexploitation
- Intensifying trade and resulting population declines threaten wild orchid diversity

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Article

Molecular evidence reveals unsustainable harvest of wild orchids

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SUMMARY

Human use of wild species has long reshaped biodiversity, but the historical dynamics of exploitation are often poorly documented. One region where this is particularly concerning is the eastern Mediterranean, where orchids are harvested for the production of salep, a traditional beverage made from dried orchid tubers. Collections of these tubers held by pharmaceutical and natural history museums provide a record of their centuries-long use, but their provenance and species identity remain largely unknown. Here, salep tubers spanning nearly 200 years were analyzed using targeted capture of orchid-specific loci to identify their likely source among 80 regional candidate species. Our approach confidently identifies up to 85% of highly degraded tubers, enabling temporal and spatial reconstructions of harvesting patterns. We reveal a rapid expansion in the diversity of collected species in recent decades that is linked to variation in flowering time. Longer harvesting seasons and universally declining tuber sizes are consistent with a scenario of intensifying exploitation. Species distribution models indicate that the diversity of salep sold in markets today exceeds local orchid availability, implying long-distance trade—while comparative phylogenomics identifies the lineages that are increasingly targeted today and are at an elevated risk of future depletion. Combined, our results show that traditional salep orchid populations are declining, driving shifts toward new species and harvesting territories. This escalating trade poses a significant and growing threat to orchid diversity.

INTRODUCTION

Overexploitation is a major driver of global biodiversity loss,[1] and continued failure to address its underlying causes risks pushing many neglected species toward extinction.[2] A key contributor is wildlife trade, a multi-billion-dollar industry that affects thousands of species each year.[3,4] Knowledge of which species are harvested and traded and at what levels is crucial for assessing the scale of overexploitation and curbing its negative ecological effects.[5] Since 1975, the Convention on the International Trade in Endangered Species of Fauna and Flora (CITES) has been the primary global policy instrument designed to protect species that are vulnerable to overexploitation by regulating their trade between countries and mandating strict reporting.[6,7] Despite this, trade in CITES-listed species is poorly monitored and enforced, and large trade volumes that fall outside CITES reporting requirements (including domestic, pre-CITES, and illegal trade) remain largely invisible.[8–10] As a result, changes in exploitation patterns and trade dynamics are unknown for most wild-harvested species, hindering the detection of shifting trends and changing conservation priorities.

Among CITES-listed species, the orchid family (*Orchidaceae*) stands out as particularly species rich and vulnerable to overexploitation due to its global relevance for horticulture, food, and medicine,[11] and its species are 50% more likely to be endangered than those of other flowering plant families.[12–14] Although most orchids are epiphytes, the subfamily *Orchidoideae* comprises a diverse group of terrestrial orchids, the underground

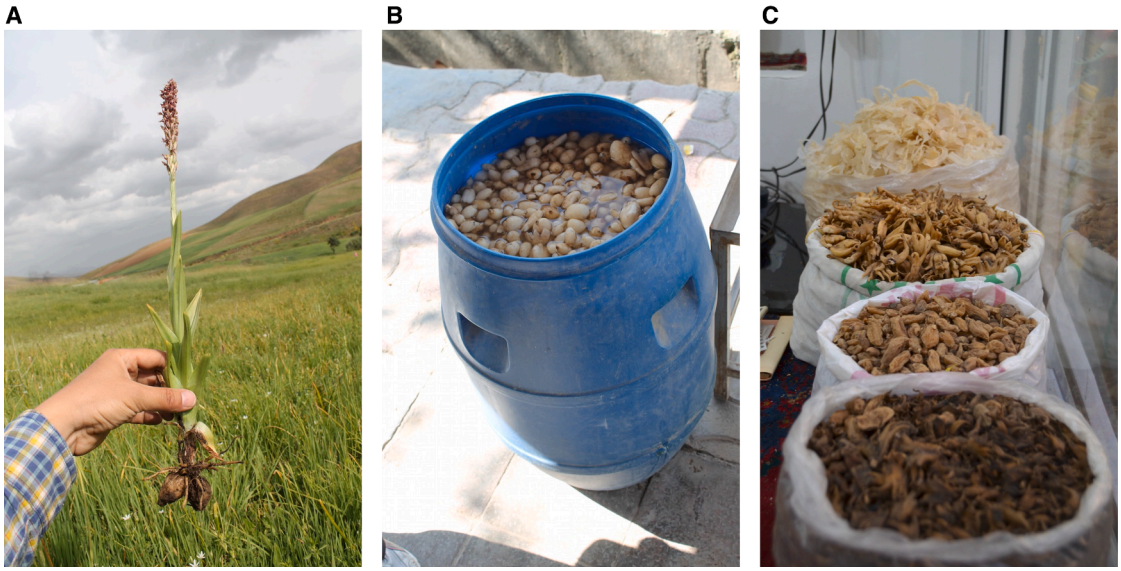

Figure 1. Harvesting and preparation of salep

(A) A recently dug up orchid (*Anacamptis coriophora*).

(B) Freshly harvested and washed tubers.

(C) Dried orchid tubers as sold in Iran at the market of Teheran.

Photos: Abdolbaset Ghorbani and Barbara Gravendeel.

storage organs of which are used for consumption on multiple continents.[15] In Southeastern Europe and the Middle East, the primary product made from such orchids is called "salep," a preparation of ground orchid tubers that is a main ingredient in the eponymous beverage and in ice cream.[16] The benefits of salep consist of its unique flavor and texture, which are thick and gelatinous, and its purported health effects, thought to aid digestion and alleviate respiratory symptoms.[17] Salep has therefore been a popular comfort drink and home remedy for centuries, with especially high usage among the peoples of the former Ottoman Empire and parts of the Arabic-speaking world, where it remains a culturally significant ingredient in local cuisine.[18]

Urbanization and migration have led to a surge in demand for salep far outside the areas where it is traditionally consumed.[19] The ubiquitous availability of powdered salep in pre-packaged form, sold by large multi-national companies in supermarkets all over Europe, the US, and online,[20,21] is a testimony to this growing popularity. Orchids are generally difficult to cultivate,[22–24] and although some salep species can be grown from seed, this production has not reached an industrial scale and most tubers still originate from wild populations. This has rendered the harvest and trade of wild orchid tubers a lucrative business with a high export value (Figure 1). It is estimated that in Türkiye[19] and Iran[25] alone, the individual tubers sold in millions and are worth over half a million USD annually. Recent evidence suggests that the finite supply of orchid tubers in areas where salep is traditionally consumed can no longer sustain demand, and that salep is now sourced from different species and even different regions or countries.[25,26] The growing interest in salep has therefore raised concerns about overharvesting and the future survival of targeted species.[26,27]

Despite reports of raw salep tubers being sold for profit across large distances, destined for consumers who are often unaware of their provenance and species identity,[20] detailed knowledge of how the exploitation of this commodity has changed over time and how it impacts the affected species is missing. Long-term and accurate monitoring of trade and population trends can reveal important insights into orchid trade and conservation,[28] but in the absence of these, historical collections offer a unique opportunity to study the genetic, phenotypic, and ecological consequences of trade. The evolutionary histories that are stored in plant repositories, such as herbaria and natural history museums, can increasingly be unlocked owing to the advances in ancient DNA techniques.[29,30] By providing a direct window into the past, genomic analyses of such repositories allow the reconstruction of past patterns of biodiversity, helping to identify historical drivers of change and future trajectories[31–34]—applying these methods to *materia medica* and ethnobotanical collections in pharmaceutical and natural history museums could yield similar insights into the evolving nature of plant use across scales.

Here, we apply targeted capture and sequencing to historical and modern collections of salep from three centuries to characterize the evolution of the salep trade from the mid-19th century to the present. Leveraging a recently developed, custom-bait kit and phylogeny of Mediterranean terrestrial orchids based on genome-wide markers,[35] we identify the assemblage of targeted species and its compositional variation through time and space and combine this knowledge with ecological and morphological data to explore the drivers and consequences of changing harvesting preferences. We infer the likely provenance of contemporary salep based on species distribution modeling and use comparative phylogenomic analyses to discover

overrepresented clades that may contain future target species. Our results strongly suggest that salep orchid populations are declining, people are turning to new areas to harvest popular species, and more species are harvested now than in the past. The combination of indiscriminate harvesting and tapping into novel sources shows that salep trade is a thriving business but a growing threat to local orchid diversity.

RESULTS

Target capture successfully enriches and identifies severely degraded DNA in orchid tubers

An inventory of tuberous orchid species native to our study area (defined as Greece, Türkiye, and Iran) yielded 82 candidate species belonging to ten genera that could be potential targets for salep harvest.[36] We supplemented existing reference sequences for the loci captured by the custom-bait kit that we generated[35] (Orchidinae-205) of 73 taxa—some of them represented by multiple samples—with seven additional species to construct a near-complete reference database of 205 loci (>300 kb) for species assignment, with a small number of taxa still missing due to restricted access to samples or poor sequence recovery. We successfully extracted DNA from 99 historical tubers sourced from pharmaceutical and natural history museums (27 collections) and 97 contemporary tubers bought at market stalls (31 batches) during fieldwork in Türkiye and Iran. This DNA was captured and enriched with the same baits. For 17 contemporary tubers with unusually intact DNA, 36%–70% of 150-bp paired-end reads mapped to the target; *de novo* assembly of these reads resulted in 300–329 kb of exon recovery. The DNA of the 186 tubers and additional reference samples was highly fragmented. Due to the difficulty of assembling ultra-short fragments, their target sequences were assembled in a reference-guided manner by alignment to the reference database. After excluding 18 samples with <40% coverage, the remaining 168 samples had a mapping rate of 42%, ranging from 7% to 67%, and an exon recovery of 156–327 kb, with a median of 318 kb. This shows that despite a 10-fold difference in enrichment, a broad coverage of >80% was achieved for the majority of tubers.

Salep tubers were identified by placing them in a shared phylogenetic framework with 89 target-enriched and five transcriptomic reference samples, including three outgroup species. Because there are different approaches to species identification (which can be distance based or clade based)[37] and species tree reconstruction (which are commonly based on maximum likelihood or multispecies coalescent approaches),[38–40] we attempted to provide a consensus identification by triangulating the results from different methods. Most tubers (75%) had consistent identifications regardless of the method employed (any distance- or clade-based method). Even more (78%) had consistent clade-based identifications regardless of using a multispecies coalescent (MSC) or maximum likelihood (ML) approach. In a few cases where the two approaches did not agree, the distance-based identification was used to achieve a consensus. In this manner, a total 81%–85% of tubers could be identified at the species level, depending on the threshold level of node support that was used for collapsing low-to-medium support nodes (0.4–0.8 posterior probability, and 80–95 ultrafast bootstrap for the MSC and ML trees, respectively), and the remainder at the genus level.

Common species are substituted as salep diversity increases

The majority of salep tubers were identified as belonging to the genus *Orchis*, most notably *Orchis mascula* (L.) L. Lower frequencies of salep were observed in other genera, dating largely to more recent time periods (Figure 2A), suggesting that modern salep collections are taxonomically more diverse than historical salep collections. Non-metric multi-dimensional scaling of all collections shows that the distance between historical collections in two-dimensional space tends to be smaller than that between modern collections, with the oldest collections clustering most tightly together and more recent collections gradually fanning out around this core historical diversity (Figure 2B). The most distant collections are three contemporary batches of salep tubers bought in Türkiye, consisting solely of *Serapias* species (*S. bergonii* E.G. Camus or *S. vomeracea* (Burm. f.) Briq., depending on the identification method)—a species that was not identified in collections from other regions or time periods. The larger variation in community composition among modern collections is confirmed by an analysis of beta diversity, which shows that the dispersion within centuries is not homogeneous, but that in each century, the variance among the distances of collections to the centroid becomes progressively higher (Figure 2C).

Analysis of species co-occurrences within collections and within time periods shows that most relationships between pairs of taxa are close to zero or negative, regardless of the chosen clustering unit. This means that the presence of one species or genus generally did not increase (but sometimes lowered) the expectation of observing another, and that no taxa were consistently found together. The largest (negative) effect sizes of species co-occurrences were found for *Orchis mascula*, with *Orchis anatolica* Boiss. and *Orchis simia* Lam. being the most common congeneric substitutes, followed by species belonging to other genera, such as *Dactylorhiza incarnata* (L.) Soó, *D. romana* (Sebast.) Soó, *Serapias vomeracea* (Burm.f.) Briq., and a range of *Anacamptis* species (Figure S1A). At the genus level, the most common substitutes for *Orchis* tubers are *Dactylorhiza* tubers, closely followed by *Anacamptis* tubers, and *Serapias* tubers to a lesser extent. Each of these substitutes was more negatively related to *Orchis* than to each other, demonstrating that they are broadly exchangeable as alternatives to the primary (historical) source of salep (Figure S1B).

Phylogenetic clustering of salep unravels over time

Breaking down the composition of species in salep collections into five discrete time periods shows that *Orchis mascula* used to make up more than half of the salep collected nearly 200 years ago, and until the mid-20th century, most salep was dominated by only a handful of species with globose tubers, mostly belonging to the *Orchis* genus. The most common (congeneric) alternatives for *O. mascula* encountered in previous centuries are *O. anatolica* and *O. adenocheila* Czerniak, with the occasional observation of *Dactylorhiza maculata subsp. saccifera* (Brongn.) Diklic and *D. sambucina* (L.) Soó. This indicates that already in the 19th century, salep was not monospecific, or even

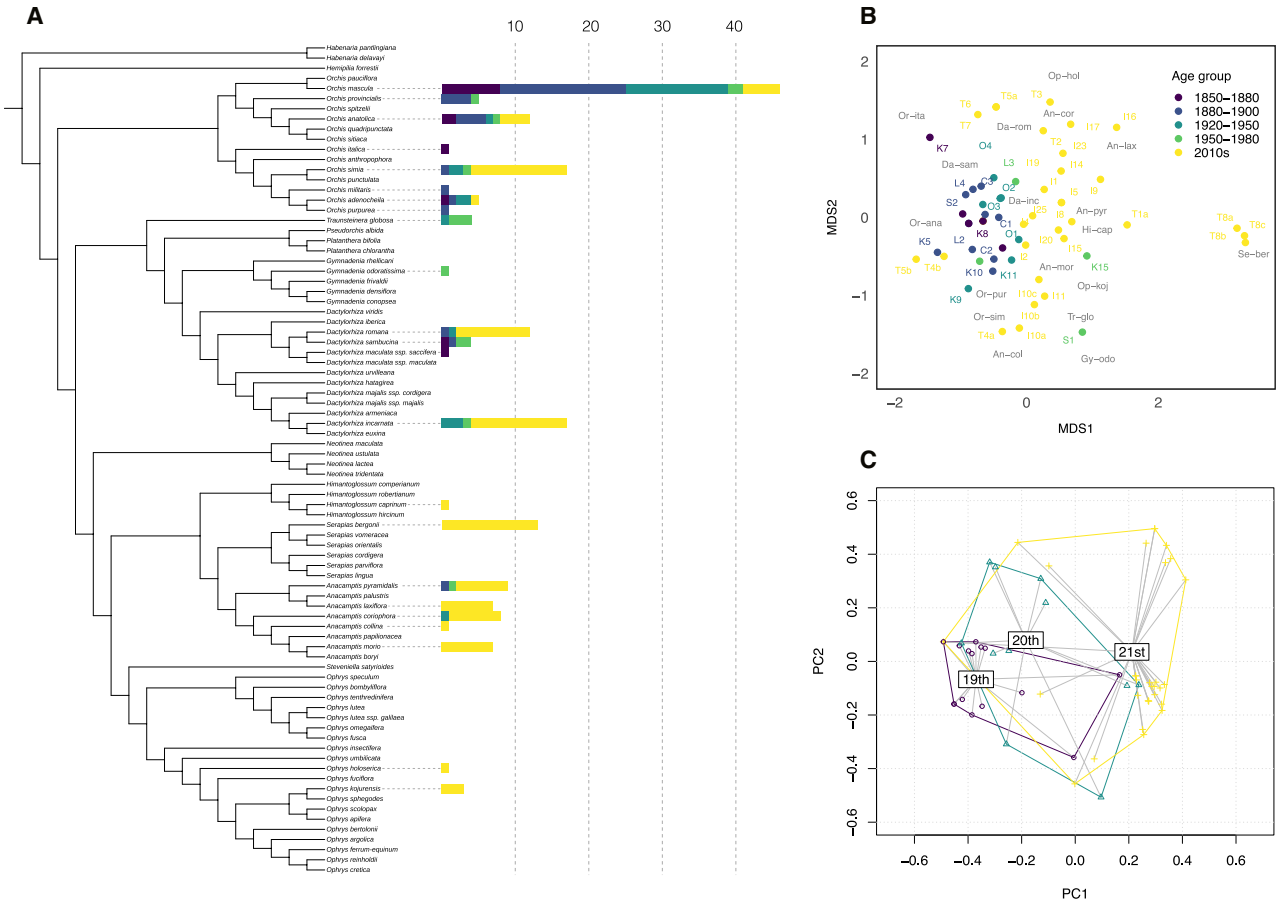

Figure 2. Heterogeneity in orchid species composition of salep collections

(A) Count of species identified by closest reference under the multispecies coalescent. Colors of the stacked bar chart correspond to the legend in (B).

(B) Non-metric multi-dimensional scaling of collection diversity, colored by age group.

(C) Within-group variance of collections, grouped by century. Colored lines indicate the circumference of the collection dispersion within each group. Gray lines indicate the distance of each collection to the centroid of the group. Distances between collections in (B) and (C) are based on the Kulczynski dissimilarity index using the species identifications made in (A).

See also Figure S1.

monogeneric. Moving toward the present, these traditional salep alternatives are increasingly being displaced by other *Orchis* species (particularly *O. simia*), *Dactylorhiza* species (particularly *D. incarnata* and *D. romana*), *Serapias* species (either *S. vomeracea* or *S. bergonii*), and *Anacamptis* species (most commonly *A. pyramidalis* (L.) Rich., *A. coriophora* (L.) R. M. Bateman, Pridgeon & M. W. Chase, *A. morio* (L.) R. M. Bateman, Pridgeon & M. W. Chase, and *A. laxiflora* (Lam.) R. M. Bateman, Pridgeon & M. W. Chase). While species turnover appears to have been gradual at first (until about the 1930s), it accelerated in the second half of the 20th century until it reached a relatively even spread among more than a dozen distantly related species in the present (Figure 3A). The share of *Orchis mascula* in the total correspondingly decreases to less than 50% in the 20th century and to as low as 5% in the 21st century, whereas the share of other genera—some with strikingly different tuber morphologies, such as the digitate *Dactylorhiza and Gymadenia*—increases from ~10% prior to 1900 to 37% in the 20th century and more than 75% in the 21st century (Figure 3B).

To test the hypothesis that there is a tendency toward phylogenetic dispersion of salep communities over the past two centuries, we conducted phylogenetic diversity analyses of tubers collected in different time periods. Two common metrics of phylogenetic diversity—mean phylogenetic distance (MPD), as measured by the net relatedness index (NRI), and mean nearest taxon distance (MNTD), as measured by the nearest taxon index (NTI)[41]—show that historical salep diversity is phylogenetically clustered, with a strongly positive NRI ($p < 0.01$) and NTI ($p < 0.05$). 19th century salep is significantly clustered for both indexes ($p < 0.05$), but in the 20th century, only NRI demonstrates significant clustering ($p < 0.05$). The difference between the two suggests that deep branching patterns play a larger role in the phylogenetic clustering of historical salep than more shallow branching patterns.[41] Although phylogenetic clustering persists until the 20th century, NRI and NTI both show a downward trajectory, and clustering breaks down completely with NRI approaching zero in the 21st century (Figure 3C). Hence, while species harvested for salep used to be more closely related

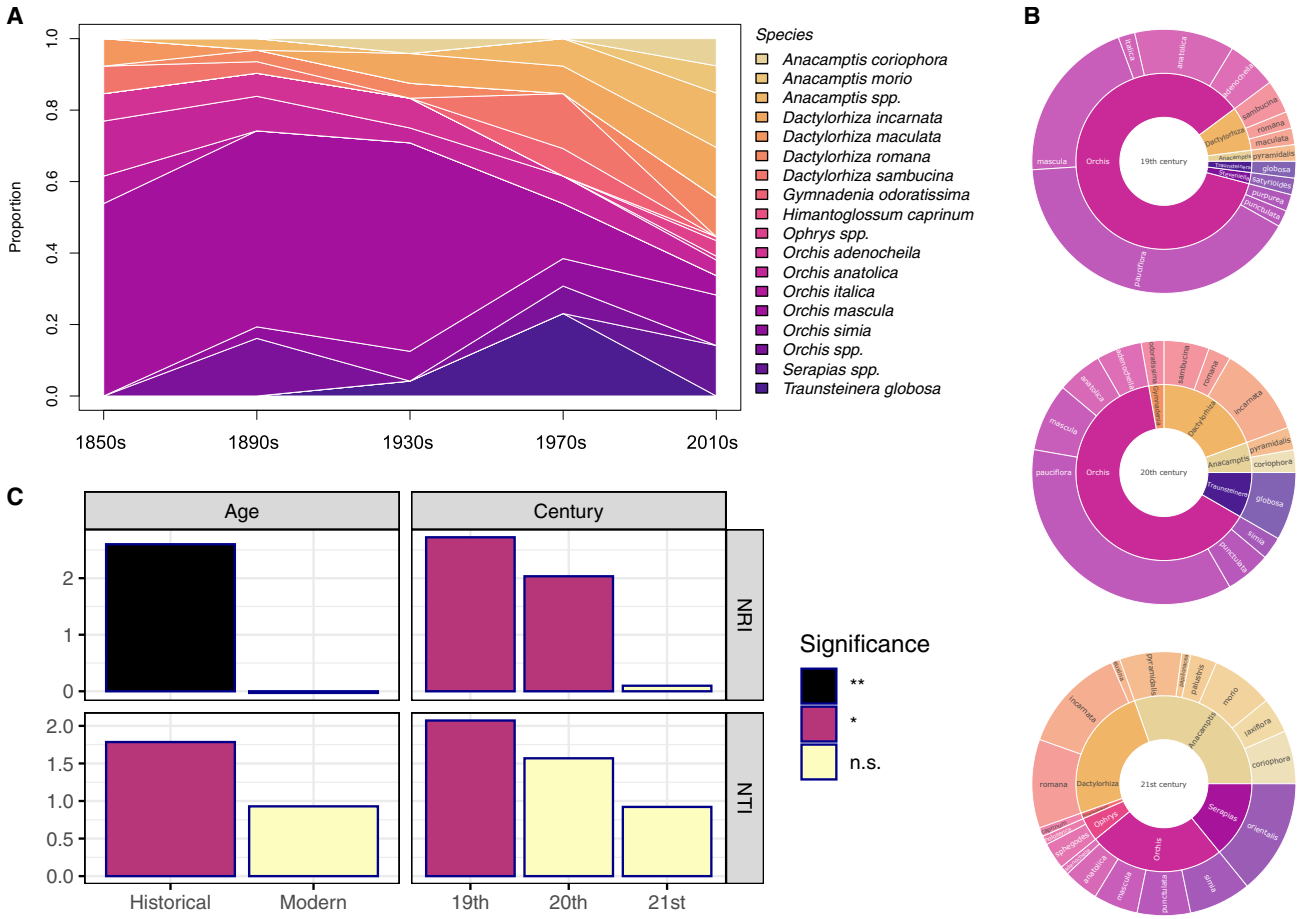

Figure 3. Phylogenetic dispersion of species sold or collected as salep from the 19th through the 21st century

(A) Relative proportion of species identified in five different time intervals, and the changes between them.

(B) Genus and species composition per century.

(C) Phylogenetic clustering of species identified as salep for different specimen age groups, as measured by NRI and NTI. Historical specimens correspond to 19th and 20th century collections, and modern specimens correspond to 21st century collections. Significance of clustering is indicated as followed: n.s. = not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

than expected by chance, this trend is slowly vanishing; simultaneously, species harvested for salep in the present day are neither significantly more closely nor more distantly related than expected by chance and hence show no sign of overdispersion, hinting that (phylogenetically speaking) species are currently selected at random.

Local availability drives species turnover

To explore whether the currently observed phylogenetic dispersion of salep is even across space, we mapped all identified tubers collected during fieldwork to the place where they were purchased from markets and subdivided the area into five regions consisting of roughly equal sample sizes (Figures 4A and 4B). We observed striking differences in species composition between these zones, a pattern that suggests there might be a longitudinal gradient in the genera preferentially targeted and/or sold (Figure 4B). This is corroborated by a LOESS regression of the generic frequencies grouped by their longitudinal coordinates, which shows a peak in common substitute genera in the middle of the range and *Orchis* attaining its maximum frequencies at both ends of the range (Figure 4C). It is particularly noteworthy that the most iconic traditional salep species, *Orchis mascula*, was sold in multiple cities in central and eastern Iran, but not in northwest Iran and eastern Türkiye where salep is traditionally consumed by local populations.[42] Since the local market for central and eastern Iran is probably negligible,[26] the majority of salep harvested there is likely exported. The fact that *Orchis mascula* was only found in the eastern range of our study area could signify its continued popularity and declining abundance (or possibly extinction) in the western range where it has long been popular, forcing an eastward expansion of the sourcing of traditional species. This is consistent with the observation that in both Türkiye and Iran, *Orchis simia* is now harvested alongside local and longstanding alternatives that are unique to these countries (*O. anatolica* and *O. adenocheila*, respectively), showing shifting targets in this genus that might be driven by changes in local availability.

To assess the possible origins of salep and their comparison with native orchid diversity, we created species distribution models to generate presence-absence maps of 80 inventoried

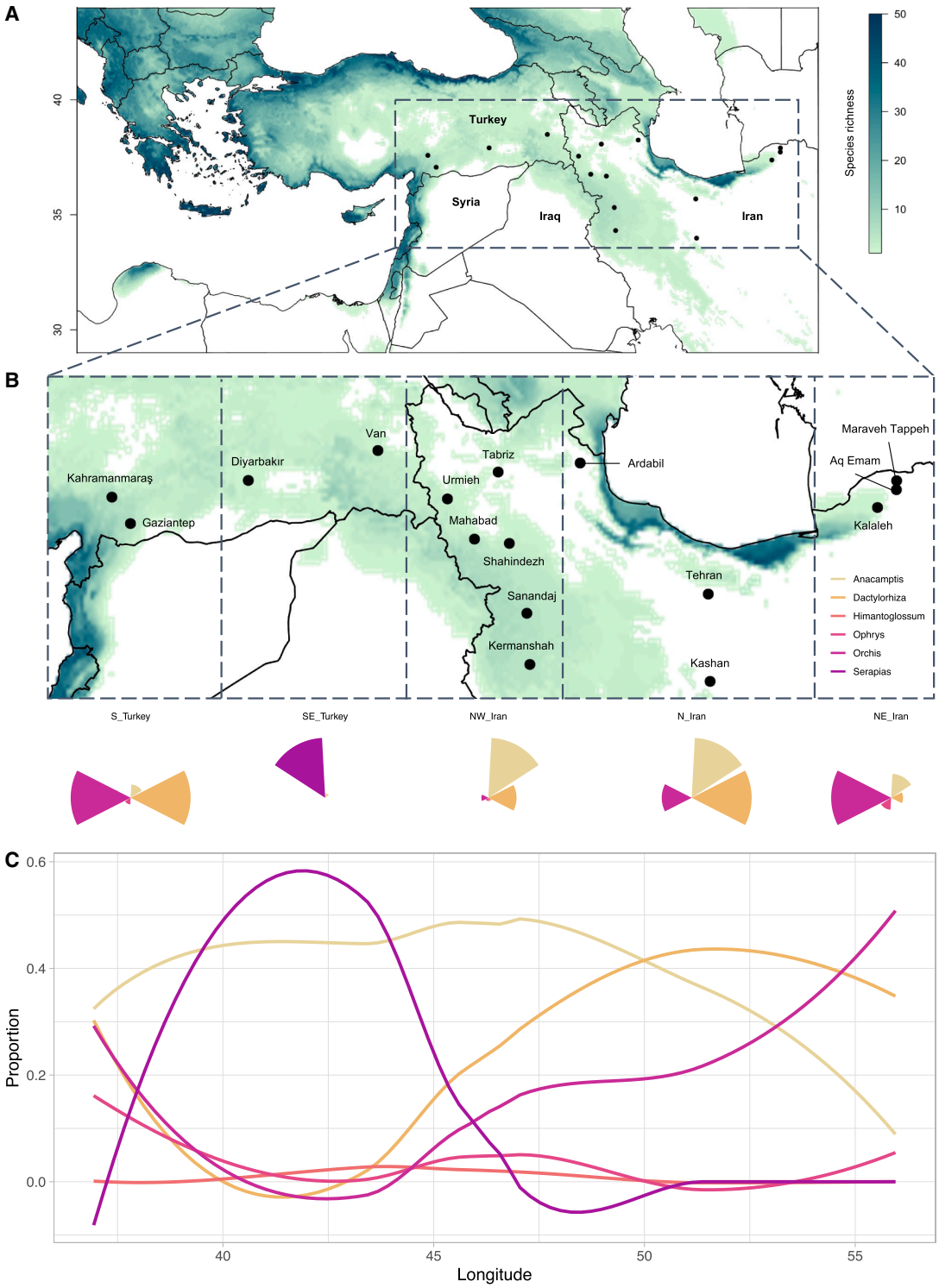

Figure 4. Geographic variation in orchid genera traded as salep in modern-day Türkiye and Iran

(A) Map of study region, with points indicating cities where markets were visited during field trips in 2013–2014 for the purchase of tubers.

(B) Close up of the area where tubers were sampled, divided into five zones with the corresponding generic composition of salep depicted below in rose charts. Each rose chart consists of six segments, one per genus, with the diameter proportional to their frequency.

(C) Longitudinal gradient of the relative frequencies with which genera were encountered, as estimated by a loess regression.

See also Figures S2 and S3.

target species for which sufficient occurrence records (sourced from GBIF and supplemented with our own field observations in Iran) were available. This yielded species richness and phylogenetic diversity estimates across our study area at 10 km resolution (Figure S2). Estimated native species richness was higher than sold species diversity in three out of four Turkish cities; nonetheless, some traditional salep species that were predicted to occur in this area were not encountered on the markets, suggesting that either they have become locally unavailable or that other species are now more preferred or more readily accessible. In contrast, in Iran, the diversity sold on markets often outstripped estimated native diversity, with the exception of two Kurdish cities in the northern Zagros mountains (Sanandaj and Kermanshah). This might be partially explained by the fact that Iran is underexplored and has fewer species occurrence records available, limiting the accuracy of predicted habitat suitability in this area, but it could also indicate that Iran is currently a thriving hub of orchid harvest and trade. While we did not find conclusive evidence of international trade based on known species distributions, some species were traded across larger distances than others, with *Serapias vomeracea* and *Orchis mascula* sold at markets furthest removed from their inferred distributional range (Figure S3).

Harvesting preferences affect species composition

In addition to patterns of local availability, we further tested whether species turnover is associated with different harvesting practices, such as when and where salep is harvested. To this end, we compared the median elevation at which species occur, as well as their flowering times, between different collection ages. Although we expected that the lack of availability might lead harvesters to go higher mountain slopes to collect different species, we observed the opposite, with harvested species found at a lower median elevation in the 21st century compared with previous time periods (Wilcoxon rank-sum test, $p < 0.01$; Figures 5A and 5B), with significant shifts also observed for the first and third quartiles (Figures S4A and S4B). While we cannot be sure at which elevation tubers were actually harvested, this shows that relatively more lowland species are currently targeted than in the past (Figure 5C). As species occurring at higher elevations tend to flower later, a possible explanation for this is a growing preference for earlier flowering species.[43]

When comparing flowering times of the species harvested in different time periods, we found that the majority of salep harvested today originates from species with longer flowering times, flowering for an average duration of 1.5 months instead of <1 months (Wilcoxon rank-sum test, $p < 0.001$; Figures 5D and 5E). Crucially, the onset, midpoint, and end of flowering have a larger spread around the median in recent decades than previously, with onset of flowering on average happening earlier in the season (although the shift in onset is not significant after correcting for multiple testing; Figures S4C and S4D), possibly explaining the over-representation of lowland species in recent years. The larger variance and longer duration of flowering times translate into a longer season during which salep species can be picked. This is a striking finding because, traditionally, tubers tend to be harvested during a narrow time window in spring when salep orchids are in flower and the new tubers of the year are sizable but not yet old.[44,45] Our results thus suggest that the observed diversification of salep is not just explained by geographic expansion and local differences in availability, but also by extended harvesting seasons, with earlier and possibly longer harvesting activity throughout the year (Figure 5F).

Morphological trends indicate population declines

To assess whether the seasonal and geographic expansion of harvesting might be caused by overharvesting and population declines of native orchid populations, we measured and weighed ~1,200 tubers taken from the same collections that were sampled for DNA extraction and sequenced. Comparison of the weight and size distributions for five discrete time periods shows a significant reduction in weight and size for each pair of consecutive intervals (Wilcoxon rank-sum test, $p < 0.05$; Figures 6A and 6B), corresponding to a 65% reduction in the median of both weight (a 0.9 gr decrease) and size (a 1.5 cm^3 decrease) between the oldest and youngest time periods (Figures 6C and 6D). Since weight and size are strongly correlated (Pearson correlation coefficient r = 0.96), and weight measurements are more precise due to shape irregularity, we conducted further statistical tests on the weight measurements. Analysis of variance shows that the time period in which tubers were collected significantly impacted their log weight ($p < 0.001$), also for the smaller subset of tubers that were sequenced; this relationship held even after correcting for species identity ($p < 0.01$). While species identity also affected tuber weight ($p < 0.01$) as expected,[43] only one species (*Himantoglossum caprinum*) had a significant effect, and there was no significant interaction between species identity and age group, suggesting that the observed weight reduction is universal across target species. Only a few species were collected in sufficient numbers to enable statistical comparison of their tuber weight and size over time. For those identified with high confidence among both the historical and modern tubers, modern tubers were significantly smaller and weighed less for *Dactylorhiza romana* (Wilcoxon rank-sum test, $p < 0.05$) and *Orchis simia* (Wilcoxon rank-sum test, $p < 0.01$); differences for other species were not statistically significant (Figure S5).

Smaller tubers can either indicate that they are harvested earlier in the growing season, before or during flowering, or that their peak size during flowering is smaller. We consider the former unlikely, as it is harder to find and recognize orchids when they are not in flower, and the sale of underdeveloped tubers would lead to lower profits because salep is sold by weight. The latter could mean that harvested plants are smaller because they are younger or have reduced vigor, possibly signaling depletion of older plants and inbreeding depression. This would be consistent with a scenario of overexploitation, in which species that have been persistently harvested for several decades or even centuries show a decline in abundance and hence a changing age composition. Another explanation could be that harvesters collect all tubers of a plant instead of only the largest, irrespective of their size. Reduced size selection by harvesters is an intriguing possibility because it would imply a departure from traditional harvesting practices that involved replanting of smaller tubers to promote regrowth.[27,46] This could lead to lower regeneration and higher plant mortality.

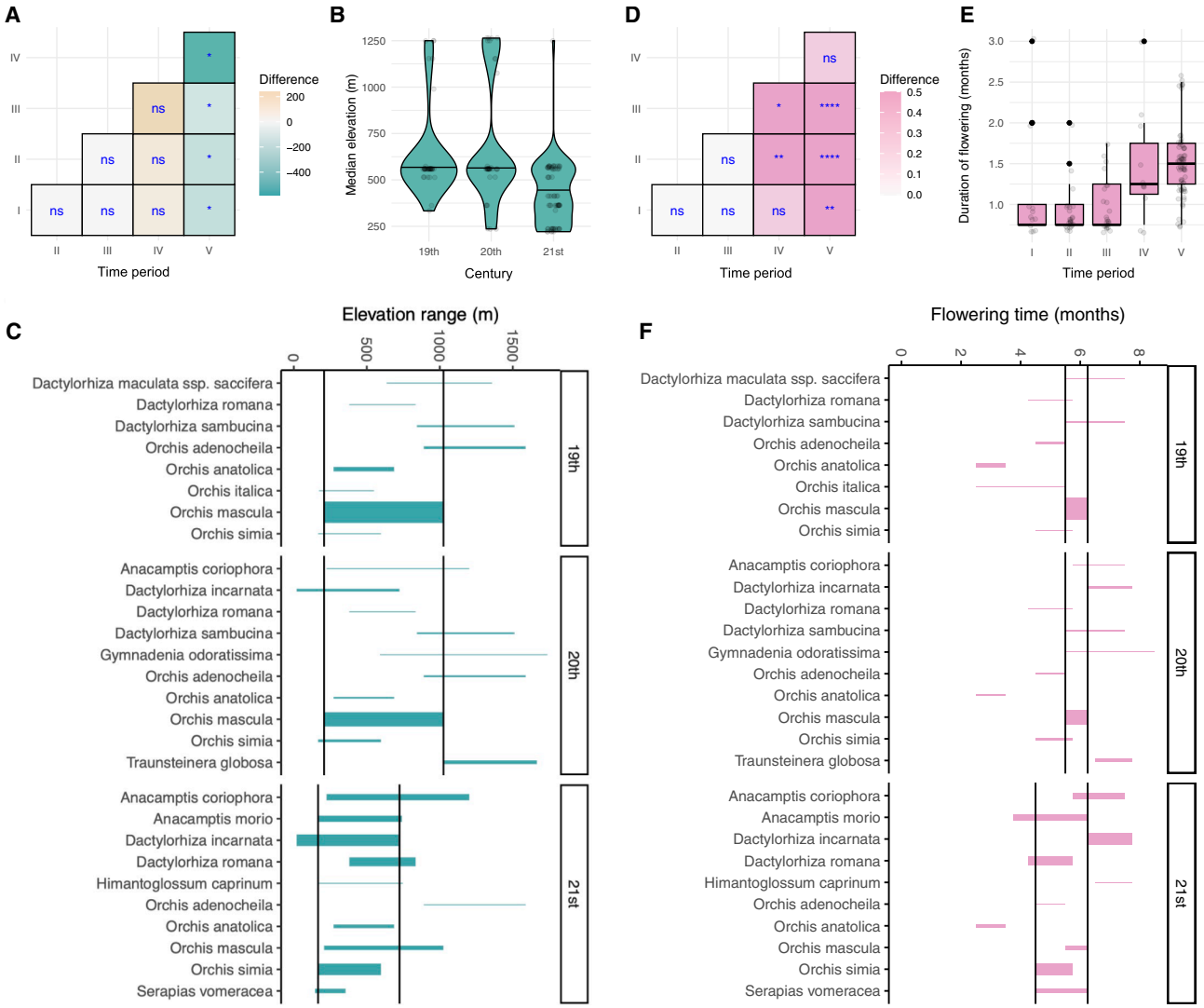

Figure 5. Variation in elevation range and flowering time of harvested species

(A) Estimated difference in median elevation of harvested species between different age groups.

(B) Median elevation of species harvested in different centuries.

(C) Interquartile range of elevation range of species harvested in different centuries. Black lines indicate the median first and third quartiles in each century.

(D) Estimated difference in flowering duration of harvested species between different age groups.

(E) Flowering duration of species harvested in different time periods.

(F) Flowering times of species harvested in different centuries. Black lines indicate the median start and end date of flowering in each century.

Age groups: I = 1840–1879; II = 1880–1919; III = 1920–1949; IV = 1950–1979; and V = 2013–2014. Distributions of the median elevation (A) and duration of flowering (D) in different age groups were compared with a Wilcoxon rank-sum test (n.s. = not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, $****p < 0.0001$). In (C) and (F), bar width indicates relative frequency of each identified species as a proportion of the total number of identified tubers.

See also Figure S4.

More lineages at risk of being harvested

Since our sampling of salep was limited and possibly non-exhaustive, there could conceivably be other species that were harvested for salep and were not included in our study. To assess the likelihood that non-identified candidate species could also be targets, we conducted a randomization test by reshuffling species assignments across the tree and testing for each node whether its descendants were significantly more often identified as salep than expected by chance. We consider these "high-risk clades," also referred to as "hot nodes" in the terminology of Saslis-Lagoudakis et al., where we define "high-risk" not as a conservation risk, but as an elevated probability of being selected for salep collection.[47] Randomization of historical and modern salep tubers (which were roughly equal in sample size) shows that in the past, the entire genus *Orchis* is significantly enriched for salep, with only one other shallow node in *Dactylorhiza* being significant (Figure 7A). This changes in the present day, where fewer *Orchis* species seem to be at risk, whereas almost all *Dactylorhiza* species are now at risk. While the most recent common ancestor of *Serapias*, *Himantoglossum* and *Anacamptis*

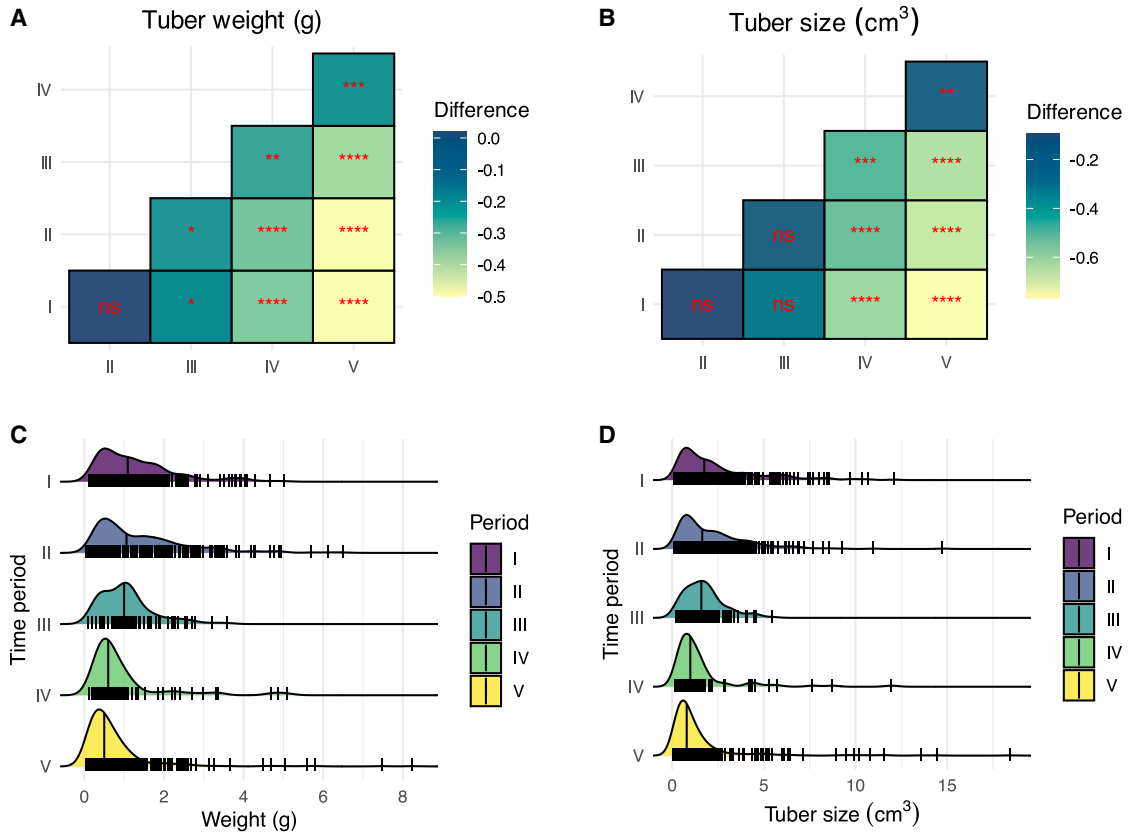

Figure 6. Reduction in tuber size and weight over time

(A) Estimated shift in median tuber weight (in grams) between different age groups.

(B) Estimated shift in median tuber size (in cm^3) between different age groups. Shifts were estimated by a Wilcoxon rank-sum test from the older to the younger age groups.

(C) Shifts in the distribution of tuber weight over time.

(D) Shifts in the distribution of tuber size (measured in three dimensions) over time. Tick marks indicate individual tubers, and the large horizontal line indicates the median. Age groups: I = 1840–1879; II = 1880–1919; III = 1920–1949; IV = 1950–1979; and V = 2013–2014. Tuber weight and size distributions of different age groups were compared with a Wilcoxon rank-sum test (n.s. = not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, $****p < 0.0001$).

See also Figure S5.

is also significantly enriched for salep tubers, this is mainly caused by the high frequency of *Serapias* and *Anacamptis* tubers, and shallower significant nodes are only observed within these two genera (Figure 7B). Several genera seem to be at a consistently low risk of being harvested, including *Ophrys*, *Neotinea*, and *Gymnadenia*, although it is impossible to test significance for the genera that are represented by only one species, such as *Traunsteinera*, *Platanthera,* and *Pseudorchis*.

The identification of hot nodes based on a randomization of observed use, instead of raw tuber counts, is less likely to be influenced by differences in frequency and was conducted for all five time periods and three centuries. This showed very few differences in the number and placement of hot nodes between different historical time intervals (Figure S6), with the entire genus *Orchis* and a fraction of (or no) *Dactylorhiza* nodes labeled as significantly enriched for salep species. The main difference between the tuber count and salep use analyses lies in the detection of high-risk *Orchis* clades in the 21st century. These are significantly enriched for count, but not for use, due to the relatively low number of species targeted. Since the low number of *Orchis* species used for salep in recent times could be explained by a drop in their availability, rather than a drop in their popularity, this by no means suggests that these species are now safe from the effects of harvesting.

DISCUSSION

More than 30,000 plant species are used by humans for food, medicine, and other purposes worldwide,[48,49] but the exploitation history of most of these plants is inaccessible except through sparsely annotated historical records and surviving specimens. In this study, we generated a genetic time series of edible orchid use over the last 175 years with a custom-built target capture bait set[35] and used the resulting compositional data to shed light on the ecological dynamics that have altered the face of the salep trade from the 19th century to the present. By integrating the analysis of historical DNA from a broad temporal range of samples with distributional, phenological, and morphological data, we show that salep harvesting has not only expanded into new territories and new species but that

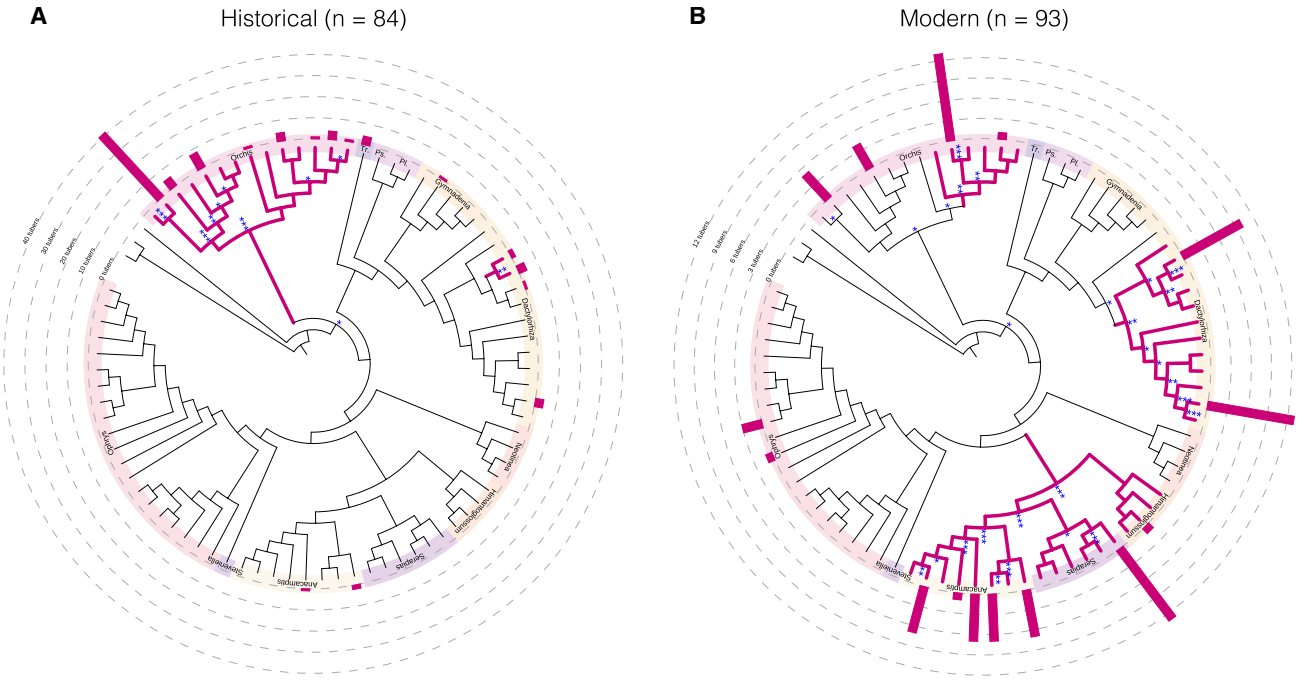

Figure 7. Orchid clades more likely to be harvested for salep than expected by chance, i.e., "hot nodes", based on species abundance

(A) Hot nodes for salep harvesting in the past (19th and 20th centuries combined).

(B) Hot nodes for salep harvesting in the present (contemporary Türkiye and Iran). Highlighted branches indicate descendants of "white hot" nodes ($p < 0.01$); the nodes themselves are labeled with asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

See also Figure S6.

this is linked to increasing and prolonged harvesting pressure throughout the season with probable detrimental effects for the health and survival of preferred orchid populations.

By capturing exon sequences and analyzing them in a robust phylogenetic framework with near-complete (>90%) taxon sampling, we were able to positively identify up to 85% of severely fragmented plant remains of centuries-old specimens. While previous efforts have been made to identify salep orchids,[25,50] these studies were conducted with traditional barcoding markers that have limited enrichment success and discriminatory power and were primarily focused on contemporary specimens, therefore lacking a historical perspective. The results presented here therefore mark a unique step forward in the analysis of traded orchids while also demonstrating the utility of target capture for museomics research beyond the use of typical herbarium leaf specimens, such as *materia medica* and ethnobotanical collections. Enrichment of low-copy nuclear loci with custom baits has proved successful in a limited, but growing, number of other cases investigating wildlife trade, including *Aloe* spp.[51] and *Anacyclus* spp.,[52] but has yet to be adopted on a larger scale. The fact that our approach worked on starting material with exceptionally low DNA quantities and high impurity is especially promising for tubers and other useful plant parts, where morphological characters often fall short in species identification. This requires recourse to molecular methods when plant vouchers or other observational field data are absent.

Even though our species identification was relatively robust, it is conceivable that the omission of a handful of reference species could have led to a small number of false-positive identifications. The most glaring absences consist of *Anacamptis sancta* (L.) R.M.Bateman, Pridgeon & M.W.Chase, *Orchis pallens* L., and *Ophrys schulzei* Bornm. & Fleischm, all of which occur in Türkiye, and the last of which occurs widely in Iran. Hence, in the absence of detailed knowledge of their phylogenetic placement and distance to neighboring reference species, we cannot completely rule out the possibility that some of the identified salep in these genera could be more accurately identified as one of these missing species. However, as most missing species belonged to *Himantoglossum* and *Ophrys*, genera that were hardly observed among our salep collections, we are confident that most of the species-level identifications of modern-day tubers from Türkiye and Iran are correct. Some of the genus-level identifications could reflect either insufficient taxon sampling or insufficient phylogenetic information contained within the target sequences presented here. The latter could cause unstable identifications, especially in species that have recently diverged and are characterized by high levels of incomplete lineage sorting[53,54] or gene flow.[55,56] While we accounted for phylogenetic uncertainty in identification by seeking a consensus between different methods of clade-based identification and distance-based identification, we were not able to eliminate all genus-level identifications. Genus-level identifications within *Anacamptis* and *Serapias* especially could be further refined by expanding the available target space, either by capturing non-exonic sequences in the flanking regions of the targeted exons or by adding additional target loci.[35,57] On the other hand, target enrichment can capture sufficient sequence variation to trace traded plant materials down to geographic subpopulations.[52]

Future studies on salep could therefore focus on commonly harvested or endangered species, to assess the likely source population(s) of harvested salep tubers against a geo-referenced reference panel.

The results presented here challenge the emerging paradigm in ethnobotany that ethnomedicinal species belong to preferred lineages that are stable over time.[47,58,59] While we see a persistent preference for one or two species and a few common alternatives, the choice for most other species harvested today is more labile, showing that determinants of plant selection are context specific, dictated by a combination of local availability of natural resources and socio-economic conditions specific to the time and place of resource use. We suspect that the ability to predict ethnomedicinal plant use through phylogenetic comparative methods is restricted to relatively large clades used over relatively long time periods in environmental systems characterized by a stable state, but may break down when socio-ecological systems are strained under external pressures that challenge this equilibrium. In the case of salep, this strain is evident from the expansion in target species and geographic source areas reported here but also in the increasing proportion of digitate-tubered species in our sample, which can be seen as bycatch of the presumably preferred globose-tubered species that dominated salep production more than a hundred years ago. This switch to less preferred and possibly lower quality alternatives could be a sign of resource scarcity and another result of the trade-offs harvesters make between search effort and yield when faced with diminishing returns, such as abandoning a resource patch in favor of another area—suggesting evolving heuristics governing foraging rationality.[60,61] The pressures tipping the ecological balance between native orchid diversity and human use likely stem from a rapidly growing global market, which is facilitated by advancements in logistics and communication technology on the supply side, and a lack of awareness of or concern for legal and sustainable sourcing of wildlife products on the demand side.[21,62,63] These forces are transforming the purpose of orchid harvest from local consumption to export and from home use to profit generation,[19,26,64] possibly explaining decreasing species fidelity and changing harvesting practices—trends that, when exacerbated by dwindling orchid availability, can result in a negative feedback loop with possibly disastrous consequences for a widening range of native orchid species.

Combined, our results provide compelling evidence that more species are being targeted for salep today than before; traditionally preferred lineages are still harvested but in lower numbers and on an eastward-moving frontier; geographic expansion and an extended harvesting season drive the recent acceleration in species turnover; and overharvesting leads to a depletion of mature individuals with smaller tubers over time. Diminished body or organ size and increased harvest of juveniles are well-known consequences of overexploitation, especially in fisheries and trophy animals,[65,66] but there is little direct evidence of this phenomenon in plants. Our study strongly suggests that prolonged harvesting pressure can have analogous demographic and phenotypic effects in harvested plants and complements rare observations of dwarfing and decreased root size in other medicinal species.[67–71] Given the decline in salep tuber weight and size, there is a real risk that current unsustainable harvest practices are rapidly exterminating the older demographic of commonly harvested species, which are subsequently unable to renew themselves at the rate required to sustain their population levels. This could potentially lead to a boom-and-bust cycle where the growing market for a particular salep species results in population collapse and forces humans to tap into novel species and areas. Compositional turnover caused by sequential species collapse and replacement has been observed for other wildlife products, including bushmeat,[72] sea cucumbers,[73] and shark fins.[74] We consider it likely that the tendency toward phylogenetic dispersion of salep over time is indicative of this phenomenon, which appears to be magnifying in intensity and affecting increasingly more target species.

In conclusion, this study provides direct and quantitative evidence of the changing relationship of humans with traditionally used plants over the course of almost two hundred years. More research is needed to investigate the social and economic drivers of salep harvesting, which are likely to change and respond to evolving conditions in the near future. The growing number of clades that are at risk of being targeted for salep now and in the future is cause for concern when care is not taken to harvest in a sustainable manner. Given the increasing demand for export and the recently observed decline in local orchid populations,[26,27] we advocate for stronger control of (illegal) international and domestic trade, while promoting local sustainability initiatives and allowing for the safe and legalized extraction of healthy orchid populations according to evidence-based best practices.[75] Community standards provided by certification schemes such as FairWild[76] could increase transparency concerning the identity and provenance of wild-collected species, while incentivizing sustainable harvesting. In addition, ongoing efforts to cultivate salep orchids[77,78] could relieve harvesting pressure but could also pose a risk for laundering of species collected from the wild.[79] Future research could extend our approach to species identification to authentication of cultivated varieties of salep and distinguish legal from illegal sources. Although vegetative propagation does not yet present an economically viable alternative to wild harvest, the development of artificial hybrids or cultivars, when genetically distinguishable from wild populations and properly certified,[80] could in the long term be successful in lowering demand for wild-harvested salep and providing a sustainable supply in the future.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Margret A. Veltman (margret.veltman@nhm.uio.com).

Materials availability

Materials generated in this study are available upon request from the lead contact.

Data and code availability

- Raw sequencing reads are deposited in the NCBI Sequence Read Archive (SRA) under project number PRJNA1403031.
- All newly generated *de novo* assembled and reference-guided target sequences generated in this study are available in a Dryad repository (https://doi.org/10.5061/dryad.mpg4f4rf5) linked to this study, together with the tuber size and weight data and the occurrence records and distribution maps of candidate target species.

- Previously generated target sequences from Veltman et al.[35] are available on Dryad (https://doi.org/10.5061/dryad.sj3tx96bn).
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

M.A.V., B.G., and H.d.B. designed and conceived the research. M.A.V., A.G., E.O., S.T., S.A.-K., S.M., M.N., B.G., and H.B. collected samples and metadata. B.A., A.S.-N., A.K., and E.Ö. performed DNA extractions and library preparations. M.A.V., A.G., S.M., and H.d.B. performed morphological measurements. M.A.V. performed genetic and statistical analyses. J.A.C.B. performed species distribution modeling and diversity analysis. M.A.V. prepared the manuscript with input from B.A., A.S.-N., J.A.C.B., M.F.F., A.A., B.G., and H.d.B. M.F.F., A.A., B.G., and H.d.B. provided supervision. All authors read and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2026.02.066.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
99 historical salep tubers	Herbarium and museum collections	See Table S1
97 modern salep tubers	Shops and markets in Türkiye and Iran	See Table S2
Critical commercial assays		
AMPure XP Beads	Beckman Coulter	Cat# A63882
Accel-NGS 2S Hyb DNA Library Kit	Swift Biosciences	Cat# 23023
Accel-NGS 1S Plus DNA Library Kit	Swift Biosciences	Cat# 10096
MyBaits Custom Hybridization Capture Kit 40–60K; Orchidinae-205	Daicel Arbor Biosciences; described in Veltman et al.[35]	Cat# 300316.v5; https://arborbiosci.com/publication/orchidinae-205-a-new-genome-wide-custom-bait-set/
Deposited data		
Raw sequencing data	This paper	https://www.ncbi.nlm.nih.gov/sra/PRJNA1403031
Assembled target sequences, curated species occurrence records, species range maps, and tuber weight and size measurements	This paper	https://doi.org/10.5061/dryad.mpg4f4rf
Assembled target sequences	Veltman et al.[35]	https://doi.org/10.5061/dryad.sj3tx96bn
Species occurrence records	Global Biodiversity Information Facility	RRID: SCR_005904; https://www.gbif.org/
WorldClim version 2 historical climate data (1970–2000)	Fick and Hijmans[81]	RRID: SCR_010244; https://www.worldclim.org/data/worldclim21.html
Software and algorithms		
Trimmomatic v0.39	Bolger et al.[82]	RRID: SCR_011848; http://www.usadellab.org/cms/index.php?page=trimmomatic
BWA v0.7.17	Li and Durbin[83]	RRID: SCR_010910; https://bio-bwa.sourceforge.net/
SAMtools v1.12	Danecek et al.[84]	RRID: SCR_002105; https://www.htslib.org/
BCFtools v1.12	Danecek et al.[84]	RRID: SCR_002105; https://www.htslib.org/
BEDtools v2.30.0	Quinlan and Hall[85]	RRID: SCR_006646; https://github.com/arq5x/bedtools2
MACSE v2.06	Ranwez et al.[86]	https://www.agap-ge2pop.org/macse/
HmmCleaner	Di Franco et al.[87]	https://metacpan.org/dist/Bio-MUST-Apps-HmmCleaner
AMAS	Borowiec[88]	https://github.com/marekborowiec/AMAS
IQ-TREE v2.1.2	Minh et al.[89]	RRID: SCR_017254; https://iqtree.github.io/
ASTRAL-III	Zhang et al.[90]	https://github.com/smirarab/ASTRAL
Newick utilities	Junier and Zdobnov[91]	https://anaconda.org/channels/bioconda/packages/newick_utils/overview
TreeShrink	Mai and Mirarab[92]	https://github.com/uym2/TreeShrink
R package: ape	Paradis and Schliep[93]	RRID:SCR_017343; https://cran.r-project.org/web/packages/ape/index.html
R package: castor	Louca and Doebeli[94]	https://cran.r-project.org/web/packages/castor/index.html
R package: vegan	Oksanen et al.[95]	RRID:SCR_011950; https://cran.r-project.org/web/packages/vegan/index.html
R package: cooccur	Griffith et al.[96]	https://cran.r-project.org/web/packages/cooccur/index.html

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
R package: picante	Kembel et al.[97]	https://cran.r-project.org/web/packages/picante/index.html
R package: Geiger	Pennell et al.[98]	https://cran.r-project.org/web/packages/geiger/index.html
R package: rgbif	Chamberlain et al.[99]	https://cran.r-project.org/web/packages/rgbif/index.html
R package: CoordinateCleaner	Zizka et al.[100]	https://cran.r-project.org/web/packages/CoordinateCleaner/index.html
R package: sf	Pebesma[101]	RRID: SCR_023393; https://cran.r-project.org/web/packages/sf/index.html
R package: raster	Hijmans et al.[102]	https://cran.r-project.org/web/packages/raster/index.html
R package: rgdal	Bivand et al.[103]	RRID: SCR_024422; https://cran.r-project.org/web/packages/rgdal/index.html
MaxEnt	Phillips et al.[104]	RRID: SCR_021830; https://biodiversityinformatics.amnh.org/open_source/maxent/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Orchid tubers aged 50-180 years old were sourced from ethnobotanical herbarium and museum collections in Norway, Sweden, Denmark, the Netherlands and England. Tuber collections were considered of interest when they were labelled as 'salep' (including various alternative spellings, such as 'saleb', 'salab' or 'sahlab'), or one of our target taxa. In total, 216 tubers were sampled from 34 museum/herbarium collections, housed in five institutions. While the exact history of many of these collections is unknown, they are acquired from diverse sources including traditional salep producing countries, such as Türkiye and Iran, but also more distant locations where they were likely imported, such as European (France, Germany) and Indian markets. Contemporary tubers were collected by purchasing them at markets in Türkiye and Iran in 2013-2014. Fieldwork in Türkiye was conducted during July and August 2014. Orchid tubers were purchased at markets in the cities of Van, Diyarbakir, Gaziantep and Kahramanmaras. Fieldwork in Iran was conducted in 2013-2014, where orchid tubers were purchased and interviews were conducted with salep vendors in 12 different cities.[25] In total, 428 tubers were collected from 40 different markets. Based on DNA quantity and quality, we selected 99 historical tubers and 97 contemporary tubers for library preparation and enrichment, aiming for a minimum of 2-3 and up to 5 tubers per market or museum collection (Tables S1 and S2). In addition, we extended a reference database for the Orchidinae subtribe generated by Veltman et al.,[35] which focusses on species occurring in regions where salep is traditionally consumed (Greece, Türkiye and Iran), by adding seven additional species of interest for which available tissue or DNA samples were too degraded to be included in the aforementioned study (Table S3).

METHOD DETAILS

DNA libraries and sequencing

Tissue was sampled from the tubers either by drilling a small hole and collecting powder or by grinding the tuber into a powder using liquid nitrogen. DNA extractions and library preparations were performed in dedicated lab facilities with established routines and procedures for molecular work on museum samples. DNA was extracted with a modified STE-CTAB protocol to minimise gelling caused by glucomannan.[105] Nonetheless, the high polysaccharide content of the tubers led to substantially lower DNA yields and purity than what is common from (fresh) leaf tissue. Leaf tissue from the seven additional reference samples was extracted with a CTAB protocol[106] with minor modifications. DNA purities, concentrations and integrities were quantified using Nanodrop One (Thermo Scientific, MA, USA), Qubit 2.0 (Life Technologies, CA, USA) and Fragment Analyzer (Agilent Technologies, CA, USA) or gel electrophoresis, respectively, where DNA content allowed this.

With the exception of 17 tuber samples that had a higher-than-average DNA quality and quantity, libraries of all tubers and additional reference samples were prepared with the Swift Accel-NGS 1S Plus DNA Library Kit (Swift Biosciences, MI, USA; Cat. No. 10096, 2021), which was chosen for its compatibility with low input and single-stranded or otherwise damaged DNA. No shearing step was carried out due to the fragmented nature of these samples and as to preserve as much DNA for enrichment as possible. Depending on initial DNA input, indexing PCR was performed with 9-14 cycles. Indexed samples were pooled in 50 equimolar groups consisting of 2-4 samples each with a total amount of 160–1560 ng DNA per group. Each group was cleaned using Ampure XP (Beckman Coulter, CA, USA) and eluted in 10 μl before performing target enrichment with the Orchidinae-205 baits following the MyBaits v5

manual. The RNA probes were hybridized at 62 °C for 24 hrs, and 14 amplification cycles were carried out after enrichment. Given their short fragment lengths, the enriched libraries were sequenced at 50bp paired-end on an Illumina NovaSeq S1 flowcell. DNA of the remaining 17 tubers was sonicated using a Covaris E220 focused ultrasonicator (Woburn, MA, USA) to approximately 400 bp fragments, prior to library preparation with the Swift Accel-NGS 2S Hyb DNA Library Kit (Swift Biosciences, MI, USA; Cat. No. 23023, 2021), enrichment with 79 other Covaris-sheared reference samples and 150bp paired-end sequencing on an Illumina NovaSeq SP flow cell, as described in Veltman et al.[35]

Sequence assembly and alignment

All 150PE reads were trimmed and assembled following the methods by Veltman et al.[35] Target exon sequences obtained in that study, which are available on Dryad,[107] were subsequently used as a reference file for mapping the 50PE reads, after trimming them with Trimmomatic v0.39[82] using the following settings: ILLUMINACLIP:"TruSeq3-PE-2.fa":2:30:10:2:TRUE LEADING:3 TRAILING:3 SLIDINGWINDOW:4:15 MINLEN:25. The reference sample with the highest mapping rate was then selected for reference-guided assembly of target loci in the following way: trimmed reads were mapped against the selected reference with the bwa-mem algorithm of the BWA short read aligner v0.7.17,[83] followed by read sorting and deduplication with SAMtools v1.12.[84] The deduplicated reads served as the basis for variant calling with the BCFftools v1.12[84] *mpileup* and *call* commands. Zero coverage regions were identified with BEDtools v2.30.0[85] and masked prior to creating a consensus sequence from the VCF file with the BCFtools v1.12 *consensus* command. Tuber sequences with less than 60% breadth of coverage were excluded from further analysis (Table S3).

Reference sequences were aligned with MACSE v2.06.[86] These alignments were enriched with the *de novo* assembled tuber sequences using the *-seq* option (for adding high quality data) and the reference-assembled tubers sequences using the *-seq_lr* option (for lower quality data). The enriched alignments were subsequently refined with the MACSE optimisation setting *-optim 2*, and exported by replacing any remaining internal stop codons with Ns (“NNN”) and frameshifts with dashes. A two-pronged trimming strategy was employed as per Veltman et al.,[35] by removing either poorly aligned segments with HmmCleaner only, or following this first trimming step with the additional removal of gappy columns with trimAl.[87,108] Given the higher level of congruent species identifications with alignments trimmed by HmmCleaner but without trimAl, we report only findings that result from the use of these alignments.

Species identification

Because species identification is sensitive to the chosen models of sequence evolution and criteria for assigning species identity, such as sequence similarity thresholds or clade membership,[37] we opted for a multi-criteria method to find a consensus between multiple competing paradigms: identification based on genetic or evolutionary distance (hereafter ‘‘distance-based’’) versus identification based on phylogenetic placement or monophyly (hereafter ‘‘clade-based’’), and for clade-based identification additionally whether it relies on a multi-species coalescent (MSC) or maximum likelihood (ML) approach. Trimmed gene alignments were concatenated with AMAS[88] and the concatenated alignment was used to calculate pairwise genetic distances between all samples using Kimura’s two-parameter (K2P) model of DNA evolution.[109] For each tuber, the reference sample with the smallest genetic distance was taken as a putative species identification. In addition to species identification based on sequence similarity, a phylogenomic framework was used to identify tubers based on species relationships in two ways: by finding the shortest path in the tree from any tuber to any reference sample (distance-based), and by finding the most recent common ancestor of a tuber with one or more reference samples (clade-based).

Gene trees were constructed with both sets of alignments using IQ-TREE v2.1.2[89] with the default options, including a model selection step, 1000 bootstrap replicates and a maximum of 1000 iterations, and running ten independent tree searches. Nodes with low support values (<30 UF-Boot) were collapsed with the Newick utilities[91] and implausibly long branches, which might indicate paralogs or spurious sequences, were removed with TreeShrink.[92] The curated sets of gene trees were used to construct species trees under the multispecies coalescent (MSC) as implemented in ASTRAL-III.[90] The gene alignments were also concatenated to construct a species tree under a maximum likelihood (ML) framework using IQ-TREE v2.1.2[89] with default settings. Likely species identities were assigned first by selecting the nearest neighbor among all reference samples in each species tree, based on cumulative branch length, with the *find_nearest_tips* function of the R package ‘castor’.[94] This resulted in an ML distance identification and a MSC distance identification. In addition, for both trees we assessed whether tubers were monophyletic with one or more reference species in well-supported clades based on two support thresholds (0.4 or 0.8 posterior probability in the MSC tree, and 80 or 95 UF-Boot in the ML tree). In case of monophyly with multiple species, a genus-level identification was assigned rather than a species-level identification. We assigned a species-level consensus identification if both clade-based identifications were in agreement with at least one distance-based method, or if one clade-based method agreed with multiple distance-based methods. In all other cases a genus-level consensus identification was assigned.

Distance-based identifications were used for summary statistics of community composition and phylogenetic diversity; only consensus species-level identifications were used for analyses linking salep species to ecological covariates (geographic coordinates, elevation and flowering time) and morphological measurements (tuber size and weight). We assessed the risk of possible misidentification due to a small number of missing reference species, by identifying outliers with an unusually large genetic distance to their nearest reference (Figure S7). We repeated all analyses without these outliers to ascertain that they did not influence the results. The species identifications for different methods and genetic distances to the nearest reference are summarised in Table S4.

QUANTIFICATION AND STATISTICAL ANALYSIS

Community ecology and phylogenetics

Species composition of salep was assessed on multiple levels: on the collection level, the temporal level, and the geographical level. For temporal analysis, salep collections were binned in five time intervals depending on their known or estimated age, of which four historical (1840–1879, 1880–1919, 1920-1949, and 1950-1979) and one encompassing all modern collections. The R package 'vegan' v2.6-4[95] was used for community ecological analysis, including the calculation of species diversity measures with the *diversity* function and assessing the homogeneity of collection dispersion with the function *betadisper*. Dissimilarity indices between collections were calculated with the *vegdist* function, and used as input for nonmetric multi-dimensional scaling (NMDS) with metaMDS. Phylogenetic diversity metrics were calculated with the R package 'picante'.[97] The R package 'cooccur'[96] was used to analyse species co-occurrences.

Hot nodes, defined by Saslis-Lagoudakis et al.[47] as "nodes on the phylogeny that include significantly more plants traditionally used in medicine", were identified using an R implementation of the *nodesig* function[110] as provided by Souza et al.[59] This function uses the R packages 'geiger'[98] and 'picante'[97] to compare the observed number of medicinally used species (i.e., species used for salep) against a probability distribution generated by randomizing the tips of the tree 1000 times. The resulting p-values indicate for each clade whether the number of species used as salep exceeds what is expected by chance. To account for the large variation in the frequencies at which species were observed, this test was adapted to randomise not only species use data (sampling of a species without replacement, where n equals the total number of species identified), but also with species count data (sampling of a species with replacement, where n equals the total number of tubers identified). Species descending from nodes that were significantly enriched for salep species ($p < 0.05$) or tubers ($p < 0.01$) in each time frame are considered likely to have been harvested in the past (historical salep) or at high risk of being harvested in present/near future (modern salep). Because the statistical power of this test is higher with larger sample sizes, it tends to be easier to detect significant deviations on deeper nodes with more descendants. For this reason, a stricter significance threshold was used for randomisation of counts rather than use data, in order to reduce the risk that significance would be inflated on deep nodes and produce false positives.

For geographic analysis, the sampling of locations of all modern salep were divided into five zones along a west to east gradient: southern Türkiye (Kahramanmaras and Gaziantep), southeastern Türkiye (Diyarbakir and Van), northwest Iran from the border with Türkiye extending along the Zagros mountains (Urmieh, Mahabad, Tabriz, Shahindezh, Sanandaj and Kermanshah), north Iran along the Caspian sea (Ardabil and Tehran), and northeast Iran along the border with Turkmenistan (Aq Eman, Kalaleh and Maraveh Tappeh). The relative frequencies of genera harvested were calculated for each city, with coordinates obtained from https://geohack.toolforge.org. The variation in frequency at intermediate points was estimated by means of a loess regression.

Morphology, flowering time and elevation data

During tissue collection, salep tubers were weighed with a precision scale at milligram precision, and their size was measured in millimeters with a caliper along three dimensions at two decimal points precision. The salep collections contained many more tubers than were selected for DNA extraction and sequencing, and in order to obtain a more comprehensive sampling of weight and volume measurements nearly all tubers were measured, yielding 1192 measurements. Flowering times of salep tubers with a positive species identification (Table S5) were taken from established field guides to orchids of the area.[111,112] The categorical variables were coded into numeric variables in the following way: each month received a number from 1-12, with decimal points corresponding to the beginning (0.25), middle (0.5) or end (0.75) of the month. For species where only the month was given, the midpoint of that month (0.5) was taken. The numerical values of the end and the start of the flowering season were then subtracted to obtain the estimated duration in number of months. Because we don't know where exactly tubers were collected from, we estimated their elevational distribution with the species occurrence records used for species distribution modelling (see below). For each species, the variation in elevation was summarised by their minimum, first quartile, median, third quartile and maximum values. For each positively identified salep tuber, the median of the corresponding species was taken as its expected elevation, or the most likely elevation at which a tuber was collected. We used the non-parametric Wilcoxon rank-sum test to identify significant differences in tuber weight, size, flowering time and elevation between different age groups, and corrected the p-values for multiple testing with a false discovery rate (FDR) of <0.05.

Species distribution modelling

Native orchid diversity in the study area was estimated by modelling habitat suitability for individual target species. The coordinates were downloaded from publicly available species occurrence records retrieved from the Global Biodiversity Information Facility (GBIF) and supplemented with records obtained during fieldwork for regions with low sampling density. The coordinates were downloaded with the package 'rgbif'[99] and subsequently filtered by setting the initial extent box to -11 to 58 longitudinally and 29 to 58 degrees latitudinally, while limiting the maximum number of coordinates per species to 50,000. This ensured that the subsequent niche models would cover a larger extent of the natural species range, which often exceeded our study area. Species with less than 10 records after cleaning with the R package 'CoordinateCleaner'[100] were dropped. The total number of records used for each species is reported in Table S6.

Eight species from different genera, with varying levels of data and distributions in space, were selected to run preliminary species distribution models with the Java version of MaxEnt[104] using the 19 historical (1970–2000) bioclimatic variables found in WorldClim[81]

in addition to altitude. Ten of these (bioclimatic variables 1, 2, 7, 9, 12, 14, 17, 18, 19 and altitude), which jointly had 86% of the explanatory power across all models, were chosen as environmental variables with which to predict habitat suitability for all available target species. The cleaned coordinates and the ten selected environmental variables were subsequently used to run the final distribution models. The models were evaluated based on their area under the curve values (AUC) and those with an AUC below 0.80 were discarded. In order to ensure the compatibility of the models for downstream analyses, habitat suitability thresholds ranging from 0.1–-0.7, at 0.1 intervals, were used to create presence-absence maps. The estimates of individual species distributions were compared with the most recent range maps based on expert opinion as presented by Kühn et al.[36] Threshold values were chosen to ensure congruence between the two; species for which all possible thresholds yielded results evidently contradicting known distributions were discarded. This left 80 species with distribution models of which 71 were represented in our phylogenomic framework.

The distributions based on the optimised thresholds were then resized to the extent of interest for the study (18 to 58 degrees longitudinally and 29 to 44 degrees latitudinally). The resized distributions were aggregated to calculate the total species richness (SR) for the target area. The phylogenetic diversity was calculated with the ML species tree generated in this study and the aggregated species distributions, using the R package 'picante'[97] *pd* function. The species present in the tree but not present in the final list of species with distributions were first dropped the R package 'ape'.[93] Local SR and PD values of different cities were extracted with the 'raster' and 'rgdal' R packages. Spatial analyses and manipulations were performed with the R packages 'raster'[102] and 'rgdal'.[103]

Provenance and trade analysis

For each modern salep sample that was positively identified, the minimum distance from the markets where it was sold to the estimated native range of the species was calculated with the *st_distance* function of the R package 'sf'.[101] To compare molecular evidence for modern salep trade with legal records of international salep trade, we downloaded comparative tabulations of commercially traded quantities of orchid roots from the start of CITES reporting (1975) to the present-day (2025) from https://trade.cites.org/, recovering 46 import and export quantities of putative salep roots reported between 1983-2024. Since none of these involved countries in our study region (Greece, Türkiye and Iran) as an exporting or originating country, we did not analyse these data further.