Arabis alpina: a perennial model plant for ecological genomics and life-history evolution

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Abstract

Many model organisms have obtained a prominent status due to an advantageous combination of their life-history characteristics, genetic properties and also practical considerations. In non-crop plants, Arabidopsis thaliana is the most renowned model and has been used as study system to elucidate numerous biological processes at the molecular level. Once a complete genome sequence was available, research has markedly accelerated and further established A. thaliana as the reference to stimulate studies in other species with different biology. Within the Brassicaceae family, the arctic-alpine perennial Arabis alpina has become a model complementary to A. thaliana to study life-history evolution and ecological genomics in harsh environments. In this review, we provide an overview of the properties that facilitated the rapid emergence of A. alpina as a plant model. We summarize the evolutionary history of A. alpina, including the diversification of its mating system, and discuss recent progress in the molecular dissection of developmental traits that are related to its perennial life history and environmental adaptation. We indicate open questions from which future research might be developed in other Brassicaceae species or more distantly related plant families.

INVITED TECHNICAL REVIEW

Arabis alpina: **a perennial model plant for ecological genomics and life-history evolution**

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Abstract

Many model organisms have obtained a prominent status due to an advantageous combination of their life-history characteristics, genetic properties and also practical considerations. In non-crop plants, *Arabidopsis thaliana* is the most renowned model and has been used as study system to elucidate numerous biological processes at the molecular level. Once a complete genome sequence was available, research has markedly accelerated and further established *A. thaliana* as the reference to stimulate studies in other species with different biology. Within the Brassicaceae family, the arctic-alpine perennial *Arabis alpina* has become a model complementary to *A. thaliana* to study life-history evolution and ecological genomics in harsh environments. In this review, we provide an overview of the properties that facilitated the rapid emergence of *A. alpina* as a plant model. We summarize the evolutionary history of *A. alpina* , including the diversification of its mating system, and discuss recent progress in the molecular dissection of developmental traits that are related to its perennial life history and environmental adaptation. We indicate open questions from which future research might be developed in other Brassicaceae species or more distantly related plant families.

arctic-alpine environment, Brassicaceae, functional experiments, gene–environment associations, local adaptation, perennial

1 | INTRODUCTION

Describing and understanding the overwhelming diversity of life forms depends on the establishment of model species as common study platforms. By focusing on a single organism with practical advantages, a wealth of knowledge can be generated. This has led to tremendous advances in the understanding of fundamental principles in many disciplines of biology (reviewed e.g. in Müller & Grossniklaus, 2010). In plant sciences, *Arabidopsis thaliana* has served as a widely used model for several decades (Weigel, 2012). It combines many key characteristics of a successful plant model: short life cycle, wide distribution, variation in life-history traits, self-compatibility, small genome size, genetic tractability, facile transformation and ease of cultivation. However, no model can cover all areas of biological interest. Consequently, the number of dedicated plant model species has increased continuously (Cesarino et al., 2020; Kane et al., 2013; Koenig & Weigel, 2015), which will benefit future research in many fields (Pyhäjärvi & Mattila, 2021).

For reasons of comparability, specific topics were initially addressed using sister species from within the genus *Arabidopsis* . *Arabidopsis halleri* , for example, contributed to understanding the molecular basis of heavy-metal tolerance (Hanikenne et al., 2008), and has been developed into a perennial model system for population ecology and adaptation (reviewed in Honjo & Kudoh, 2019). *Arabidopsis arenosa* originally served as a model for polyploidy associated with hybridization (Monnahan et al., 2019; Yant & Bomblies, 2017), and more recently for evolutionary ecological genomics (Kolář et al., 2016). *Arabidopsis lyrata* has attracted attention for studies on mating system shifts (Mable, Dart, Berardo, & Witham, 2005), phylogeography (Schmickl, Jørgensen, Brysting, & Koch, 2010), adaptation (Kemi et al., 2013) and population genomics (Hämälä & Savolainen, 2019). Similarly, more distantly related *Cardamine hirsuta* has been used to study compound leaf development and seed dispersal (Hay et al., 2014).

The fact that most of the species mentioned above are studied more broadly today might indicate a change of paradigm in plant sciences. For species with sufficient knowledge on mechanistic underpinnings, and where increasingly powerful analytical methods are available, studies can address more systemic questions such as trait evolution or developmental biology in relation to environmental variation. Here, and particularly in the study of closely related species, *A. thaliana* serves as reference to identify, for example, gene orthologs and address gene function in phylogenetically closely related species that vary for a trait of interest. The knowledge gained with *A. thaliana* and its relatives is also extremely valuable when performing comparative studies on even distantly related species.

Arabis alpina L. (Brassicaceae), the Alpine Rockcress, has emerged as a model species for ecological genetics and life-history evolution during the past fifteen years. Research on *A. alpina* started nearly 60 years ago with taxonomic studies by Hedberg (1962), who compared populations from Africa and Scandinavia. About 50 years later, phylogeographic studies inferred the species' Pleistocene and postglacial history (Ehrich et al., 2007; Koch et al., 2006), and experimental studies highlighted that the differential breakdown of self-incompatibility has led to populations with varying degrees of self-compatibility (Ansell, Grundmann, Russell, Schneider, & Vogel, 2008; Tedder et al., 2015).

Arabis alpina is diploid with a base chromosome number of $n = 8$, and its karyotype resembles the putative ancestral state of the Brassicaceae, which is in contrast to its *Arabidopsis* relatives with $n = 5$. The species can equally be genetically manipulated by *Agrobacterium-* mediated transformation and, hence, is amenable to the toolkit of molecular biology. Consequently, the species has developed into a model system for addressing the molecular mechanisms of perenniality (R. Wang et al., 2009). With the release of a first reference genome assembly (Willing et al., 2015), comparative genomic analyses have become possible, and similar to the development in the genus *Arabidopsis* , studies have widened to include other species from the genus *Arabis* (e.g. Kiefer et al., 2017).

The arctic-alpine *Arabis alpina* has a wide geographic distribution in the European Alps, Spain, Arabia, East Africa, and extends into Scandinavia, southern Greenland and northern parts of North America (cf. Ansell et al., 2011; cf. Figure 1). Corresponding to its broad range, habitats of *A. alpina* span a wide ecological amplitude and elevation. Typically, plants occur on calcareous scree slopes and rocky debris, where they can persist by elongating shoots between the unstable substrate. However, individuals also thrive in more sheltered areas where nutrients often accumulate due to dung deposition of cattle, wild ungulates or birds, and they can tolerate very moist conditions in moss-dominated communities along creeks or ravines (Figure 1). Many of these habitats are transient and can restrict the lifespan of individual plants, which exemplifies the need for a developmental flexibility. Given its wide distribution and broad ecological niche, *A. alpina* complements the aforementioned model species by expanding into the extremes of plant occurrence, both in latitude and elevation.

Here, we provide an overview of current knowledge on *A. alpina* and introduce the various types of resources recently developed. We summarize the species' phylogeographic and evolutionary systematic history and discuss its use as a model for studies of adaptation, mating system evolution and the dissection of complex developmental traits. Moreover, we include the latest progress in understanding its perennial life history under natural conditions and the molecular and physiological underpinnings of it, and finally provide perspectives on potential future research.

FIGURE 1 HERE

2 | EVOLUTION, SYSTEMATICS AND PHYLOGEOGRAPHY

Tribe Arabideae, which includes *A. alpina* , is one of the most prominent tribes within the Brassicaceae family. It is a monophyletic assemblage with roughly 545 species distributed among 18 accepted genera, and convergence of morphological traits and trait complexes is found in all main lineages (Walden, German, et al., 2020). Based on recent cytogenetic evidence, Arabideae has been considered one of the early emerging tribes among the evolutionary lineages described in Brassicaceae, that is likely basal to all lineages except Aethionemeae (Walden, Nguyen, Mandáková, Lysak, & Schranz, 2020). However, this finding contradicts phylogenomic analyses (e.g. Kiefer et al., 2019; Mabry et al., 2020; Nikolov et al., 2019; Walden, German, et al., 2020) that placed the tribe close to Brassicaceae evolutionary lineage II (Box 1, Figure A-A). Despite this uncertainty, stem group and crown group ages of the tribe can be roughly estimated at 20 mya and 18 mya, respectively (Huang, German, & Koch, 2020; Walden, German, et al., 2020).

Genus *Arabis* , which forms the core of tribe Arabideae, is a well-studied para- and polyphyletic set of approximately 100 species (Karl & Koch, 2013), for which *A. alpina* serves as the type species. However, the genus at present does not form a monophyletic group and will likely undergo further taxonomic revision. Even among the taxa currently considered as closely related, including *A. caucasica* that is often used as

ornamental plant, there is ample taxonomic uncertainty that still requires to be resolved. Nevertheless, this taxonomic group encloses species with a great variety of life-history characteristics that may serve as comparative study systems. A detailed account of the systematic and taxonomic state of knowledge—and uncertainty—is given in Box 1.

BOX 1 HERE

Phylogeographic studies on chloroplast and nuclear DNA indicate that *A. alpina* originated in Anatolia. Present-day distribution was established with three ancestral lineages (Ansell et al., 2011; Koch et al., 2006) that diverged about 2-2.7 million years ago, at the Pliocene–Pleistocene transition. This period was marked by rapid cooling (Webb & Bartlein, 1992) and the expansion of habitats suitable for alpine plants. During the Pleistocene, a fragmented network of local survival centres persisted in Anatolia, possibly undergoing local elevational migrations during fluctuations between warmer interglacial and colder glacial periods (Ansell *et al.,* 2011).

From Anatolia, a first lineage migrated to the Caucasus and the Iranian Plateau through the Anatolian diagonal. This high-elevation mountain system likely provided stepping-stone habitats for *A. alpina* to eventually reach the East African high mountains (Ansell et al., 2011; Koch et al., 2006). Within this lineage, the populations of the Anti-Taurus and Mount Lebanon ranges form an independent clade (Ansell et al., 2011). A second, more southern lineage formed two phylogeographic groups in Ethiopia, which likely resulted from previously isolated populations that came into secondary contact with the East African lineage (Assefa, Ehrich, Taberlet, Nemomissa, & Brochmann, 2007; Koch et al., 2006). From Western Anatolia, a third lineage gave rise to all central and northern European populations through multiple immigration events, and also served as a source for the populations in Northwest Africa (Koch et al., 2006). Migration to Europe probably occurred through the region around the Sea of Marmara during colder glacial periods, when alpine habitats were located at lower elevations (Ansell et al., 2011). Within this third lineage, populations of *A. alpina* in the Alps and the Carpathians show high levels of overall genetic diversity and form a mosaic of differentiated groups with an East–West spatial structure (Alvarez et al., 2009; Ehrich et al., 2007). This pattern might result from multiple recolonizations from different refugia around and possibly within the Alps, the Carpathians and the Tatras (Ansell et al., 2008; Ehrich et al., 2007; Rogivue, Graf, Parisod, Holderegger, & Gugerli, 2018).

In more remote regions with milder climate, such as the Pyrenees and the Mediterranean, *A. alpina* might have persisted *in situ* during glacial periods (Ehrich et al., 2007). Northern European and North-American populations, by contrast, show very low levels of genetic diversity (Ehrich et al., 2007). The authors propose colonization from a single refugium in Europe. However, this scenario appears unlikely given the vast periglacial area that expanded from the northern edge of the Alps to the northern European glaciers. Alternatively, multiple migrations with strong selection for colonization ability might have led to a selective sweep decreasing genomic diversity (Ehrich et al., 2007).

Detailed knowledge on the spatial genetic structure and the underlying demographic history is a valuable foundation for investigating hypothesis-driven questions in ecological genetics. Likewise, knowledge of the neutral genetic structure is essential when inferring signatures of selection, because genomic imprints of past demographic processes such as genetic drift may mimic selective processes at neutral loci. Corresponding analyses require solid genomic resources, and a major step in this direction was the establishment of a high-quality reference genome for *A. alpina* , as described below.

3 | REFERENCE GENOME AND APPLICATIONS

With 475 Mbp, the genome of *A. alpina* is roughly 3.5 times the size of that of *A. thaliana* (Willing et al., 2015). This difference in genome size largely relates to the accumulation of retrotransposons in both hetero- and euchromatic regions of the genome, exceeding that of other Brassicaceae species (Willing et al., 2015). Usually, transposable elements are not randomly distributed across the genome, but often accumulate within pericentromeric regions (e.g. The Arabidopsis Genome Initiative, 2000). In *A. alpina* , an evolutionarily recent transposition burst of *Gypsy* elements has led to the expansion of pericentromeric regions and, consequently,

about half of the gene space of *A. alpina* is contained in the heterochromatic compartment of the chromosome. By contrast, only a few genes are located in the short pericentromeres of *A. thaliana*(Willing et al., 2015).

Pericentromeric regions can be characterized by low meiotic recombination rates; hence, expansion of pericentromeric regions can alter the recombination landscape (Tanksley et al., 1992). Transposon density was shown to be correlated with patterns of linkage disequilibrium along all chromosomes in natural *A. alpina*populations within the Swiss Alps, and a large proportion of the linked blocks showed signatures of selective sweeps; those regions were enriched for genes that are underlying adaptive traits, which implies that transposon-mediated genome dynamics play a key role in natural selection (Choudhury, Rogivue, Gugerli, & Parisod, 2019). Such genomic features might complicate future genetic mapping experiments, which depend on breaking up linkage groups to identify causal polymorphisms that underlie signatures of selection.

The most recent release of the reference genome and other resources can be accessed at*www.arabis-alpina.org* (Jiao et al., 2017). Subsequent re-sequencing of 35 and 304 individuals from across the species range (Laenen et al., 2018) and the western Swiss Alps (Rogivue et al., 2019) represented outstanding sequencing efforts of natural plant populations, and the publicly available data offer ample opportunities for in-depth population genomic analyses. Additional genomic resources for *A. alpina* include the whole-chloroplast genome sequence (Melodelima & Lobréaux, 2013) and a more fragmented reference genome assembly using individual and pooled-sample sequencing of a Swiss population (Rellstab et al., 2020). Future studies might benefit from further, phylogenetically structured resources. For example, tetraploidy of *A. nordmanniana* , which is the perennial sister species of *A. alpina,* and the much smaller genome of*A. montbretiana* (Kiefer et al., 2017), which is the annual sister of *A. alpina* , suggests that other species from tribe Arabideae could be used to study genome evolution. Only recently, phylogenetic coverage has been expanded by studying genomic properties of *A. sagittata* and *A. nemorensis,* illustrating how genomic resources can allow for interspecific comparisons and eventually assist conservation efforts (Dittberner et al., 2019).

4 | MATING SYSTEM EVOLUTION

Understanding the processes governing mating-system evolution is pivotal, because the mating system influences the distribution of genetic diversity (Hamrick & Godt, 1996) and, thus, opportunities for adaptive evolution (Charlesworth, 2006; Hartfield, Bataillon, & Glémin, 2017). One ubiquitous pattern among angiosperm plants is the repeated transition to self-compatibility and increased selfing (Barrett, 2002), which is commonly observed also in Brassicaceae (Mable, 2008).

Similar to *Arabidopsis* , *A. alpina* has a sporophytic self-incompatibility system that partially has lost its function (Tedder, Ansell, Lao, Vogel, & Mable, 2011) resulting in fully outcrossing, fully selfing, but also mixed-mating populations. Hence,*A. alpina* offers a suitable platform for studying mating-system variation within an evolutionary lineage. Until now, such studies have been done at the interspecific level (e.g. *Capsella* spp.; Bachmann et al., 2019), but only few have targeted mating-system variation within species (e.g. *A. halleri* ; Griffin & Willi, 2014).

Comparative approaches have shown differences in flower morphology between outcrossing and selfing populations, with the latter ones having e.g. markedly smaller flowers and lower pollen production (Tedder et al., 2015). Moreover, subtle differences in stigma–anther distance and anther orientation translated into differential pollination success between largely selfing populations from Scandinavia, France and Spain (Toräng et al., 2017). On a local scale in the Swiss Alps, Buehler, Graf, Holderegger, & Gugerli (2012) found evidence for mixed mating, but inbreeding was predominant with 84% of collected seeds originating from selfing. Nevertheless, these paternity analyses indicated effective mating events over distances up to 1 km.

Based on F_{IS} values, Ansell et al. (2008) suggested that, after postglacial recolonization from southern Italian refugia, self-incompatibility was lost when the species reached the Alps, which was subsequently confirmed by pollination trials (Tedder et al., 2011). Such a loss of self-incompatibility might assure reproduction when chances for mating are restricted, e.g. during migration. However, negative consequences of selfing, such as inbreeding depression, might counterbalance this advantage. In a field experiment in Scandinavia, Toräng et al. (2017) showed that the capacity for self-pollination conveyed a fitness advantage in the pollinator-poor

tundra, leading to selection for flowers with more introrse anthers and reduced anther–stigma distance. This observation may imply that detrimental alleles, potentially inducing inbreeding depression, had been purged in Scandinavian populations. However, Laenen et al. (2018) could not substantiate this: by using genome resequencing data, they demonstrated that Scandinavian populations had strongly reduced genetic diversity and increased genetic load resulting from increased selfing and a strong bottleneck, likely associated with post-glacial recolonization. By contrast, genetic diversity and load of mixed-mating French and Spanish populations were similar to the obligate outcrossing Italian and Greek populations, suggesting a reduced cost of self-compatibility in mixed-mating populations (Laenen et al., 2018).

Information on the causes and consequences of varying mating systems eventually will help evaluate how *A. alpina* may cope with environmental changes, e.g. due to climate warming. A local population may increase its persistence by pollinator-independent reproduction including asexual growth, in combination with phenotypic plasticity, or through spreading potentially beneficial alleles by pollen and seed. Here, newly arising mutations or standing genetic variation may form the basis for local adaptation. The latter has become a prime topic in evolutionary research, including a series of early studies involving *A. alpina,* as outlined in the following section.

5 | ADAPTATION TO ARCTIC AND ALPINE ENVIRONMENTS

Alpine environments are ideal settings for studies on local adaptation due to large habitat diversity over short distances (Scherrer & Körner, 2011), and patterns of differentiation were found in alpine plants along geographically narrow gradients (Byars, Papst, & Hoffmann, 2007; Kim & Donohue, 2013; Leempoel, Parisod, Geiser, & Joost, 2018). The broad distribution of *A. alpina* offers many opportunities to investigate adaptive processes at different spatial scales. Habitats located on a latitudinal gradient from the Alps to Scandinavia are expected to share typical features, such as a low annual mean temperature and a short growing season, while photoperiod length, but also light intensity, is strongly differentiated. Habitats located in the Cantabrian mountains, the Pyrenees, the Central Alps and the Carpathian Mountains share aspects of alpine habitats, but differ in the degree of continentality. These clines can be exploited to test for broad-scale natural variation in *A. alpina* . Moreover, local surveys can be replicated to test for convergent evolution or the contribution of biogeographic history to local adaptation. Consequently, *A. alpina* has been extensively used for studies on local adaptation and has become a showcase for landscape genomic analyses.

5.1 | Experimental approaches: reciprocal transplantations and common gardens

In a classical long-distance reciprocal transplantation experiment, strong local adaptation was detected between populations from the Spanish and Scandinavian edges of the European range of *A. alpina* (Toräng et al., 2015). At both transplantation sites, fitness parameters were consistently higher for local than for foreign provenances (*sensu* Kawecki & Ebert, 2004), while differences between regional replicate populations were negligible. This suggested adaptation towards large-scale habitat differences, such as winter minimum temperature, which was lower in Scandinavia than in its southern counterpart, and the intensity of summer drought, which was more pronounced in Spain than in the North. Both temperature and precipitation were previously identified as key environmental parameters shaping adaptive differentiation in plants and animals across the globe (Siepielski et al., 2017), in several alpine plant species (Manel et al., 2012) and also in *A. alpina* within the European Alps (e.g. Manel, Poncet, Legendre, Gugerli, & Holderegger, 2010).

Significant signatures of local adaptation were also detected on a regional scale within the French Alps (de Villemereuil, Mouterde, Gaggiotti, & Till-Bottraud, 2018). A comparison of plants from six populations in two different mountain ranges in common gardens close to the natural sites revealed phenotypic differentiation in traits related to vegetative and reproductive performance. Again, temperature was the key environmental parameter explaining the observed patterns: Plants originating from low-elevation sites grew more vigorously and had higher reproductive output than those from high-elevation populations, which may relate to respective higher average temperatures and longer growing seasons.

In the study of de Villemereuil et al. (2018), the degree of phenotypic plasticity depended on the population of origin, with plants from higher elevations showing less plasticity for the measured traits, suggesting another

layer of adaptation to contrasting environments. Phenotypic plasticity was also detected in the comparison of Scandinavian and Spanish accessions (Toräng et al., 2015): the onset of flowering differed markedly between local and foreign populations at the Scandinavian, but not so much at the Spanish site. Hence, it is likely that adaptation on both the large and regional scales includes specific cues that are only partially fulfilled in the foreign transplantation site. Given the latitudinal distance between Spain and Scandinavia, it might be expected that temperature interacts with photoperiod to synchronize flowering phenology with regional conditions (King & Heide, 2009).

The mentioned studies on local adaptation in *A. alpina* focused on abiotic drivers and traits that show variation in relation to latitudinal and elevational contrasts. Buckley, Widmer, Mescher, & De Moraes (2019) also considered elevational clines, but combined field observations and climate chamber experiments using populations of *A. alpina* to investigate variation in traits related to growth and herbivore defence. In this yet single study including biotic drivers of adaptation, the authors found a link between herbivore pressure, leaf traits and defence compounds, which they associated to growth–defence phenotypes. Moreover, signals of adaptation were site-specific even among populations located at the same elevation.

5.2 | Landscape genomics

Earlier studies attempting to identify genomic signals of local adaptation, commonly referred to as landscape genomics, relied on genome scans using amplified fragment length polymorphisms (AFLPs). In *A. alpina,* outlier AFLP loci, considered to be adaptive due to significantly higher genetic differentiation than others, indicated temperature and precipitation as the main environmental drivers of local adaptation (Manel et al., 2010; Poncet et al., 2010; Zulliger, Schnyder, & Gugerli, 2013). In two cases, such outlier loci were sequenced and found to be located within gene regions: one matched the SIT4 phosphatase-associated family protein known from *A. thaliana* and *A. lyrata* (Buehler et al., 2013), and the other one was homologous to a nucleotidyltransferase family protein in *A. thaliana* (Zulliger et al., 2013). However, genotyping an independent set of populations (Buehler, Brodbeck, Holderegger, Schnyder, & Gugerli, 2014) could not confirm SIT4 variants to associate with contrasting habitat types as in the original study, suggesting that local adaptation to similar environmental cues may involve different genes in different independent sets of populations (Rellstab et al., 2017).

More recent studies made use of whole-genome sequencing data. A genome scan based on reduced representation sequencing data identified a candidate gene associated with growth performance in *A. thaliana* , which could explain the observed patterns in vegetative performance in *A. alpina* (de Villemereuil et al., 2018). Additional 19 genomic regions associated with temperature, precipitation and snow cover (Lobréaux, Manel, & Melodelima, 2014; Lobréaux & Miquel, 2020), and these included orthologs of genes involved in abiotic stress response and the regulation of flowering in *A. thaliana* . By increasing both genomic and spatial resolution, Rogivue et al. (2019) identified candidate SNPs for local adaptation to stress and defence response. Interestingly, this study also identified transposable elements largely shared among populations and corresponding to temperature response terms.

In an alpine environment, similar environmental factors are relevant for many plant species (Körner, 2003; Manel et al., 2012). It is hence possible that selection targets the same genes or pathways in phylogenetically distant species that occupy similar ecological niches (Stern, 2013), even though this general assumption may not hold true (see above). Two studies compared the genes involved in adaptation to the Arctic environment in different species including *A. alpina* and found that adaptation involved similar functional pathways, but most adaptive genes remained species-specific (Birkeland, Gustafsson, Brysting, Brochmann, & Nowak, 2020; Rellstab et al., 2020).

In summary, it appears that common environmental drivers, such as temperature and precipitation, are associated with adaptive differentiation in *A. alpina* . This might not be unexpected for an arctic-alpine pioneer plant that has specific, but broad habitat preferences. While most of the discussed regional and local findings were uncovered within the French and Swiss parts of the European Alps, it remains to be tested if similar patterns exist elsewhere, taking full advantage of the broad distribution range of *A. alpina* and

including populations that have evolved within a tremendously different environment

6 | POPULATION DYNAMICS AND DEMOGRAPHY

Demographic dynamics of natural populations contribute to shaping and partitioning natural variation within and among populations at the local and regional scale. Over six years, Andrello et al. (2020) studied demographic parameters (survival probability, growth variables, reproduction probability, fecundity) of individuals in six natural sites representing the species' elevational range in the Alps. These authors found mostly consistent values for mean annual survival probability ($S = 0.5$) and mean probability of reproduction ($F_0 = 0.5$) across populations. Moreover, demographic rates were related to environmental conditions in these populations: Survival tended to increase, while growth and fecundity tended to decrease with elevation. These findings in *A. alpina* reflect common patterns in life histories of herbaceous plants: Small, long-lived species tend to inhabit high elevations, and vice-versa (Laiolo & Obeso, 2017; Nobis & Schweingruber, 2013). Andrello et al. (2020) also observed that individual *A. alpina* plants frequently grew larger and produced more fruits when the surrounding vegetation was composed of tall-growing species with large specific leaf areas. This could indicate a response to competition with other plants or an effect of temperature, because vegetative height and specific leaf area commonly increase with temperature (Read, Moorhead, Swenson, Bailey, & Sanders, 2014; Rosbakh, Römermann, & Poschlod, 2015).

Despite marked clines in demographic rates along elevation, *A. alpina* showed surprisingly little variation in population growth rates across its full elevational range (Andrello et al., 2020). This lack of spatial variation in growth rates could be partly ascribed to demographic compensation among different life-cycle components (Andrello et al., 2020). In particular, increased survival probabilities at higher elevation compensated for lower fecundity. Moreover, interannual variation in survival probabilities, which reduces population growth rates, was smaller at higher than at low elevation and further contributed to compensation. Such negative correlations between life-cycle components can result from opposite responses to shared environmental drivers or from trade-offs between different life-cycle processes (Knops, Koenig, & Carmen, 2007; Williams, Jacquemyn, Ochocki, Brys, & Miller, 2015). In addition to showing little spatial variation, population growth rates were all negative, suggesting that populations are declining and might eventually go locally extinct. Accordingly, the persistence of metapopulations of *A. alpina* depends on recruitment from the seed bank and/or immigration from nearby sites. However, strong genetic differentiation between the six studied populations ($F_{ST} = 0.6$; de Villemereuil et al., 2018) suggests low dispersal rates, and hence strong effects of genetic drift likely combined with inbreeding through selfing. Conversely, viable seeds of *A. alpina* were observed in the seed bank of several arctic-alpine soils (Diemer & Prock, 1993; Philipp et al., 2018), which can also be seen as a genetic legacy of former local occurrences.

From such demographic observations, we can infer a differential contribution of individual plant life-cycle components to population persistence. The time at which any individual enters a particular stage of its life cycle and the time it spends within that stage can vary according to the prevalent environmental conditions and the genetic composition of the individual. Hence, understanding the developmental biology of traits that interact with demographic trajectories is pivotal, as exemplified in the next section.

7 | PERENNIAL GROWTH HABIT AND TRAIT EVOLUTION

Polycarpic plants such as *A. alpina* can flower and reproduce several times during their lifetime, whereas monocarpic plants like the classical plant model *A. thaliana* are commonly annual and reproduce only once before they die (for details on modes of parity see Hughes, 2017). One major difference between these two life strategies is that senescence after flowering is restricted to reproductive branches in polycarpic plants, whereas it is global in monocarpic plants. Within the Brassicaceae, the transition from polycarpic to monocarpic life history has occurred many times (Kiefer et al., 2017). It is now possible to dissect the mechanisms that contribute to life-history evolution at the molecular level using comparative studies between *A. alpina* and its annual relatives *A. montbretiana* and *A. thaliana*. Below, we showcase some important traits described in *A. alpina* that contribute to the polycarpic perennial life history.

FIGURE 2 HERE

7.1 | Juvenile phase length

Physiological experiments under controlled environmental conditions have demonstrated that seedlings of the Spanish *A. alpinaPajares* reference accession require a minimum of five weeks of growth in long-day conditions before they are competent to respond to flower inductive stimuli (R. Wang et al., 2011). The molecular mechanisms regulating juvenile–adult phase change are similar to those described in *A. thaliana* ; in both species, this trait is regulated by the sequential action of two microRNAs, miR156 and miR172 (Wu et al., 2009). Typically, miR156 accumulates in the apices of young seedlings and decreases as plants become older and reach reproductive maturity, while at the same time levels of miR172 increases (Wu et al., 2009). miR156 targets a family of SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE (SPL) transcription factors, whereas miR172 regulates a sub-clade of AP2 transcription factors which include APETALA2 (AP2) and the AP2-like SCHLAFMÜTZE (SMZ), SCHNARCHZAPFEN (SNZ), TARGET OF EAT1-3 (TOE1-3; Aukerman & Sakai, 2003; J. W. Wang, Czech, & Weigel, 2009; Wu et al., 2009). Orthologs of some of these genes have also been functionally characterised in *A. alpina* and it has been demonstrated that they contribute to the age-dependent control of flowering. These factors include the *A. alpina* orthologs of *SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE15* (*AaSPL15*), *PERPETUAL FLOWERING2* (*PEP2* , the *A. alpina* ortholog of *AP2*) and *TARGET OF EAT2* (*AaTOE2* ; Bergonzi et al., 2013; Hyun et al., 2019; Lazaro et al., 2019; Zhou, Gan, Viñegra de la Torre, Neumann, & Albani, 2021).

Although the role of these genes in the age-pathway is conserved between*A. thaliana* and *A. alpina* , they additionally contribute to the polycarpy of *A. alpina,* which maintains vegetative growth after flowering (Table 1). For example, polycarpy is compromised in*pep2* and *toe2* mutants, and in transgenic lines that express microRNA resistant forms of AaSPL15, in which all axillary branches become reproductive (Table 1; Hyun et al., 2019; Lazaro et al., 2019; Zhou et al., 2021). These additional roles of age-related factors in polycarpic *A. alpina* may result from a more prominent role of the age-pathway than in *A. thaliana,* in which the age-pathway cannot be bypassed by other flowering-time pathways (Hyun, Richter, & Coupland, 2017; Hyun et al., 2019).

7.2 | Ecological significance of flowering behaviour

Cold is a major environmental factor that plants have to cope with, but at the same time it provides a distinct cue for synchronizing flowering with favourable environmental conditions. *Arabis alpina* requires exposure to prolonged cold to flower, a process known as vernalization in *A. thaliana* and other temperate perennials. Alpine environments are characterised by long winters and unpredictably short growing seasons, which puts additional constraints on alpine species. Hence, many plants from alpine habitats initiate floral organs several months or years before anthesis, so that they can flower rapidly once environmental conditions are benign (Billings & Mooney, 1968; Diggle, 1997; Körner, 2003). In experimental conditions, flower buds are formed during cultivation at 4°C (Lazaro, Obeng-Hinneh, & Albani, 2018; R. Wang et al., 2009) and in natural populations of *A. alpina* , flower buds can already be observed in autumn (S. Wötzel, personal observation), suggesting that *A. alpina* plants can be vernalized and initiate flowering before winter. Experiments characterizing the flowering response of the reference accession *Pajares* to different durations of cold treatment indicated that exposure to less than 12 weeks of cold leads to asynchronous flowering among individuals and floral reversion, thereby reducing reproductive output (Lazaro et al., 2018; R. Wang et al., 2009). These results suggest that natural populations may require locale-specific cold periods for optimal reproduction.

Flowering in response to long cold in *A. alpina* is mediated by the MADS box transcription factor PERPETU-AL FLOWERING 1 (PEP1; R. Wang et al., 2009), which is the orthologue of the *A. thalianaFLOWERING LOCUS C* (*FLC* ; Michaels & Amasino, 1999; Sheldon, Rouse, Finnegan, Peacock, & Dennis, 2000) . Similar to*FLC* , *PEP1* acts as a floral repressor and is transcriptionally regulated by vernalization. In *A. alpina* plants of the reference accession (wild type), *PEP1* transcript abundance decreases during cold exposure and plants form flower buds (Lazaro et al., 2018; R. Wang et al., 2009). In addition, *pep1* mutants and accessions with non-functional alleles of *PEP1* (AaFLC) flower early and without cold exposure (Albani et al., 2012; R. Wang et al., 2009), resembling the early flowering phenotype of *A. thalianaflc* mutants (Michaels & Amasino,

1999).

Vernalization stably silences *PEP1* only in mature meristems, which initiate reproductive development during cold exposure, but not in juvenile meristems, which remain vegetative (Lazaro et al., 2018). This suggests that besides the age-pathway, differences in vernalization-mediated *PEP1* stable silencing by vernalization, as observed between reproductive and vegetative meristems, may also contribute to the polycarpic growth habit of *A. alpina* (Table 1; reviewed in Soppe, Viñegra de la Torre, & Albani, 2021). *PEP1* mRNA levels are upregulated in meristems that did not commit to flowering during vernalization to ensure the maintenance of vegetative growth habit the following year (Lazaro et al., 2018; R. Wang et al., 2009). This role of PEP1 may also pleiotropically contribute to maintain dormant buds by ensuring the continuous supply of auxin from vegetative axillary branches even after flowering (Soppe et al., 2021; Vayssières et al., 2020). In common garden trials, accessions with non-functional *PEP1* alleles showed increased mortality, suggesting that PEP1 function is relevant for plant survival (Albani et al., 2012; Hughes, Soppe, & Albani, 2019). This is probably related to the reduced vegetative perseverance observed in *pep1* mutants. In addition, seed longevity and dormancy have been found to be reduced in *pep1* mutants (Table 1; Hughes et al., 2019), suggesting a potential shift towards a rapid-cycling life strategy that closely resembles the monocarpic growth habit.

Arabis alpina has also been used to study further developmental traits (exemplified in Fig. 2), which include leaf trichome formation (Chopra et al., 2019, 2014), leaf senescence (Wingler, Juvany, Cuthbert, & Munné-Bosch, 2015; Wingler, Stangberg, Saxena Triambak, & Mistry, 2012), secondary growth (Sergeeva et al., 2021) and adventitious rooting (Mishra, Roggen, Ljung, & Albani, 2020). For the latter, natural variation has been detected under controlled environmental conditions (Mishra et al., 2020). This finding might indicate a potential adaptive significance for that trait, with different phenotypic optima for individual populations. Observations in natural alpine environments suggest that adventitious roots in *A. alpina* may primarily serve for attaching the growing plant body to unstable substrate (Figure 1H), an adaptation similar to those found in other scree-inhabiting plant species (Körner, 2003).

In summary, comparative physiological studies between *A. alpina* and *A. thaliana*, chemically induced mutants, functional studies and the observation of natural accessions of *A. alpina* have resulted in a detailed understanding of perennial life-history traits at the molecular level. Many, if not all, of these traits may be of adaptive significance, and the examples of flowering time and duration have highlighted the crucial role of naturally occurring variants for characterising gene functions. Future studies will be motivated by the functional characterization of candidate loci that were identified by landscape genomics methods (see above). In return, molecular-physiological approaches can provide the proof-of-concept data that is often the step remaining to be completed in contemporary studies of adaptation. Further synergies might result from comparing trait expression and gene function between annual and perennial life histories within the Arabideae. Introgression lines of *A. alpina* that contain genomic regions of the annual close relative *A. montbretiana* in a common genetic background have been developed as a tool to understand the divergence of annual and perennial life histories (Hyun et al., 2019; Kiefer et al., 2017). It will be interesting to see to which extent the relevant traits can be related back to the environments in which the contrasting life histories have evolved.

8 | PERSPECTIVES

In this overview, we demonstrate that *A. alpina* is well suited to answer general questions related to the adaptation of plants to harsh arctic-alpine environments and the evolution of perennial life-history. However, there still are many unknowns that await to be addressed using the wealth of available biological resources to expand current knowledge. Here, we formulate some avenues that may guide future research in the fields of ecological, evolutionary and molecular genetics in *A. alpina* and other taxa.

Predominant selfing has been considered as a drawback for the study of adaptation (Yant & Bomblies 2017), but the very availability of outcrossing populations endorses *A. alpina* as a model for studying mating system evolution *within* a single species. Similarly, it can be tested whether *inter* specific differences in life-history and functional traits (e.g. Adler et al., 2014; Nobis & Schweingruber, 2013; Read et al., 2014) can be observed at the *intra* specific level. One could, for example, specifically address adaptation to extreme environmental

factors such as high irradiance, low temperatures, persistent snow cover and short growing season: How similar is the genomic basis of evolutionary solutions to these ecological challenges in species that inhabit arctic and alpine habitats? Do different strategies exist, are differences found within the same genes or gene networks, or were complementary pathways involved in these adaptive processes? What is the molecular basis of highly specialized physiologies, such as the ability of the alpine snow-bed specialist *Soldanella pusilla* to grow at freezing temperatures (Körner et al., 2019)? Here, lessons learnt from an arctic-alpine model system may help pinpointing the genomic particularities that also govern physiological processes in other taxa (cf. Park, Kim, & Lee, 2017).

A broad variety of landscape genomic approaches and genome-wide studies have identified polymorphisms within genes that are promising candidates for being involved in adaptive processes. Future research might further address the molecular genetic basis of ecologically relevant traits besides the regulation of flowering, which is increasingly well understood. There are still many traits that are relevant in view of adaptation to arctic-alpine environments, in particular regarding biotic stress such as pathogens and herbivory (but see Buckley et al., 2019). Initial physiological studies have addressed response to cold stress and detected clinal variation with increased frost tolerance at high elevations, suggesting adaptive significance of that trait (Kolaksazov, Ivanova, Stanev, Markovska, & Ananiev, 2017). A similar trajectory was identified by Wingler et al. (2015), who found higher cold stress tolerance in plants from high compared to low elevations, likely mediated by higher leaf sucrose levels. However, at warmer temperatures, sugar accumulation led to accelerated leaf senescence, suggesting a physiological trade-off with frost protection shaping natural variation (Wingler et al., 2012). Moreover, the physiology of storage metabolites has been addressed in relation to secondary growth and perennial behaviour (Sergeeva et al., 2021). However, there are yet further eco-physiological studies needed to better understand the functional aspects of adaptation to cold in *A. alpina* .

Environmental stress has been shown, e.g. in *A. thaliana* , to induce enhanced activity of transposable elements (TEs), which in turn affects gene integrity or the regulation of gene expression. Epigenetic transmission can then lead to an acquired adaptive response in the next generation (Thieme & Bucher, 2018; Thieme et al., 2017). At present, we are unaware of any investigation that evaluates how epigenetic changes (Richards et al., 2017) contribute to the ability of *A. alpina* to cope with environmental stressors. Here, we see great potential in establishing links between genome-wide methylation patterns and the pertinent information on the types, activity and distribution of TEs (Choudhury, Neuhaus, & Parisod, 2017; Choudhury et al., 2019).

Another key to the adaptive success of plants is their ability to associate with mutualistic organisms. In many taxa, fungi or other microbiota associate with plant roots to form close mutualistic symbioses. To date, only limited information is available on how *A. alpina* may benefit from such root associates. For example, Almario et al. (2017) characterized fungal microbiota on *A. alpina* roots and found certain taxa to be dominant on soils with low phosphorus content. Their results indicate microbial support for phosphorus uptake under limiting conditions and suggest that taxa growing on alpine, often nutrient-poor soils, can evolve alternative solutions to the otherwise common mycorrhizal symbiosis. Nevertheless, it remains unclear how common these associations are, whether they lead to co-adaptations in the involved physiological pathways, and to which degree they influence the evolutionary trajectory of the host plant. Here, hypotheses could be developed in relation to the extended phenotype concept (Gugerli et al., 2013; Whitham et al., 2006) and tested using *A. alpina* .

While most of the aforementioned research is centred on populations from the European Alps and the Spanish reference accession *Pajares* , future studies should expand along the phylogeography of *A. alpina* . Accessions from the Anatolian mountains and African sky islands might contain unexpected genetic variants underlying traits that provide adaptation to a strongly divergent habitat. Particularly the equatorial daytime climate, to which the African populations are exposed, radically differs from the extreme seasonal habitats of Northern latitudes. Moreover, analyses of such distinct lineages might change the understanding of the species' evolutionary history, similarly to what has been shown for the example of *A. thaliana* after including previously neglected accessions from Africa (Durvasula et al., 2017). It is also possible that accessions from

more southerly climates contain genetic variants that may provide adaptive advantages for cold adapted species that are threatened by global warming.

Biological discoveries can be expanded from *A. alpina* to closely related sister species within the Arabideae, and to those in other well-studied genera of the Brassicaceae such as *Arabidopsis* ,*Capsella* , *Boechera, Cardamine* and *Brassica* (Krämer, 2015; Rushworth, Song, Lee, & Mitchell-Olds, 2011). With more and more plant species being fully sequenced, comparative genomics are becoming increasingly feasible. Studies of such kind have just begun to address principles of adaptation in the Brassicaceae (Birkeland et al., 2020; Nowak et al., 2020; Rellstab et al., 2020) and provide opportunities for understanding the adaptive evolution of life-history traits.

Taken together, widening the phylogenetic and environmental scales will further help understanding fundamental processes in adaptation. The marked variation in life-history traits encountered across the natural range of *A. alpina* , together with the publicly available genomic resources established in recent years, will serve as a comprehensive basis for comparative studies. With this overview on the evolutionary and ecological genomics of *A. alpina* , we demonstrate that this species is a valuable emerging model system in plant biology. Together with a suite of other taxa, *A. alpina* complements the hitherto outstanding *A. thaliana* , on which a huge array of research is still relying, to address complementary ways of evolutionary responses to environmental cues. Additional, intensively studied taxa will enrich the field of evolutionary plant biology and contribute to knowledge about the manifold ways plants cope with their abiotic and biotic environment.

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Author contributions

SW, MA, MCA, GC and FG conceived the outline, SW, MA, MCA, MAK and FG wrote the article with contributions from GC, and all authors read and approved the final version.

Supporting Information

Additional supporting information may be found online in the Supporting Information section.

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Box 1. Evolution and systematics of *Arabis*

Evolution of tribe Arabideae

Among the 18 genera and 545 species within tribe Arabideae (Walden, German, et al., 2020), 63% are neopolyploids, and its mean net diversification rate is more than three times higher than the family mean (Huang et al., 2020), highlighting the evolutionary dynamics of this lineage. Research of the past two decades resulted in a well-resolved phylogenetic tree that demonstrates paraphyly of the genus *Arabis* and established a new systematic concept (Karl & Koch, 2013). Multiple radiations in various clades involved a split between lowland annual and montane/alpine perennial sister species, in which increased speciation rates occurred frequently.

The center of origin of tribe Arabideae is the Irano-Turanian region (Figure A), which ranges from the eastern Mediterranean and Saharo-Arabian regions to the Tian Shan and Pamir Mountains (for a detailed review on this floristic region: Manafzadeh, Staedler, & Conti, 2017). From there, the different clades independently colonized the temperate and alpine mountain regions of the world (Karl & Koch, 2013). Generally, numerous morphological trait characteristics have evolved convergently and are often linked, e.g. in annuals *vs.* perennials. In contrast to perennial species, annuals exhibit a complete selfing syndrome, have wider and lowland distribution ranges, did not undergo subsequent radiations, and exhibit lower genetic variation that might, among others, result from the selfing syndrome (Karl & Koch, 2013, 2014).

Systematic and taxonomic considerations of genus Arabis

The type species of genus *Arabis* is represented by the Linnean holotype of *A. alpina* (Species Plantarum 2: 664, 1753). However, if future taxonomic work aims for a monophyletic genus *Arabis,* then most of the species contained in the genus at present will have to be transferred into new genera. The resulting monophyletic set of species would contain the type *A. alpina* together with approximately 20 additional species that are: (i) *A. alpina* and its closest relatives (ca. 10-12 species), (ii) its sister clade including *A. nordmanniana* (*A. nordmanniana* clade; 5 species), and (iii) the *A. auriculata* clade (3 species; Karl & Koch, 2013; Kiefer et al., 2017). Among those closest relatives of *A. alpina* are the red or pink flowering taxa *A. purpurea ,A. cypria* and *A. aubrietoides.* Moreover, *A. deflexa , A. ionocalyx, A. caucasica* and *A. tianchanica* (Kyrgyzstan) are found within the same phylogenetically unresolved clade. If all of those were included into *A. alpina* to establish monophyletic entities, subspecies concepts would have to be applied (Karl, Kiefer, Ansell, & Koch, 2012).

Arabis caucasica has also been introduced in synonymy as *A. alpina* ssp. *caucasica* (additional synonyms are *A. albida ,A. billardieri* ; Koch, German, Kiefer, & Franzke, 2018). Although taxonomically accepted, there is no supporting genetic, geographic or morphometric information. The same applies to *A. alpina* ssp. *brevifolia* , which has been described from Eastern Mediterranean areas (Greuter & Raus, 1983), but also without any further complementary details. Consequently, there is no reliable and convincing infraspecific taxonomic system for *A. alpina* to date, and further taxonomic work is needed to correctly relate morphological variation with genetic make-up and biogeographic patterns.

The entire species assemblage likely originated in the Pleistocene (Karl & Koch, 2013), and the three remaining species or taxa (*A. montbretiana , A. nova* ssp. *iberica , A. kennedyae*) build up a well-defined sister clade of exclusively annuals (Karl & Koch, 2013) that provide an excellent source for comparative evolutionary research (Kiefer et al., 2017, 2019). This sister clade split in the Late Pliocene or at the onset of early Pleistocene glaciation/deglaciation cycles (Karl & Koch, 2013).

FIGURE A HERE

FIGURE A (A) Different phylogenetic positioning of tribe Arabideae within Brassicaceae core groups depending on the marker set used, indicating a biological phenomenon rather than an analytical artifact (following Walden, Nguyen, et al., 2020). (B) Summary of present-day phylogenetic knowledge on clade relationships in Arabideae (species number given). Clade definition follows Karl & Koch (2013) and Kiefer et al. (2017). (C) Ancestral areas of the clade including *Arabis alpina* and its sister clades, highlighting the

"Irano-Turanian region" as a source of origin. The timeline indicates stem and crown group ages (including confidence intervals; Karl & Koch, 2013).

TABLE 1 Conserved and diverse roles of genes functionally characterized in *Arabis alpina* (Aa) compared to *Arabidopsis thaliana* (At).

Gene (At)	Gene (Aa)	Trait (At)	Trait (Aa)
FLC	PEP1	Flowering, seed dormancy	Flowering, polycarpy, duration of flowering episode, Seed do
TFL1	AaTFL1	Flowering	Age-dependent response to vernalization, polycarpy
SPL15	AaSPL15	Flowering	Age-dependent response to vernalization, polycarpy
AP2	PEP2	Flowering	Age-dependent response to vernalization,p
TOE2	AaTOE2	Flowering	Age-dependent response to vernalization, polycarpy
BRC1	AaBRC1	Bud dormancy	Bud dormancy
TTG1	AaTTG1	Trichome & root hair formation	Trichome & root hair formation
GL2	AaGL2	Trichome patterning	Trichome patterning

FIGURE 1 Sampled populations of *Arabis alpina* cover large parts of its global range (cf. Ansell *et al.* , 2011) and indicate a focus on the European Alps (A). Points represent coordinates of published populations (data listed in Supporting Information), and darker red colour indicates higher density of studies in given areas. Top row photos show typical alpine habitats of *A. alpina* : calcareous scree (B), moist habitats along small creeks (C), and areas of nutrient sinks such as road verges (D). Bottom row photos illustrate morphology of intermediately sized vegetative (E), flowering (F) and fruiting (G) individuals. The close-up photo (H) shows adventitious roots growing from a mature shoot at the base of vegetative rosettes. Photos: F. Gugerli and S. Wötzel; map made with Natural Earth.

FIGURE 2 Examples of developmental traits studied using *Arabis alpina* (A-D): Flowering time in the glasshouse varies between plants from the same population (A, B), adventitious rooting (arrow) at lateral branches (C), naturally occurring variant with low trichome density (D). Illustration of large-scale glasshouse survey testing for naturally occurring variation in developmental traits (E). Photos: S. Wötzel.

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