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The late rise of sky-island vegetation in the European Alps

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Our understanding of the emergence of mountain floras rests on our ability to infer how orogeny, landscape dynamics and climate change altered their evolutionary trajectories. Here we reconstruct the assembly of the diverse sky-island flora of the European Alps and test the impact of key geo-climatic events. We use a dated 5,231-species phylogeny, including 96% of the sky-island flora. The assembly of this flora occurred through the colonization of over a thousand distinct lineages, of which 46% speciated from their lowland or non-Alpine ancestor and 6% underwent in situ cladogenesis. The young ages of extant sky-island lineages show that their accumulation was decoupled from ancient geo-climatic events but accelerated throughout the Plio-Pleistocene. The sky-island vegetation therefore assembled through recent lineage turnover, which was triggered, rather than impeded, by Pleistocene glacial intensification. This perspective challenges previous assumptions and highlights the complex interplay of geo-climatic factors in shaping the intricate tapestry of alpine floras.

One of the most conspicuous characteristics of the biosphere is the uneven spatial distribution of biodiversity, which is intrinsically linked to the history of landscape change[1,2]. In hyper-diverse mountain regions, the combination of orogenic processes such as surface uplift and erosion, together with past global climate change, is thought to have primarily driven the accumulation of biodiversity over the course of millions of years[3]. In disparate geographical contexts, such physical processes have recurrently shaped sky islands, which are isolated or fragmented mountain ranges often harbouring unique and species-rich biotas[4,5]. Due to their geographical setting, sky-island biotas provide unique insights into the fundamental processes that underlie the evolutionary assembly of biodiversity hotspots, such as the immigration of new lineages into sky islands (here termed 'colonization'), which can be followed by the evolution of a single new endemic species (here termed 'single speciation') or by the evolution of multiple endemic species in situ (here termed 'cladogenesis') (see Fig. 1a for an explanation

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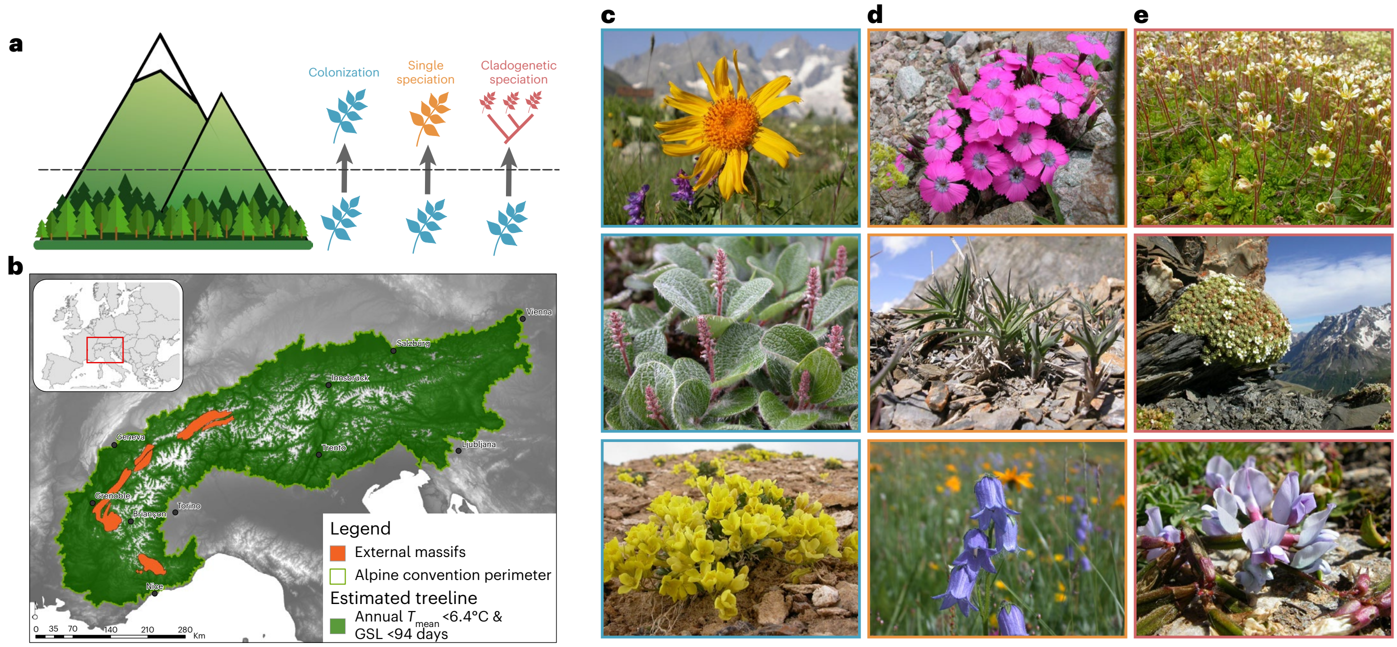

Fig. 1 | Flora of the European Alpine sky islands (EASI). **a**, The three main processes that led to the assembly of the EASI flora, whose boundary (dashed line) is defined by the treeline. Colonization is the arrival of a lineage in the Alpine sky islands, which typically results in a species occurring both above and below the treeline. Single speciation is the generation of a new endemic species due to the arrival of a lineage which diverges 'across' the boundary of the Alpine sky islands, potentially due to ecological (for example, divergence across the treeline) or geographic (for example, vicariance between biogeographic regions) drivers. Our data, however, do not allow us to infer the precise mechanisms driving speciation events. Finally, cladogenetic speciation is the diversification of a lineage within the sky islands resulting in a high-elevation clade. **b**, Map of the Alps where the present-day extent of the sky islands is illustrated by areas in white. The sky islands represent all areas above the treeline, defined by an annual mean temperature (T_{mean}) of 6.4 °C and growing season length (GSL) of <94 days (ref. 76). The external crystalline massifs, shown in red, constitute some of the highest mountains in the Alps, and their uplift 16–8 Ma is probably relevant in the history of the sky-island flora. **c**, Examples of colonist species, from top to bottom: *Arnica montana*, *Salix reticulata* and *Brassica repanda*. **d**, Examples of single-speciation species, from top to bottom: *Dianthus pavonius*, *Trisetum distichophyllum* and *Campanula barbata*. **e**, Examples of cladogenetic species, from top to bottom: *Saxifraga bryoides*, *Androsace helvetica* and *Oxytropis helvetica*. All photographs copyrighted by Jardin du Lautaret. See Extended Data Fig. 8 for more examples of EASI species.

of these three fundamental processes). How exactly these stages of evolutionary assembly were affected by past orogenic evolution and landscape dynamics is difficult to decipher, given the inconsistent results observed across various different mountains and lineages[6–8]. For example, while the evolution of some high-elevation lineages shows a strong correlation with mountain orogeny (for example, Neotropical tanagers and bellflowers in the Andes[9,10]), others arrived and diversified long after their mountain ranges attained their maximum topographic elevation[11,12].

The idiosyncratic response of lineages to past orogenic landscape change complicates the determination of the overall relationship between the assembly of sky-island biodiversity and the physical stages of orogeny when inferred from a subsample of biota. Previous reconstructions of flora assembly processes often focused on either the analysis of larger clades with extensive cladogenesis (for example, refs. 7,13), or used a more fragmentary sampling of many different genera (for example, refs. 11,14). In such cases, the colonization and subsequent speciation of lineages into sky-island endemics have been frequently underestimated despite their potentially substantial contribution to local diversity[15]. Here we aim to address this gap by using the first species-level phylogenetic analysis of an entire regional flora to reconstruct the evolutionary assembly of the European Alpine sky-island (EASI) flora.

The EASI flora comprises over 1,300 cold-tolerant plant species thriving in diverse alpine habitats above the treeline. Despite being extensively studied for more than 250 years (refs. 15–18), there is no comprehensive analysis regarding the relative contribution and timing of different assembly processes, or the biogeographic origins of the EASI flora. Although it is generally accepted that many of the larger Alpine genera originated either through migration from central Asian mountain ranges, for example, *Gentiana* and *Primula*[17,19,20], or through adaptation of Mediterranean ancestors, for example, *Globularia*[21], the absence of phylogenetic data has constrained the generalization of these findings across the entire flora[15]. Unlike the large radiation events described in the Andes and Tibeto-Himalayan region[22], diversification events in the European Alps (hereafter the Alps) are relatively small and only comprise a minor proportion of the EASI flora[15]. Consequently, although the diversification dynamics of the larger endemic genera have been extensively studied, for example, *Androsace*, *Primula*, *Saxifraga*[6,23,24], their macroevolutionary history may not entirely represent the history of the EASI flora as a whole.

The geo-climatic history of the Alps is complex, commencing ~35–30 million years ago (Ma) with the collision of the Adriatic and European plates. The climate during this period was warm and humid, and pollen records suggest that the flora had subtropical affinities[25]. By 23 Ma, the Alps had become strongly mountainous[26] and by the mid-Miocene they had attained or exceeded modern-day elevations[27]. This was followed by a period of considerable geomorphological change (16–8 Ma), which included the exhumation of the highest external crystalline massifs (for example, Mont Blanc, Fig. 1b)[28,29], as well as the establishment of new drainage patterns[30]. Concurrently, 15 Ma saw the start of a sudden drop in global temperatures by ~3 °C within 2 million years (Myr), known as the Mid-Miocene Climate Transition (MCT)[31]. The decreased temperature resulting from the MCT may have created ecological opportunities for the diversification of cold-adapted lineages both in the Alps and in other mountain ranges[24,32,33], but whether this major climatic transition triggered the development of sky-island floras remains unknown.

The MCT was followed by a gradual cooling phase, culminating in the Pleistocene glacial cycles. Initially mild and short, punctuated

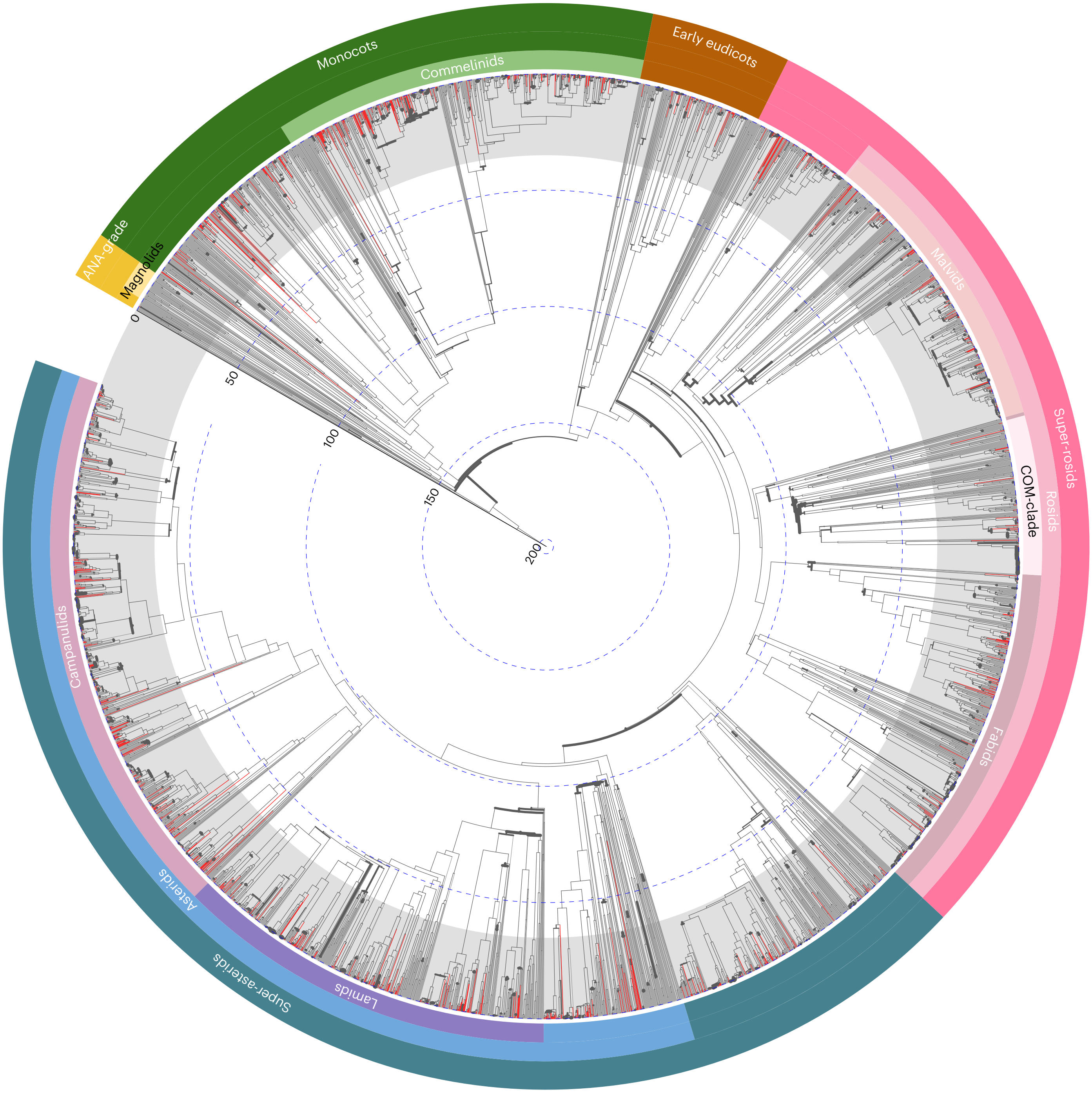

Fig. 2 | Time-calibrated ML phylogeny (branch lengths in Myr) containing 5,231 angiosperm species from 394 families. The orogeny of the Alps started ~35 Ma and is represented by the grey shaded area. Dashed blue circles indicate time in million years before the present. Red branches show EASI species and clades that were used in this study. Although the stem branches of these lineages are occasionally (14 out of 1,100 lineages) older than the initial orogenic phase of the Alps, they are constrained to a maximum age of 35 Myr in the analyses. Branch size is inversely correlated with node support. The colourful bands below the tips delimit different taxonomic groups.

by long interglacials, these cycles intensified ~1 Ma, contributing to massive and unprecedented erosion and to the relief development that ultimately shaped present-day Alpine landforms[34,35]. Pleistocene climate fluctuations triggered speciation in mountain regions globally by altering connectivity patterns[11,36,37]; in the Alps, they left a clear impact on species distributions and spatial genetic diversity[38–42]. Their net effect on biodversity accumulation within the EASI flora is, however, still debated, as some authors suggest that the glaciations caused pervasive extinction, or at least negligible diversification[15,24,43]. Others find evidence for speciation[21], particularly due to recurrent isolation in peripheral refugia[44], or on high peaks protruding from ice caps[45].

In this study, we aimed to address the above controversies by uncovering how historical environmental change has altered the evolutionary assembly of the EASI flora. To do so, we developed an unprecedented data set comprising the chloroplast genomes of 5,231 angiosperm species, which was used to reconstruct a dated phylogeny that comprehensively covers the flora of the Alps and the Arctic, both above and below the treeline, as well as close relatives from other

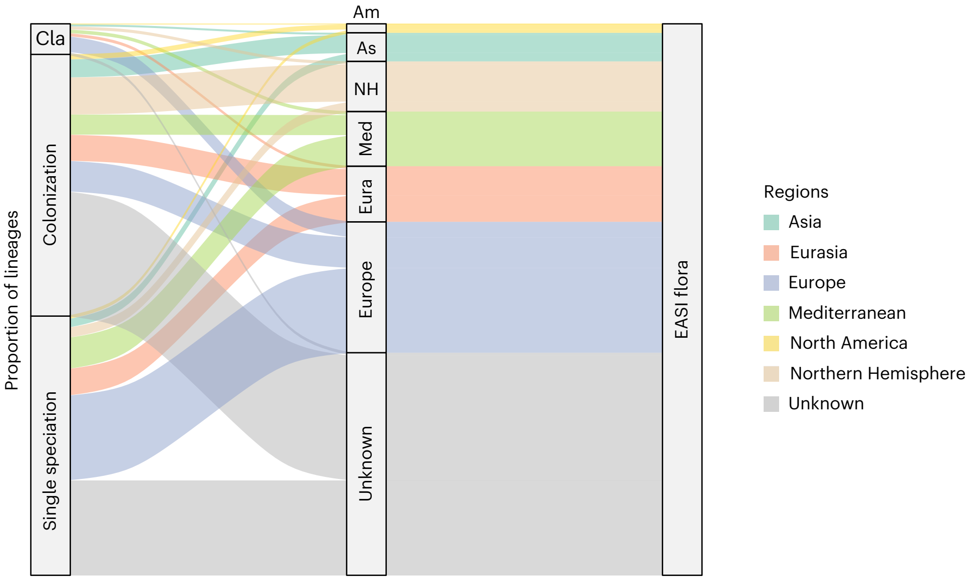

Fig. 3 | The biogeographic origins of all EASI lineages based on a literature search. The thickness of the bars and ribbons is proportional to the number of lineages of each category in the EASI (n = 1,100). The category 'Unknown' includes lineages where there was no biogeographic reconstructions available or whose reconstructions were ambiguous. Cla, cladogenesis; As, Asia; Eura, Eurasia; Med, Mediterranean; NH, Northern hemisphere; Am, North America. See also Supplementary Table 2 for a more detailed breakdown of biogeographic origins.

mountain ranges such as the Pyrenees, Carpathians, Balkans and Apennines (Extended Data Fig. 1)[46–48]; the ~1,300 species that make up the EASI flora are deeply embedded within this sampling scheme. Biogeographic and elevational ancestral state reconstructions were used to characterize the assembly processes (for example, colonization, single speciation or in situ cladogenetic speciation, Fig. 1a) that led to the formation of EASI lineages, here defined as all descendants of a sky-island colonization event (see Extended Data Figs. 2 and 3, and Methods section 'Defining assembly processes' for the inference of these processes). These data were supplemented by using existing literature to source the biogeographic origins of EASI lineages.

We hypothesize that four key events in the Alpine geo-climatic history may have altered the rates of assembly processes in the EASI flora. First, we hypothesize that the early orogeny of the Alps (30–23 Ma) initiated the assembly of the flora, as mountain uplift is typically associated with diversification due to the creation of new environmental niche space and the initial formation of elevational zones. Second, that rates of colonization and speciation increase after the MCT ~15–13 Ma, as lower temperatures may have led to an expansion of alpine habitats, and thus an increased ecological opportunity for colonization and local speciation. Third, that lithological and geomorphological changes associated with the increased exhumation of the external massifs (16–8 Ma) may have further expanded alpine habitats, creating geological and topographical opportunity and altered connectivity patterns, and consequently increasing assembly rates. Although we test the latter two hypotheses separately and alone, their nested timing requires them to be interpreted together. Lastly, we hypothesize that glacial intensification and associated Alpine relief development starting 1 Ma may have increased net diversification rates through repeated geographical isolation and mixing of different lineages, or alternatively, slowed down net diversification due to extreme environmental conditions causing widespread extinction.

Results

Phylogeny

Our work relies on a large-scale effort of sampling and genomic sequencing targeting the European Arctic–Alpine flora of vascular plants, conducted by the PhyloAlps and PhyloNorway initiatives (https://phyloalps.osug.fr/, Extended Data Fig. 1)[4648]. These initiatives recently contributed a megaphylogeny of 7,697 plant accessions (5,600 species) inferred using maximum likelihood on a concatenated DNA matrix of 83 coding and non-coding chloroplast genes (59,903 bp in total, ref. 48). This megaphylogeny was subset to obtain an angiosperm-only phylogeny of 5,231 species (hereafter called the ML phylogeny), which includes 82% of the flora of the Alps[49] and 96% of all sky-island species of the Alps (Fig. 2). The ML phylogeny included accessions from 394 angiosperm families, therefore allowing dating using TreePL (v.1.0)[50] with 130 fossil constraints (Extended Data Fig. 4)[51]. In general, our inferred node dates subtending alpine plant clades correlated well with those previously published (Extended Data Fig. 5).

The assembly of the EASI flora

On the basis of the dated ML phylogeny and species' geographical and elevational distributions, we infer that the Alpine sky-island flora was assembled through 1,100 distinct colonization events (Fig. 2 and Extended Data Fig. 2). After colonization, 48% of the lineages failed to differentiate (same species found below and above the treeline), while 46% underwent single speciation (speciation across the treeline, leaving one species endemic to the sky island) and 6% underwent in situ cladogenetic speciation (several EASI species descending from the same colonization event; Fig. 3). Of the 347 genera present in the sky islands, 166 (48%) have colonized the sky islands multiple times, with genera such as *Carex*, *Festuca*, *Hieracium*, *Ranunculus*, *Salix* and *Saxifraga* having more than 20 colonization events each (Extended Data Fig. 6, see also refs. 52–54). Clades that diversified in situ tended to be small, with a median of three species per clade. Only four EASI clades in the genera *Gentiana*, *Pedicularis*, *Phyteuma* and *Primula* contained over 15 species (Extended Data Fig. 7).

Biogeographic origins of EASI lineages

A comprehensive literature search for the biogeographic origins of the EASI flora revealed Europe as the predominant origin for lineages for which data were available (Fig. 3). The coarse scale of many biogeographic reconstructions makes it challenging to discern whether these lineages have arrived from other mountains across the European Alpine System, or from the temperate lowland flora. Relatively few sky-island

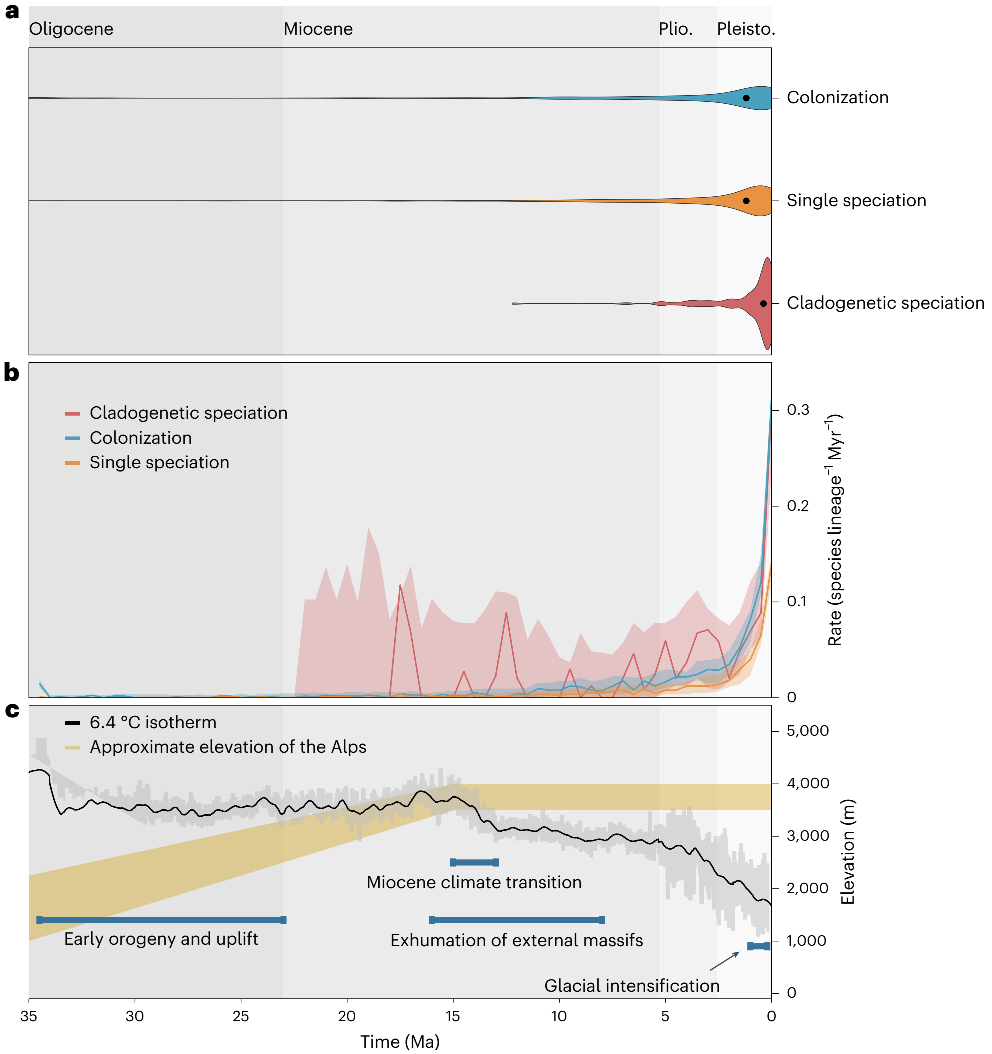

Fig. 4 | Rates of assembly of the EASI flora in relation to major climatic and geological events. a, Violin plots of the distribution of individual species ages in the EASI flora for species originating through in situ cladogenesis ($n = 281$), single speciation ($n = 508$) and colonization ($n = 531$). Black points indicate the median species age. **b**, Rates of assembly processes through time, calculated in 500-kyr intervals. Solid lines show rate estimates derived from the ML phylogeny, shaded ribbons represent the full range of rate estimates at each time point calculated across 100 bootstrap phylogenies. **c**, Timeline of selected geo-climatic events in the European Alps. The time intervals of major climatic and geological events that we hypothesize affected the assembly rates of the EASI flora are shown as blue horizontal bars that are vertically displaced for legibility. We define the sky islands to be all areas above the 6.4 °C isotherm. Therefore, for the sky islands to exist, the Alps need to have areas of greater elevation than the elevation of the isotherm. The estimated elevation of the 6.4 °C isotherm is shown by the solid black line (using temperature data smoothed at 1-Myr resolution) and by the grey bands (using temperature data smoothed at 20-kyr resolution[77]). The yellow band shows the range of maximum elevations for the Alps through time: when the band extends above the 6.4 °C isotherm, sky islands have the potential to form. Note that this maximum elevation of the Alps is approximate, as few estimates of paleo-elevation exist. We do, however, know that the elevation of the Alps had reached 4,000 m by 15 Ma, and that relief greatly increased during the Pleistocene[26,27,35]. Plio., Pliocene; Pleisto., Pleistocene.

lineages and only four clades (within *Aconitum, Callianthemum, Gentiana* and *Rhododendron*) directly originated in Asia.

Temporal assembly dynamics of the EASI flora and the impact of past geo-climatic events

The temporal variation in different assembly rates unveiled intriguing patterns. Cladogenetic speciation events first occurred ~17.5 Ma (Fig. 4b), suggesting that the ancestors of the extant EASI flora only appeared after the early orogenic phase of the Alps. Around 7 Ma, cladogenetic speciation rate began to rise consistently, culminating in a threefold increase within the past 2 Myr. Colonization rate (as estimated from the stem age of all sky-island lineages) and single-speciation rate remained close to zero for much of Alpine history. Only during the Pliocene did these rates begin to increase, followed by an exponential increase at the beginning of the Pleistocene (Fig. 4b). The recent rise in the rates of assembly processes is reflected in the young age of most EASI species (Fig. 4a), as colonization and single-speciation events both have a median age of 1.19 Myr. Similarly, the median age for an extant species derived from in situ cladogenesis is 380,000 years, with 71% being younger than 1 Myr. Finally, an island biogeography model[55] showed that the average extinction rate (0.80 species lineage^{-1} Myr^{-1}) was considerably higher than the cladogenesis rate (0.38 species lineage^{-1} Myr^{-1}) during the EASI flora's evolution (Extended Data Table 1).

We tested whether certain geo-climatic periods influenced assembly processes by conducting breakpoint analyses on the temporal variation of the rates of colonization, single speciation and cladogenesis. We found that for all three assembly processes, models that incorporated a break point associated with glacial intensification had a substantially better fit than those without (Fig. 5, and Supplementary Fig. 1 and Supplementary Tables 3–5). The addition of break points associated

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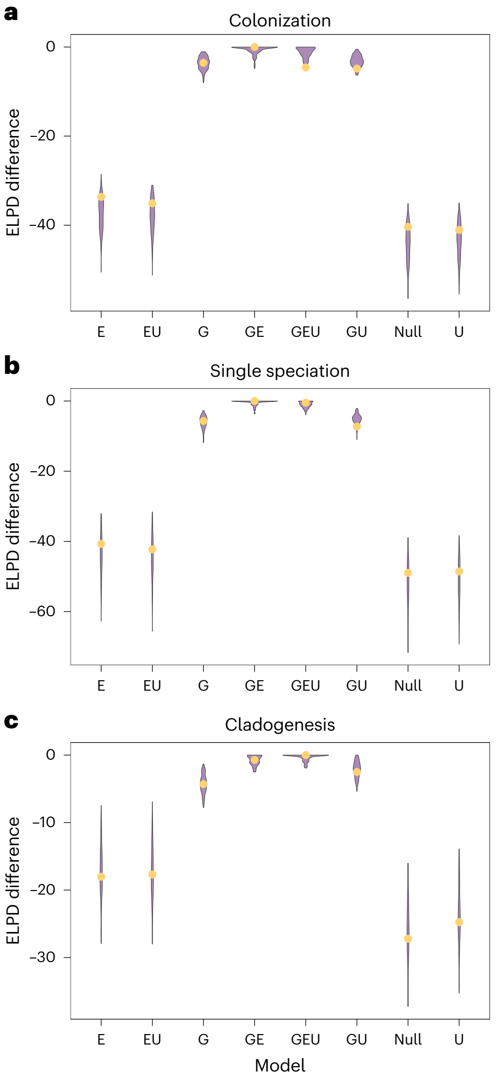

Fig. 5 | Model evaluation for breakpoint regression analyses. a–**c**, Break point regression analyses using Bayesian inference on colonization (**a**), single speciation (**b**) and cladogenesis (**c**) assembly rates estimated from both 100 bootstrap trees (purple violin plots) and the ML tree (yellow points). Models with an estimated log posterior density (ELPD) difference of zero are considered to be the optimal model. Codes on the *x* axis denote model parameters: G, model contains a break point between 1.2 and 0.8 Ma, representing the period of glacial intensification and relief development; E, model contains a break point between 16 and 8 Ma, an interval that contains the exhumation of the external massifs and the Miocene Climate Transition; U, model contains a break point between 35 and 23 Ma, representing the early orogeny and uplift of the European Alps; Null, model contains no break points.

with the other periods of interest (early orogeny, MCT and the exhumation of the external massifs) tended to slightly improve model fit over glacier-only models. Of these, however, none are clearly better, as their estimated log posterior density differences were all close to zero. Models containing only the early orogeny of the Alps, the exhumation of the external ranges and/or the MCT performed similarly to a null model without break points.

Discussion

Our study stands out for its unprecedented scale, by using a species-level phylogeny with a nearly complete coverage of the sky-island flora of the Alps. Our primary objective was to systematically assess how past landscape and climate change shaped the evolutionary trajectory of a biodiverse mountain region. Despite the inherent limitations and uncertainties associated with large-scale phylogenetic analyses, our results offer novel insights into the tempo and drivers of temperate sky-island assemblages. We observed that the EASI flora is notably young and that its origin predominantly occurred after the major phases of Alpine orogeny. Instead, its assembly was primarily driven by the extensive colonization of mainly European lineages that underwent frequent events of single speciation, or more rarely cladogenesis, coinciding with the Pleistocene glacial intensification.

The origins of high-elevation floras have traditionally been linked to orogeny, but our findings challenge this notion, revealing that the majority of current plant lineages colonized or speciated in the sky islands within the past 5–10 Myr, that is well after the early orogeny and uplift of the Alps. Our results thus corroborate the increasingly frequent reports of a temporal disjunction between orogeny and the accumulation of high-elevation lineages, particularly in older mountain ranges such as the African sky islands[11,12,14,56,57]. We propose that a plausible explanation for this temporal disjunction is that the warmer climate and lower elevations of the Alps during the late Oligocene and early Miocene would have prevented the formation of an alpine zone, which is a necessary precondition for the assembly of a sky-island flora. Comparing the 6.4 °C isotherm through time to a point estimate of paleo-elevation from the Mid-Miocene[27] does indeed suggest that the sky islands may only have started to form 15 Ma (Fig. 4c), which coincides with the appearance of some of the oldest EASI lineages.

Another, non-exclusive, explanation for the temporal disjunction is that extinction may have eliminated many of the original EASI lineages. The late rise of the sky-island flora, together with the abundance of single-species lineages and small clades, implies a large overall turnover in biodiversity where the continual extinction of previous lineages left room for the current vegetation. This interpretation is supported by our island biogeography model, which inferred that rates of extinction exceeded rates of cladogenesis. The Pleistocene climate cycles are the most plausible contributors to extinction. However, the initial recruitment and long-term persistence of plant lineages into the sky islands may also have been difficult. High-elevation zones across the Alps were potentially less extensive during the Miocene[26]. As a result, alpine habitats may have been small and fragmented, making them extinction prone and less likely to be colonized[58]. The later uplift of the external massifs (16–8 Ma) and of the Eastern Alps 6–5 Ma (ref. 59) would have increased the total area of high-elevation zones across the Alps, which, coupled with a lower treeline driven by cooler Pliocene temperatures, may have expanded existing alpine habitats. In turn, this could have created increased opportunities for speciation and colonization into the sky islands, and enabled the persistence and accumulation of alpine lineages from 5 Ma onwards.

We found that the climatic instability of the Quaternary, rather than orogeny, was the primary driver of the contemporary EASI flora. The vast majority of EASI species originated within the past 1 Myr, a date that coincides with the intensification of the Pleistocene glacial cycles. During this period, extensive and persistent glaciers reached into the Alpine forelands[60] and had a profound effect on the topography of the Alps. Glacial erosion incised valleys at a rate of 1 km Myr^{-1} to create the strong relief present in the Alps today[35]. The greater relief, coupled with the climate fluctuations, would have worked together to create a ‘species pump’ effect[61]. As Alpine plant distributions retreated and expanded in response to temperature changes, their movement across the rugged landscape would have modified their degree of connectivity and isolation, driving population divergence[39,40,62]. The species pump effect is increasingly recognized as a major driver of Quaternary speciation in mountains worldwide[37,56,57] and appears likely to be a primary driver of diversification in European sky islands as well.

The recent rise in net diversification rate challenges past research that showed that the diversification of plant clades was either slowed or remained constant during the Quaternary[15,23,24,63]. We, however, find that the majority of diversification events within the EASI flora occurred in clades of 2–3 species (61% of all clades), despite our relatively poorer sampling of the regional species pool predisposing our analyses to reconstruct larger clades. Previous phylogenetic studies tended to concentrate on species-rich lineages (for example, ref. 24), which, at least in the Alps, do not appear to be representative of the flora. We therefore suggest that caution should be used when extrapolating clade-specific results to the evolution of an entire flora, and that the overall contribution of species-poor lineages to assembly processes should not be underestimated. This finding also emphasizes the utility of biodiversity genomics, that is, the systematic sampling and sequencing of entire floristic regions, to provide novel insights into macroevolutionary patterns.

We highlight an unexpectedly large contribution of colonization to the assembly of the EASI flora. Over 90% of lineages arrived through colonization, eventually followed by single-speciation events, while in situ cladogenesis only played a relatively minor role. Most lineages originated in Europe, although the coarse nature of many biogeographic reconstructions prevents speculation over whether the main source is the lowland temperate flora or other European mountains. We expected stronger migration links with Asia, since several of the larger EASI genera, such as *Primula*, *Androsace*, *Pedicularis* and *Gentiana*, have their centres of diversity in the Tibeto-Himalayan region. Of these genera, we find that only *Gentiana* has directly dispersed into the EASI flora; the rest probably arrived through either stepping-stone migration via other regions or through direct dispersal to lower elevations in the Alps before moving into the sky islands (for example, *Androsace* and *Pedicularis*).

Our reconstruction of the timing of colonization is probably overestimated. By using stem node ages as the measure of colonization date, we infer the maximum possible age of colonization. Incomplete sampling of closely related lineages compounds this problem, as missing lineages effectively increase the length of the stem branch subtending the focal group. Despite this, we find that colonization rate peaked during the past 1 Myr, when the expansion and retreat of the glaciers would have caused waves of species to arrive and disappear with each climate oscillation. Recolonization after the last glacial period is still an ongoing process, as many high-elevation plant species in the Alps have not yet occupied their full potential niche[64]. Interestingly, the treeline does not appear to be a major environmental barrier to colonization, as it was breached multiple times in nearly half of the genera present on the sky islands. The permeability of the Alpine treeline, in comparison with that of tropical sky islands[11], is probably due to a long-postulated idea that regional temperate floras that are already pre-adapted to cold and open habitats find it easier to colonize alpine zones[65–68]. It therefore appears that in general, the EASI flora consists of a subset of the European flora[18], potentially filtered by the ability to disperse and maintain viable populations into the sky islands after the disturbance of the Pleistocene glacial cycles[64].

Our study provides an unprecedented reconstruction of the history of an entire high-elevation mountain flora and demonstrates that Quaternary climate dynamics left a stronger signature on the assembly and composition of the EASI flora than older geo-climatic events. Most extant lineages assembled through recent colonization and local speciation, against the backdrop of a high extinction rate, a pattern previously unknown among temperate mountain systems. It is, however, possible that similarly large contributions of colonization in other mountain regions remain undetected due to a sampling bias towards large clades. We therefore encourage future studies to include species-poor lineages, as their cumulative effect can have a substantial impact on the interpretation of past biotic assembly.

Methods

Sampling and sequence data

This work uses a recently released database of low-coverage shotgun sequencing of whole-cell DNA and inferred megaphylogeny for 7,697 Arctic–Alpine accessions[48]. The data are based on a nearly complete sampling of all vascular plant species occurring in the European Alps (4,640 samples, PhyloAlps project), to which were added all Arctic species (2,070 samples, PhyloNorway project), and 421 species from related lineages occurring outside the Alps in the European Alpine System (Carpathians, Pyrenees, Apennines, Balkans) and even Asia (for example, genus *Braya*). The collection also includes 566 plant accessions from families not represented in our sampling, to allow further fossil dating. All raw reads data generated by the PhyloAlps and PhyloNorway projects are available at the EMBL-EBI Short Read Archive under the following bioprojects: PhyloAlps (PRJEB30497, PRJEB48874, PRJEB50489, PRJEB82787), PhyloNorway (PRJEB43865, PRJEB48693, PRJEB50550).

Plastid gene capture

We performed in-silico capture of 79 coding DNA sequences and four non-coding rRNA genes from the chloroplast using the software ORTHOSKIM (v.1.6)[69] using a reference database of 577 annotated cpDNA genomes and 738 rDNA regions, previously produced in ref. 46. ORTHOSKIM is effective in capturing sequence data for organisms with complex cpDNA structures while dealing with issues emerging from paralogy, contamination, inter-organelle sequence transfer and biased predictions of the intron–exon junctions. BLAST tests against the NCBI database suggested that 219 libraries had dubious taxonomic assignation and were further discarded from the analyses.

Alignment and phylogenetic inference

All obtained sequences were aligned and cleaned within ORTHOSKIM using MAFFT[70] and trimAl algorithms[71], and paralogous sequences were identified and removed using a custom algorithm[69]. All genes were concatenated in a partitioned supermatrix, except for ycf1 and ycf2 because of their high-sequence variability among plants. Libraries with more than 70% of missing data were removed from phylogenetic analyses, except for parasitic taxa. Maximum likelihood analyses were performed using IQ TREE 2 (v.2.1.2)[72] under the GTRGAMMA model on the partitioned supermatrix. Node supports were assessed using 1,000 ultrafast bootstrap (UFBoot) replicates along with the Shimodaira–Hasegawa (SH)-like approximate likelihood ratio test under 1,000 replicates. We used the hill climbing nearest neighbor interchange (NNI) search option to reduce the risk of overestimating branch supports and the -wbtl option to compute branch length on each bootstrap tree.

Dating the phylogenetic tree

We trimmed the megaphylogeny and 100 bootstrap replicates of ref. 48 to only include seed plants, with *Ginkgo biloba* as the root. Divergence time estimates for the phylogeny and bootstrap replicates were calculated using a penalized likelihood method implemented in TreePL (v.1.0)[50]. To determine the appropriate level of rate heterogeneity across the phylogeny, a cross-validation step was conducted to find the optimal smoothing parameter. The analysis was calibrated using all fossils from the database of ref. 51 that were able to be unambiguously placed on the phylogeny, coming to a total of 130 fossils (Supplementary Table 6, Appendix 3). We used information from this database to determine the minimum age of each calibration point, while the maximum age of all calibrations was set to 247 Ma, that is, the minimum age of most recent common ancestors of all living flowering plants[51,73], except for the maximum age of the crown of angiosperms, which was left unconstrained. When there were multiple fossils that could be assigned to a node, the fossil with the oldest minimum age was used.

Defining assembly processes

We considered a species to be part of the EASI flora if it commonly occurred in any elevational zone from the subalpine zone and above, regardless of whether it also occurred at lower elevations. We used Flora Alpina[49], supplemented when necessary, by GBIF (www.gbif.org) and Inventaire National du Patrimoine Naturel (https://inpn.mnhn.fr/, France) to determine the elevational and geographic distribution of each species in our data set. The taxonomy of these databases was updated using the Euro+Med PlantBase (http://www.europlusmed.org) as our reference.

We aimed to evaluate the relative contributions of different assembly processes (colonization, single speciation, cladogenesis) to the formation of the EASI flora. As the flora of the Alps is strongly linked with that of the broader European Alpine System (EAS)[15,18], we wanted to consider this shared biogeographic history when defining the assembly processes. Our definitions of the assembly processes were therefore based on (1) past and present elevational distribution in the Alps and (2) past and present geographic distributions across the EAS. Past distributions were inferred with ancestral state estimations, run using the 'ace' function in the R package 'ape' (v.5.7-1)[74] with marginal estimation and an all-rates-different model. The full phylogeny was sliced into large clades originating at 35 Ma for this analysis to allow for variation in the rates of transition in and out of the sky islands, and to restrict the maximum age of all assembly events to the age of the Alps. We opted for this method over the ClaSSE-based analysis of ref. 7 due to computational constraints.

A species was considered a colonist if its current elevational distribution extends into the sky islands, but both its current and past geographic distribution included non-EAS regions. Examples of colonists include *Arnica montana* and *Salix reticulata*, which occur throughout Europe and the Northern Hemisphere, respectively (Fig. 1a). We defined single-speciation species as sky-island species whose core distribution is currently in the EAS, but their ancestor had either non-EAS or low-elevation distributions. Thus, a single-speciation event represents a colonization event into the sky islands across elevational or geographic boundaries, which was then followed by speciation. Examples of single-speciation events include *Campanula barbata* and *Dianthus pavonius* (Fig. 1b). Lastly, we deemed in situ cladogenesis to have occurred if all ancestors of a clade of sky-island species had diversified in the EAS (that is, their ancestors were both high-elevation and EAS species), for example, *Androsace helvetica* and *Euphrasia picta* (Fig. 1c). Any speciation events within such a clade that led to a non-sky-island species were not counted as a speciation event in the sky islands. Importantly, the creation of an EASI clade implies one initial colonization event into the sky islands. See Extended Data Figs. 2 and 3 and Supplementary Methods for a more detailed explanation of this classification system. We use the term lineage to refer to all descendants of a sky-island colonization event. Note also, that our data do not allow us to infer the mode of speciation (parapatry, allopatry, founder effect and so on), and therefore we chose to use terminology that is agnostic to how speciation occurred.

Incomplete sampling has the potential to alter the results of ancestral state reconstructions described above[75]. For instance, two different sky-island lineages could be reconstructed as a single EASI clade because closely related lowland and/or non-EAS species had not been included in the analysis. Although we had a thorough sampling of the Alpine flora, including most species from lower elevations, we did not necessarily have a thorough sampling of closely related species that occur outside of the Alps. Where possible, we therefore compared our results to published biogeographic studies and changed our assignations of colonist, single-speciation or cladogenetic events if necessary (Supplementary Table 1). For example, we reconstructed most Alpine *Gentiana* as a single large sky-island group, but then split it into several smaller clades, as the more thorough sampling of Asian *Gentiana* in ref. 20 showed that the genus had multiple entries into Europe.

Biogeographic origins of sky-island lineages

To find the area of origin of each EASI lineage, we conducted a literature search for studies that contained biogeographic reconstructions of the ancestor of the lineages of interest (that is, the lineage's stem node). In the case of a lineage containing multiple species, at least one of the species had to have been present in a given study for it to be used as a source of information. Often, we were only able to find phylogenetic information. In these cases, we searched for the geographic distribution of the larger clade in which our focal species or clade was embedded using the Plants of the World Online database (https://powo.science.kew.org/) and the Euro+Med online database (http://ww2.bgbm.org/EuroPlusMed). We then deemed the geographic origin of the taxon in question to be the union of geographic ranges of the majority of all taxa that were closely related to it. When our focal Alpine taxon was part of a large polytomy with an unclear biogeographic distribution, had no closely related taxon, or no satisfying phylogenetic or taxonomic information could be found, then its ancestral area was classified as unknown. By choosing to do a literature search over inferring ancestral areas on the basis of our phylogeny, we aimed to reduce the impact of bias due to any incomplete sampling of closely related non-Alpine lineages.

Temporal reconstruction of assembly processes

To calculate the average per lineage rate of assembly processes over the past 35 Myr, we used DAISIE (Dynamic Assembly of Islands through Speciation, Immigration and Extinction)[55], a likelihood-based method implemented in the R package 'DAISIE' v.3.0.1. DAISIE combines island biogeographic theory with phylogenetic information, and unlike most phylogenetic comparative methods, has the advantage of being able to incorporate multiple species-poor lineages into a single analysis. Since there is evidence that carrying capacity in the Alps has not been reached[64], we ran all models without diversity dependence. We assumed that the regional species pool contained 2,300 species, that is, all Alpine species that do not occur in the sky islands, and that the age of the sky islands was equivalent to the age of the Alps (35 Myr).

We calculated the temporal rate of colonization and single speciation by counting the number of new lineages generated by these processes in 500,000-year time intervals from 35 Ma to the present, and standardizing by a regional species pool that we assumed has stayed constant at 2,300 species (the approximate number of non-sky-island species in the Alps)[49]. The calculation of colonization rate here includes all arrivals into the sky islands over time, that is, it includes the arrival of all lineages that would remain colonists, together with the predecessors (stem lineages) of sky-island clades and single species. Note that the time of colonization is a maximum age estimate, as we assume colonization occurred at the same time that a given lineage originated. Finally, the rate of cladogenesis was calculated by dividing the number of new cladogenetic lineages originating in each 500,000-year time interval by all colonist, single species and cladogenetic lineages present on the sky islands in the previous time interval. The temporal reconstructions of the three assembly processes were repeated on the 100 dated bootstrap trees, with the range of temporal rates across the bootstrap results used as a measure of dating and phylogenetic uncertainty.

Timeline of sky-island appearance

We estimated when areas suitable for the formation of sky islands may have existed over the course of the Alpine orogeny by comparing the elevation of the 6.4 °C isotherm (treeline temperature limit)[76] to the maximum elevation of the Alps. If the maximum elevation of the Alps exceeded the elevation of the 6.4 °C isotherm at a given time period, it is theoretically possible that the sky-island flora could start to form as there would be available area above the treeline. We calculated the isotherm's elevation, z, with the following formula:

$$z(6.4\,^{\circ}\mathrm{C}) = \frac{(17\,^{\circ}\mathrm{C} + \mathrm{DT} - 6.4\,^{\circ}\mathrm{C})}{4\,^{\circ}\mathrm{C}\mathrm{km}^{-1}} \qquad (1)$$

where 17 °C is the present-day temperature at sea level, DT is the global temperature anomaly with respect to the temperature of today, inferred from δ^{18}O levels in benthic foraminifera[77], 6.4 °C is the treeline temperature limit[76], and 4 °C km^{-1} is the environmental lapse rate, which we assumed to remain constant over time.

Very few estimates of Alpine paleo-elevation currently exist. Reference 27, however, estimated that 15 Ma, the Alps had reached maximum elevations of >4,000 m, which is similar to the present-day maximum elevation. We, therefore, assumed that the elevation of the Alps increased at a steady rate from the start of the orogeny until 15 Ma, whereafter elevation remained approximately constant[26]. During the Pleistocene, relief substantially increased due to glacial erosion[35].

Influence of geo-climatic processes on the formation of the EASI flora

We used a hypothesis testing framework to find whether four historical events have impacted the rates of sky-island assembly processes. These events were (1) the uplift of the Alps at 35–23 Ma, (2) the MCT at 15–13 Ma, (3) the exhumation of external massifs at 16–8 Ma and (4) the intensification of the glaciers at 1.2–0.8 Ma. To do this, we conducted a breakpoint regression analysis using Bayesian inference with the R package 'mpc' (v.0.3.2)[78]. Strong uniform priors were set across the time intervals of interest to force a break point in that interval. We fitted models with one to three break points containing all combinations of the historical events, except that the MCT and the exhumation of external massifs were never included in the same model, as their time intervals overlapped. Models were parameterized with unconnected intercepts and slope values set to zero. We then found the optimal model of our model set by using leave-one-out cross-validation implemented in the R package 'loo' (v.2.5.1)[79]. This process was repeated on the temporal rates from the 100 bootstrap trees for each of the three assembly processes.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data needed to replicate the findings of this study are available on figshare at https://doi.org/10.6084/m9.figshare.25459135 (ref. 80). All raw reads data generated by the PhyloAlps and PhyloNorway projects were submitted to the EMBL-EBI Short Read Archive under the following bioprojects: PhyloAlps (PRJEB30497, PRJEB48874, PRJEB50489, PRJEB82787), PhyloNorway (PRJEB43865, PRJEB48693, https://www.ebi.ac.uk/ena/data/view/PRJEB50550). An online database of genome skimming of Arctic–Alpine plants, representing all information regarding samples, extraction, sequencing and reconstructed genomic data for the PhyloAlps and PhyloNorway projects can be found at https://phyloalps.osug.fr/main/home (ref. 81). Source data are provided with this paper.

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Competing interests

The authors declare no competing interests.

Additional information

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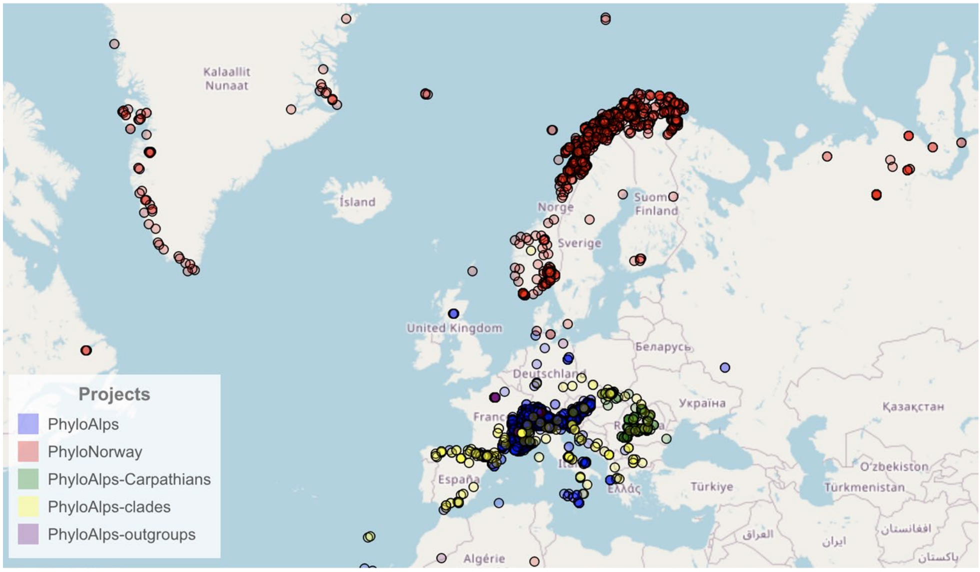
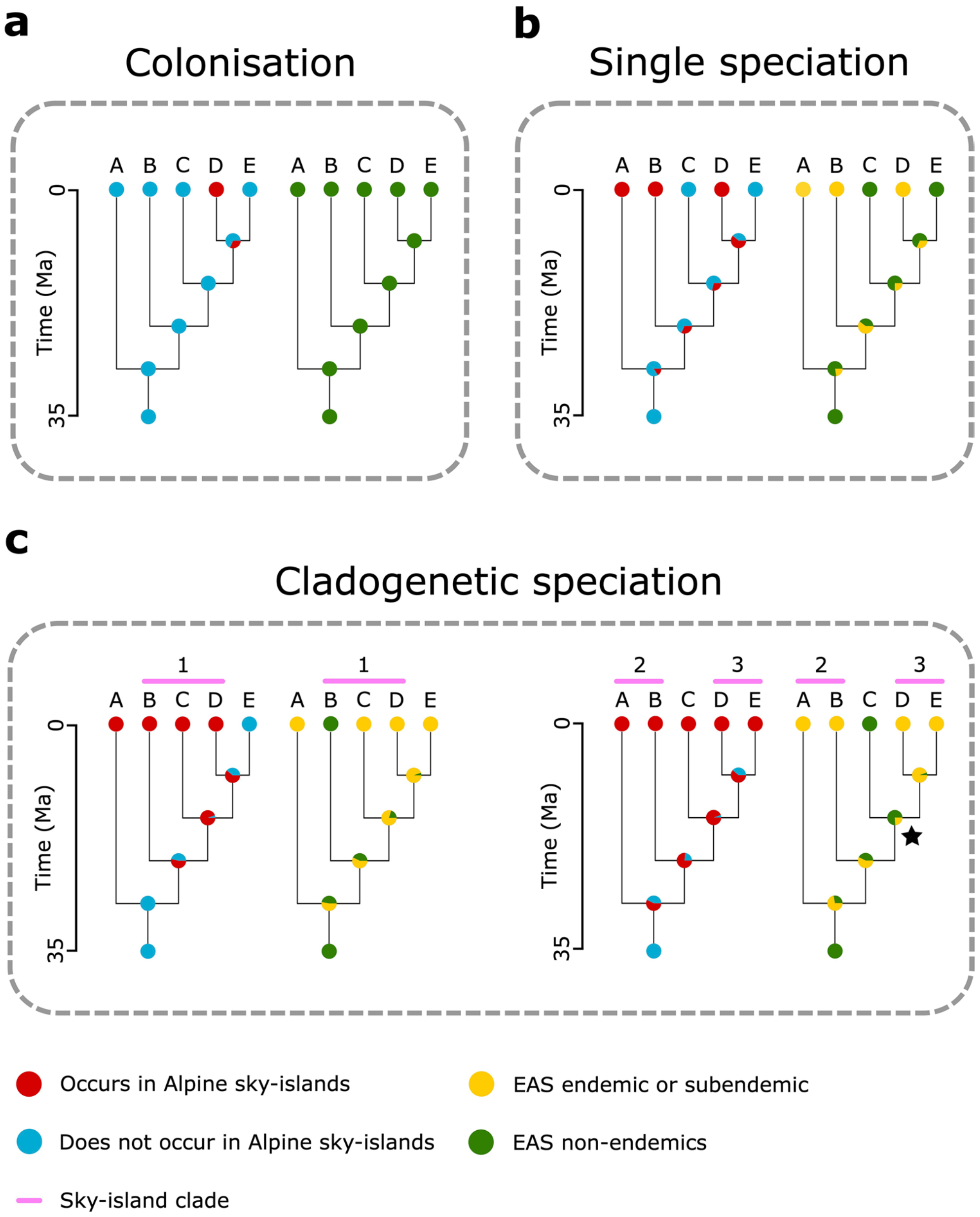
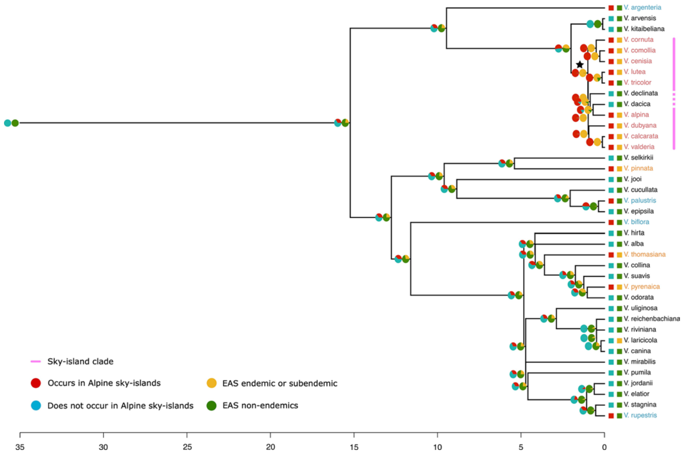


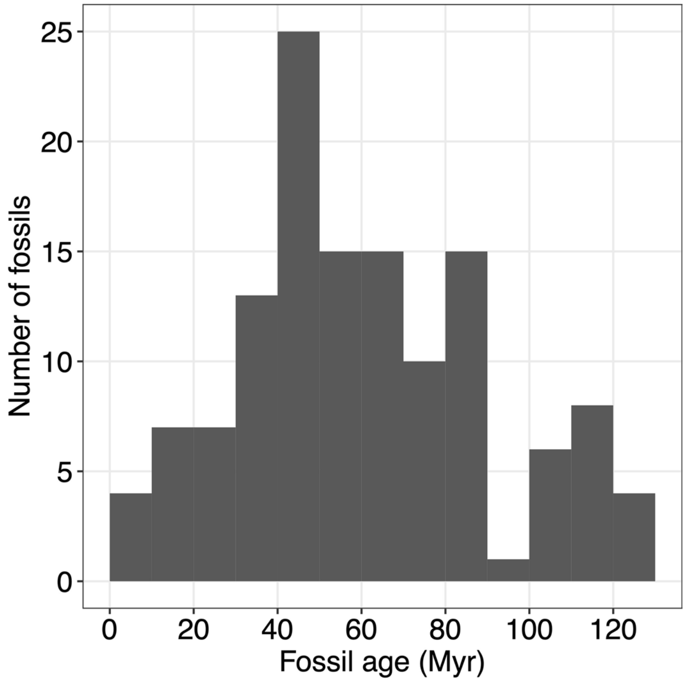
Extended Data Fig. 1 | Map of the PhyloAlps and PhyloNorway sampling. A geographically-constrained map of the PhyloAlps and PhyloNorway sampling effort. While sampling was focused on the Alps and the Arctic, the data set contains many samples from other European mountain system ranges, such as the Pyrenees, Carpathians, Balkans and Apennines. To visualise the full data set, and explore the data further, please visit the PhyloAlps website (https://phyloalps.osug.fr/).



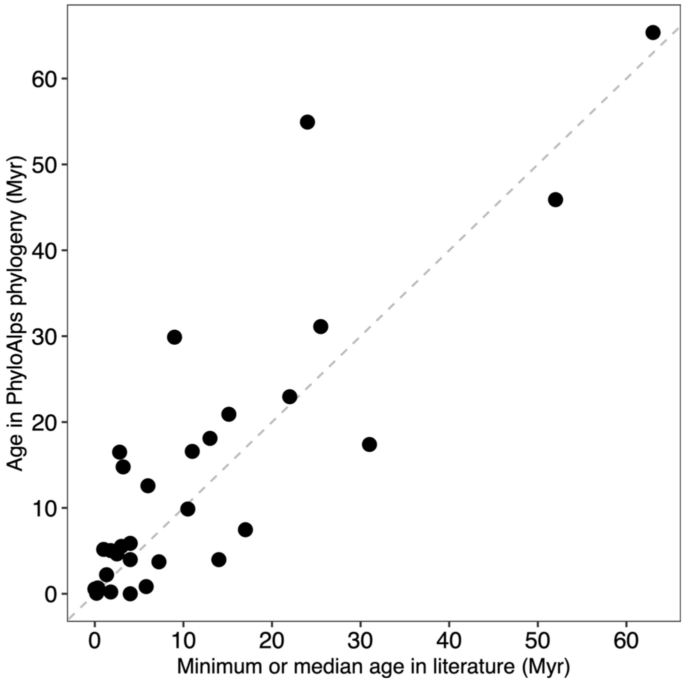
Extended Data Fig. 2 | A schematic of the decision-making process for defining colonisation, single speciation and cladogenetic speciation. Examples of the decision process for defining assembly processes. For each clade we combined two ancestral state reconstructions, shown here on two adjacent trees: one of elevational distribution (red and blue tip states) and the other of geographic distribution (yellow and green tip states). The ancestral state reconstructions were run on 35 Myr time slices of the phylogeny, with the state of stem node forced to be either low-elevation or non-EAS as relevant. **a**. A colonisation event is defined as the arrival of a lineage in the Alpine sky-islands. We consider that a sky-island species has originated via colonisation if its most recent common ancestor (MRCA) occurred at low elevations or in non-EAS regions, and its current distribution includes non-EAS regions, as illustrated by species D. **b**. We define a single speciation event as the generation of a new species due to a lineage splitting across the boundaries of the Alpine sky-islands. Species A, B, and D are all considered single-speciation species. Species A originated via single speciation as it has speciated across both elevational and geographic boundaries, its MRCA occurring at low elevations in non-EAS regions. Species B split across elevational boundaries, likely speciating during a transition from lower elevation zones to sky-islands within the EAS. Conversely, species D had a high-elevation ancestor, but likely underwent geographic divergence after arriving from a non-EAS mountain range. **c**. We define a cladogenetic speciation event as lineage splitting within the boundaries of the Alpine sky-island. In the left-hand example, species B, C, and D are considered a sky-island group that originated through cladogenetic speciation, as their MRCAs are all reconstructed to occur in the sky-islands and the EAS. In this scenario, species B is assumed to have originated in the sky-island and since extended its range to include non-EAS regions. Species E is not considered part of the group, as it does not occur in the sky-islands. Although species E has sky-island and EAS ancestors, its non-sky-island distribution suggests that speciation occurred across the treeline rather than within the sky-island boundaries. Species A is not included in the group as it does not have sky-island ancestry. In the right-hand example, all five species have sky-island ancestry. Non-EAS ancestry is reconstructed at the starred node however, suggesting that at this node lineage splitting did not occur in a sky-island context. Therefore, we circumscribe two groups, the first containing species A and B, and the second containing species D and E. Species C is then considered a single speciation event.



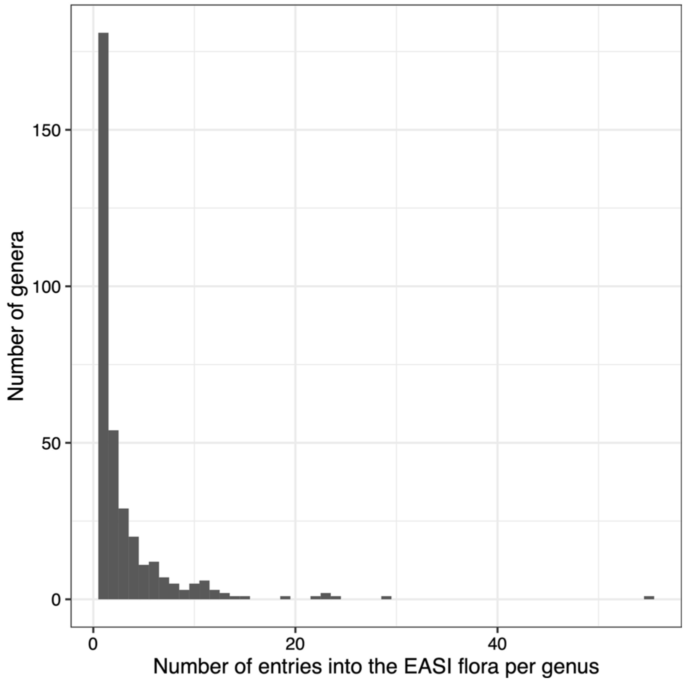
Extended Data Fig. 3 | A worked example for defining assembly processes. A worked example for defining assembly processes within *Viola*. The coloured squares on the tips represent the current elevational and geographic states for each species. The pie charts on the internal nodes display the likelihoods of each state based on ancestral state reconstructions. All species that occur in the sky-islands (denoted by red squares) are considered sky-island species. Endemism status (green and yellow squares) allow us to differentiate between species that have assembled in the sky-islands through colonisation or through single speciation. Blue text on tip labels represent colonist species (for example *V. palustris*). Colonists are not endemic to the EAS (green squares) and their ancestors occurred at low elevations or in non-EAS regions. Orange text on tip labels represent species that originated via single speciation (for example *V. thomasiana*). Single-speciation species are endemic to the EAS (yellow squares) and their ancestors occurred at low elevations or in non-EAS regions, but they are not (yet) part of an EASI clade. Red tip labels represent cladogenetic species (for example *V. cenisia*). Cladogenetic species are endemic to the EAS (yellow squares) and their ancestors occurred at high-elevations and were EAS endemics. The size of a sky-island clade is determined by the node depth to which high-elevation and EAS endemism is reconstructed. In this example, all nodes between the tips and the starred node are reconstructed as high-elevation EAS endemics, and therefore all species below the starred node (with the exceptions of *V. declinata* and *V. dacica*) are considered to be part of a single clade that diversified in situ. *V. declinata* and *V. dacica* do not occur in the sky-islands, and thus are not considered part of the sky-island clade. The speciation events leading to their formation are not used in our calculation of cladogenetic rate. All other branching events within the clade are, however, used in the calculation of cladogenetic rate.



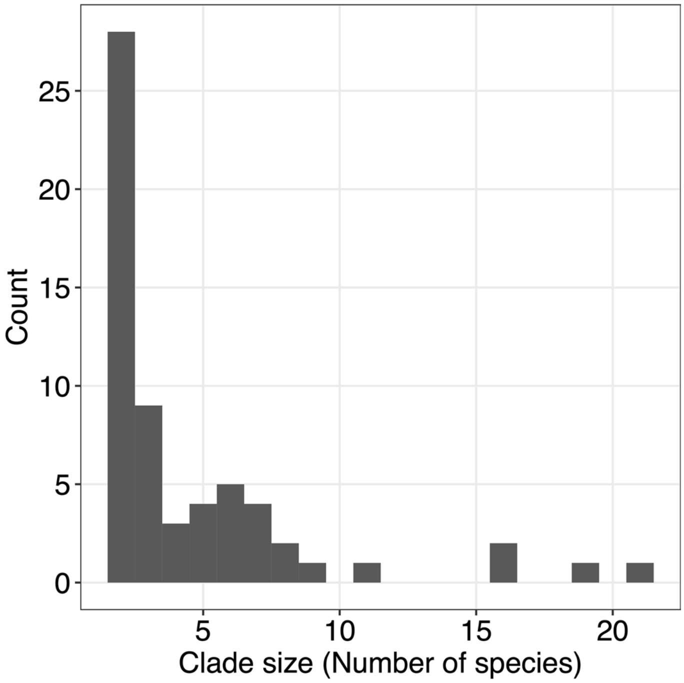
Extended Data Fig. 4 | Distribution of the ages of the fossils used to calibrate the dating analysis. Distribution of the ages of fossils used to calibrate the dating analysis. In total, 130 fossils were used, spanning 45 different orders and 96 different families. All fossils were sourced from the database of [51].



Extended Data Fig. 5 | Comparison of node ages recovered in the dating analysis of this study to those sourced from previously published phylogenies. Comparison of selected node ages ($n = 29$) recovered in the dating analysis of this study to those sourced from dated phylogenies across 19 different articles from the literature search described in the section 5.3 of the methods. Each article is represented by 1-5 points in the figure. The dashed grey line represents a 1:1 reference line.



Extended Data Fig. 6 | EASI colonization events per genus. Number of times each sky-island genus has independently entered the sky-islands.



Extended Data Fig. 7 | Distribution of clade sizes in the EASI flora. Distribution of clade sizes in the EASI flora, demonstrating that cladogenetic speciation in the sky-islands has occurred predominately in small clades of 2-3 species.

Extended Data Fig. 8 | Examples of EASI plant species. Examples of Alpine plant species occurring in the sky-islands which originated through colonisation (left column, top to bottom: *Allium oleraceum, Primula farinosa, Eleocharis quinqueflora, Lilium martagon, Laserpitium latifolium*), single speciation (centre column, top to bottom: *Artemisia glacialis, Potentilla delphinensis, Trifolium alpinum, Myosotis alpestris, Soldanella alpina*), and cladogenesis (right column, top to bottom: *Scabiosa lucida, Homogyne alpina, Phyteuma scheuchzeri, Festuca alpina, Rhinanthus glacialis*). All photographs copyright Jardin du Lautaret.

Extended Data Table 1 | Assembly rate estimates for the EASI flora using an island biogeography model

Species pool	Island age (Myr)	Cladogenesis	Extinction	Colonisation	Single speciation	log likelihood
2300	35	0.46	0.84	0.29	1.50	-5393.76
2300	23	0.45	0.87	0.31	1.52	-5306.75
2300	18	0.45	0.89	0.32	1.53	-5269.99
5000	35	0.46	0.86	0.13	1.44	-6243.14
10000	35	0.47	0.86	0.07	1.42	-7003.54

Assembly rate estimates (per lineage rate) for the EASI flora using an island biogeography model (DAISIE, [55]). All models were run without density dependence and carrying capacity fixed to Inf ($n = 1320$ species).

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software were used for data collection
Data analysis	MAFFT v.7.429 TRIMAL v1.4.22 IQ-TREE-2 v.2.1.2 ORTHOSKIM v.1.6 TreePL v.1.0 R v.4.1.2 MonoPhy R package v.1.3 ape R package v.5.7-1 DAISIE R package v.3.0.1 mcp R package v.0.3.2 loo R package v.2.5.1

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All data supporting the findings of this study are available in Figshare with the identifier https://doi.org/10.6084/m9.figshare.25459135. Taxonomic information is available from Euro+Med PlantBase (http://www.europlusmed.org). Data on plant occurrences are publicly available on the Global Biodiversity Information Facility (www.gbif.org), the Inventaire National du Patrimoine Naturel (https://inpn.mnhn.fr/) and the Plants of the World Online database (https://powo.science.kew.org/). Fossil information was sourced from the database of Ramírez-Barahona, S., Sauquet, H., and Magallón, S., 2020. The delayed and geographically heterogeneous diversification of flowering plant families. Nature Ecology & Evolution 4.9, pp. 1232–1238. doi: 10.1038/s41559-020-1241-3. All raw reads data generated by the PhyloAlps and PhyloNorway projects are available at the EMBL-EBI Short Read Archives, under the following bioprojects: PhyloAlps (PRJEB30497, PRJEB48874, PRJEB50489, PRJEB82787), PhyloNorway (PRJEB43865, PRJEB48693, PRJEB50550).

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	Not applicable
Reporting on race, ethnicity, or other socially relevant groupings	Not applicable
Population characteristics	Not applicable
Recruitment	Not applicable
Ethics oversight	Not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Ecological, evolutionary & environmental sciences study design

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Study description	This study is based on a data paper that will be submitted separately. Here we use these data to reconstruct the past phylodynamics of the entire sky island flora of the Alps, as a function of past geological and landscape changes.
Research sample	This study is based on a data paper that will be submitted separately. These data comprise of low coverage shotgun sequencing of 7,697 accessions, which includes 82% of the flora of the Alps and 96% of all sky-island species of the Alps, with a number of additional related species from the Arctic, Pyrenees, Carpathians, Balkans and even Asia. In general, one sample was collected per species, but for species with subspecies or uncertain taxonomy that number was increased.
Sampling strategy	This study is based on a data paper that will be submitted separately. Sampling was based on a comprehensive list of all vascular plants occurring in the European Alps and the Arctic, plus some additional lineages from aforementioned mountain ranges chosen to increase our pool of lineages that are closely related to Alpine lineages, as well as to maximise our ability to place fossils on the phylogenetic tree.
Data collection	This study is based on a data paper that will be submitted separately. DNA extraction, whole-cell DNA sequencing, genome reconstructions, and in silico gene capture were performed to retrieve phylogenetically informative regions.
Timing and spatial scale	This study is based on a data paper that will be submitted separately. Sampling was conducted across the European Alpine system and Arctic realm, from 2008 to 2015, sequencing from 2015 to 2020, and downstream analyses from 2020 onwards.

Data exclusions	A number of bioinformatic tests have been performed to pinpoint and exclude samples with DNA contamination, sequencing errors, uncertainty of genome reconstructions, inter-compartments gene transfers and phylogenetic misplacement. Although it depended on the test, exclusion criteria were not always pre-established. In addition, for the purposes of the current paper, only one accession per species was included, and this accession was chosen at random.
Reproducibility	This study is based on a data paper that will be submitted separately, and for which all genomic data are submitted to international public repositories. All other data and phylogenetic trees required to replicate the analyses in the current study have been uploaded to Figshare.
Randomization	*Describe how samples/organisms/participants were allocated into groups. If allocation was not random, describe how covariates were controlled. If this is not relevant to your study, explain why.*
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Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
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☒ ☐ Confer resistance to therapeutically useful antibiotics or antiviral agents
☒ ☐ Enhance the virulence of a pathogen or render a nonpathogen virulent
☒ ☐ Increase transmissibility of a pathogen
☒ ☐ Alter the host range of a pathogen
☒ ☐ Enable evasion of diagnostic/detection modalities
☒ ☐ Enable the weaponization of a biological agent or toxin
☒ ☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	Sampling consisted of collecting sufficient leaf material per specimen for DNA extraction and storing it in silica. Sampling was conducted across the European Alpine system and Arctic realm, from 2008 to 2015.
Novel plant genotypes	Not applicable
Authentication	Not applicable