Journal of Experimental Botany, Vol. 70, No. 1 pp. 55–67, 2019
doi:10.1093/jxb/ery340 Advance Access publication 27 September 2018

REVIEW PAPER

The plant model system *Arabidopsis* set in an evolutionary, systematic, and spatio-temporal context

Marcus A. Koch*

Centre for Organismal Studies (COS) Heidelberg, Department of Biodiversity and Plant Systematics, Heidelberg University, D-69120 Heidelberg, Germany

* Correspondence: marcus.koch@cos.uni-heidelberg.de

Received 29 July 2018; Editorial decision 21 September 2018; Accepted 21 September 2018

Editor: Frank Wellmer, Trinity College Dublin, Ireland

Abstract

***Arabidopsis thaliana* is one of the prevailing plant model systems used for most facets of plant molecular, cell, and evolutionary biology. There are good reasons for that, such as easy cultivation, short generation time, a selfing reproductive system, and a wide geographic distribution with easy access to respective germplasm material. For the last two decades, the entire genus *Arabidopsis* with its various species has emerged as a model system allowing the study of additional traits and characters not found in *A. thaliana*. These species grow naturally under very different environmental conditions and mostly underwent independent evolutionary histories. Accordingly, consideration of their respective biogeographic and phylogenetic (taxonomic) context is important for any study aiming to explore fully the potential of comparative studies. Here, we review current understanding of spatio-temporal patterns of *Arabidopsis* evolutionary history and introduce the various taxa in more detail, including those traits well studied by the scientific community. The significance of polyploidization and interspecies gene flow is also discussed.**

Keywords: *Arabidopsis*, biogeography, evolutionary history, phylogeny, speciation, taxonomy, trait evolution.

Introduction

The taxonomy of Arabidopsis *as an emerging study and model system*

The genus *Arabidopsis*, and in particular *Arabidopsis thaliana* (Brassicaceae), is among the few prevailing plant model species for studying fundamental biological processes from molecule to population level (Weigel, 2012; Provart *et al.*, 2016). An excellent historical overview of how *A. thaliana* found its way into thousands of labs of plant molecular biologists has been provided by Koornneef and Meinke (2010). Its career as a model system started with Laibach's work using the species as a genetic system (Laibach, 1943), followed by renewed interest in a 'renaissance period' in the late 1970s and 1980s (reviewed in Meyerowitz, 2001; Koornneef and Meinke, 2010), and accumulated into >55 000 indexed papers having *Arabidopsis* in the title, abstract, or keywords (Provart *et al.*, 2016).

During most of this time, systematics and the evolutionary history of the genus *Arabidopsis* were not an issue and they were not much taken into account until recently. Consequently, there is a parallel and often confusing taxonomic history regarding species and genus delimitations. Here, a benchmark was set upon entering the new millennium when a comprehensive new circumscription of the entire genus was introduced (reviewed in Koch *et al.*, 2008). This had some serious consequences for >60 *Arabidopsis* species (excluding *A. thaliana*) recognized at that time, most of which have been transferred to very different genera (Al-Shehbaz *et al.*, 1999). On

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the other hand, the newly circumscribed genus *Arabidopsis* gained species because species shown by molecular markers to be the closest relatives of *A. thaliana* (O'Kane and Al-Shehbaz, 2003; Koch *et al.*, 2008) were incorporated. This taxonomic history—changes of names on the genus and species level following distinct rules provided by the 'Code of nomenclature' (Turland *et al.*, 2018)—is recapitulated here in in some detail, and it should be kept in mind that previous work published under species names such as *Arabidopsis pumila*, *Arabidopsis griffithiana*, or *Arabidopsis wallichii* (to name just a few) is in fact focused on species that are only distantly related to *A. thaliana*, and belong to different genera such as *Olimarabidopsis* or *Crucihimalya* (Kiefer *et al.*, 2014; Koch *et al.*, 2018). The confusion that can arise from assuming close relatedness based on genus names alone emphasizes the fact that reliable taxonomy and systematics are key to the interpretation of biological, especially evolutionary, information (Koch and German, 2013; Koch *et al.*, 2018).

The taxonomic confusion surrounding *A. thaliana* started soon after 1872. Many species were transferred into a genus *Arabidopsis* based on a few simple morphological characters (latiseptate siliques terete to quadrangular in cross section; and branched trichomes) and, therefore, some 60 species were recognized in *Arabidopsis* (German and Ebel, 2005). With the pioneering work of O'Kane and Al-Shehbaz (1997) and Al-Shehbaz *et al.* (1999), this concept was completely changed and nine 'new' *Arabidopsis* species with several subspecies, mostly from the former genus *Cardaminopsis*, were recognized together with *A. thaliana*. This taxonomic revision was based on initial phylogenetic analysis using the nuclear-encoded internal transcribed spacer of rDNA (O'Kane *et al.*, 1996) and later confirmed with a broader taxon sampling (O'Kane and Al-Shehbaz, 2003). It has to be noted that earlier, Hedge (1968) proposed a closer relationship between *Arabidopsis* and *Arabis*, while recognizing that the two genera differ only in the position of the cotyledons relative to the radicle in the seeds. Meanwhile we know from a series of phylogenetic studies that *Arabis* is also not monophyletic, and it was at that time that species from the whole Brassicaceae family (Karl and Koch, 2013) were resampled. It is curious to see that Hedge (1968) claimed that the Himalayan species *A. wallichii* (now *Crucihimalya wallichii*) is essentially an intermediate between the two genera. However, as molecular data were not available, Hedge and others could not have been aware that, in fact, the genus *Arabis* at that time was comprised of various unrelated evolutionary lineages (see Koch *et al.*, 1999, 2000, 2001; Bailey *et al.*, 2006). Nowadays the historical concept of a monophyletic genus *Arabis* no longer exists (Karl and Koch, 2013). Because taxa from both genera, *Arabidopsis* and *Arabis*, share this taxonomic history, they frequently exhibit related taxonomic nomenclatural problems with numerous misleading phylogenetic implications.

In a review entitled '*Arabidopsis* and its poorly known relatives', it is >10 years ago that the closest relatives of *A. thaliana* were introduced in more detail (Clauss and Koch, 2006), with some particular focus on *Arabidopsis lyrata*, with >600 papers published using this species between 2000 and 2018, and >1350 papers published between 2000 and 2018 dealing with any of the 'true wild relatives' (Web of Science, accessed 7 July 2018).

The new concept of the genus *Arabidopsis* was presented 15 years ago (O'Kane and Al-Shehbaz, 1997, 2003) paralleled by a contribution from Koch *et al.* (1999) in which some taxonomical problems including both *Arabis* and *Arabidopsis* have been unravelled. Some species and subspecies were added later, either because of a transfer of taxa previously never associated with *Arabidopsis* (Warwick *et al.*, 2006) or because of the description of a new species (Kadota, 2007). Changes since 1997 were mostly due to changing the rank of taxa as subspecies or recognizing synonyms (Dorofeyev, 2002; Marhold *et al.*, 2003; Shimizu *et al.*, 2005; Kolník and Marhold, 2006; Kadota, 2007; Elven and Murray, 2008). As a result, depending on the applied species concept, *Arabidopsis* can be considered as a genus comprising at least nine species and six subspecies (O'Kane and Al-Shehbaz, 1997); additionally, 15 species and 16 subspecies are presented with the latest and most up-to-date taxonomic status report (e.g. summarized in Koch *et al.*, 2008; Hohmann *et al.*, 2014) (Table 1).

An introduction to the biological system

The phylogenetic context

The genus *Arabidopsis* belongs to tribe Camelineae, and among its closest sister groups is the genus *Capsella*. The name is derived from *Arabis* (a genus of Brassicaceae, from which it cannot be distinguished by any unique character) and Greek *opsis*, in reference to this similarity. Members are mostly perennial and rarely annual or biennial. Multicellular glands are absent and trichomes are simple and mixed with stalked 1–3(or 4)-forked trichomes. Petals are white, pink, or purple, and nectar glands are confluent and subtending bases of all stamens. Fruits are dehiscent and formed as capsular, linear siliques. Other closely related genera are *Neslia* and *Camelina*. All three of them, *Capsella*, *Neslia*, and *Camelina*, are characterized by silicules. Recent phylogenetic data indicated incongruencies among gene trees comparing plastome and nuclear genome data and questioning the monophyly of tribe Camelineae and the sister relationship of *Arabidopsis* to a clade consisting of *Neslia–Camelina–Capsella* (Hohmann *et al.*, 2015; Huang *et al.*, 2016). However, Beilstein and co-workers have shown that the *Arabidopsis* versus *Neslia–Camelina–Capsella* relationship is the most likely sister relationship scenario, and this might be masked because of ancient gene flow among lineages predating most of the species considered (Forsythe *et al.*, 2017, Preprint). In our current circumscription, tribe Camelineae is species poor (~50 species) (Koch *et al.*, 2018), comprised of nearly 50% of neopolyploids, and its average 1 C*x* (monoploid) genome size is ~0.36 pg (equals 300 Mbp, compared with 0.16 pg in A. *thaliana* representing ~135 Mbp) (Hohmann *et al.*, 2015). The base chromosome number of *Arabidopsis* is n=8, with *A. thaliana* showing a derived situation with n=5 chromosomes (Table 1). Within the genus *Arabidopsis*, phylogenetic analyses have recognized seven major lineages, with all of them also comprising diploid taxa: *Arabidopsis halleri* lineage, *Arabidopsis lyrata* lineage, *Arabidopsis arenosa* lineage, *Arabidopsis pedemontana*, *Arabidopsis cebennensis*, *Arabidopsis croatica*, and *A. thaliana* (Koch and Matschinger, 2007;

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Table 1. *The genus* Arabidopsis *and its various taxa*

***Arabidopsis thaliana* L.**		**2*x***	**Native range almost all Europe to Central Asia**
***Arabidopsis arenosa* group**			
A. arenosa (L.) Lawalrée[a]		(2*x*) 4*x*	
	subsp. *borbasii* (Zapał.) O'Kane & Al-Shehbaz		Mountain ranges in Central and Western Europe
	subsp. *arenosa*		Central and Western Europe, Scandinavia at lower altitudes
A. carpatica nom. prov.		2*x*	Carpathian Mountains in mountain ranges on calcareous bedrock
A. neglecta (Schult.) O'Kane & Al-Shehbaz			Carpathian Mountains
	subsp. *robusta* nom. prov.	4*x*	Alpine regions and only occasionally at lower altitudes
	subsp. *neglecta* nom. prov.	2*x*	Alpine regions on siliceous bedrock types
A. nitida nom. prov.		2*x*	Carpathian Mountains
A. petrogena (A. Kern.) V.I. Dorof.			Carpathian Mountains
	subsp. *petrogena* nom. prov.	2*x*	Carpathians and Pannonian lowland
	subsp. *exoleta* nom. prov.	4*x*	Carpathians at lower altitudes
***Arabidopsis halleri* group**		2*x*	
A. halleri (L.) O'Kane & Al-Shehbaz			
	subsp. *dacica* (Heuff.) Kolník		Carpathians, Romania
	subsp. *gemmifera* (Matsum.) O'Kane & Al-Shehbaz		Russia Far East, NE China, Korea, Japan, and Taiwan
	subsp. *halleri*		Europe
	subsp. *ovirensis* (Wulfen) O'Kane & Al-Shehbaz		Austria (taxon and its distribution is unclear)
	subsp. *tatrica* (Pawł.) Kolník		Tatra mountains, Slovakia
A. umezawana Kadota			Japan, Hokkaido (alpine zone of Mt. Rishirizin)
***Arabidopsis lyrata* group**			
A. lyrata (L.) O'Kane & Al-Shehbaz			
	subsp. *lyrata*	2*x* (4*x*)	Alaska, Canada, USA
	subsp. *petraea* (L.) O'Kane & Al-Shehbaz	2*x*	Europe
	subsp. *umbrosa* nom. prov.	2*x*	Arctic NE Asia, Siberia, Alaska, Canada
	subsp. *septentrionalis* nom. prov.	4*x*	Arctic NE Europe, European Russia to Siberia (may be admixed populations between subsp. *lyrata* and *umbrosa*)
A. arenicola (Richardson) Al-Shehbaz *et al*.		2*x*	Arctic Canada and Greenland
Endemic diploid taxa			
A. croatica (Schott) O'Kane & Al-Shehbaz		2*x*	Bosnia, Croatia
A. cebennensis (DC.) O'Kane & Al-Shehbaz		2*x*	SE France
A. pedemontana (Boiss.) O'Kane & Al-Shehbaz		2*x*	NW Italy
Allopolyploid taxa			
A. suecica (Fr.) Norrl.		4*x*	Fennoscandinavia and the Baltic region
A. kamchatica (DC.) K. Shimizu & Kudoh subsp. *kamchatica*		4*x*	Boreal Alaska, Canada, E Siberia, Russian Far East, Korea, Japan, Taiwan
A. kamchatica subsp. *kawasakiana* (Makino) K. Shimizu & Kudoh		4*x*	Japan, winter annual (coastal, lowland)

Species-level taxonomy refers to Al-Shehbaz *et al.* (1999), Koch *et al.* (2008), and Hohmann *et al.* (2014). The most recent treatment of subspecies within *A. halleri* has been proposed by Kolnik and Marhold (2006). *Arabidopsis arenicola* has been introduced by Warwick *et al.* (2006) on the species level. Ploidal levels (diploid=2*x*, tetraploid=4*x*) are summarized from Hohmann *et al.* (2014) and Kolár *et al.* (2016*b*). Base chromosome number is n=8 (2n=2x=16), with *A. suecica* (2n=4x=26) and *A. thaliana* (2n=2x=10) as the only exceptions.

[a] There is another variety still treated under the old genus name Cardaminopsis: *C. arenosa* var. *intermedia* (Neilr.) Hayek from high alpine regions in the south-eastern Austrian Alps (Seckauer Tauern).

Hohmann *et al.*, 2014; Novikova *et al.*, 2016) (Fig. 1, Table 1). Although substantial ancient [million(s) of years ago] and contemporary gene flow (past and interglacial) has been demonstrated (e.g. Jørgensen *et al.*, 2011; Arnold *et al.*, 2015; Novikova *et al.*, 2016; Hohmann and Koch, 2017), these major lineages are well defined, genetically, ecologically, and taxonomically. Also it becomes evident that this source of natural variation including *A. thaliana* itself may serve as an excellent system to study evolutionary processes and ecological strategies within an environmental context (reviewed for *A. thaliana* by Takou *et al.*, 2018).

Species and subspecies in *Arabidopsis* are taxonomic units and are defined by morphological descriptions including information on cytology, ecology, or distribution. Accordingly, any validly described taxon—which refers to species but also to subspecies and varieties—following the rules of botanical

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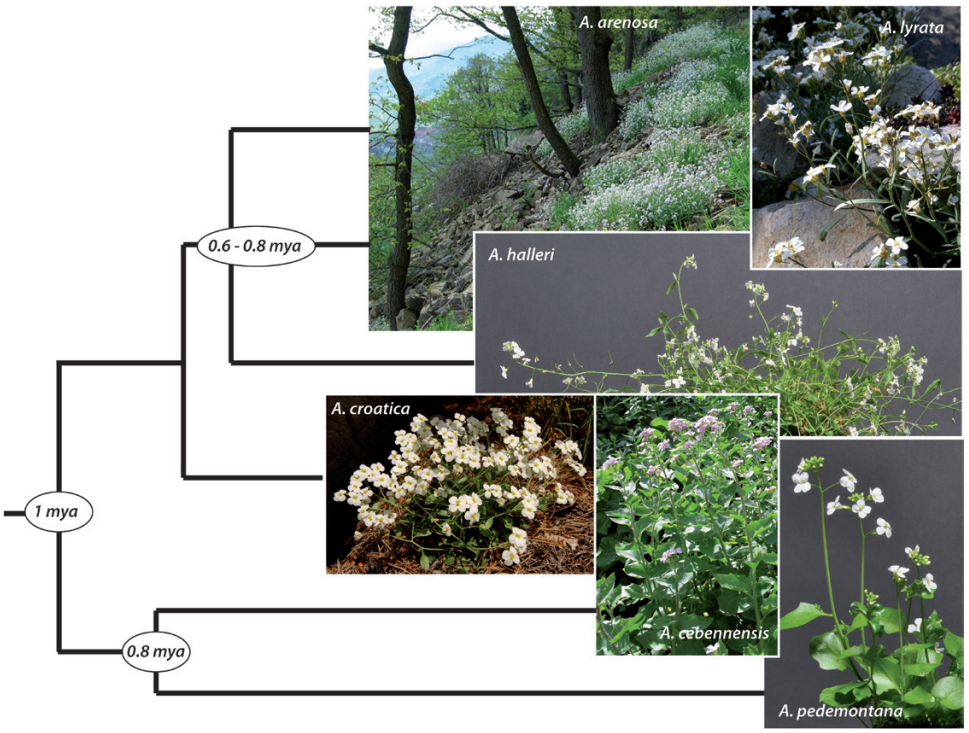

Fig. 1. Schematic phylogenetic relationships among lineages of relatives of *Arabidopsis thaliana*. *Arabidopsis thaliana* split from this entire group during Early Pliocene/Late Miocene ~5.8 million years ago (mya). Divergence times are summarized from Hohmann *et al.* (2015), Arnold *et al.* (2015), Hohmann (2016), and Hohmann and Koch (2017).

nomenclature can serve as accepted taxon. As a consequence, there is no general agreement or taxonomic concept when a subspecies should be considered on species rank or vice versa. Obviously, this needs to be kept in mind for the genus *Arabidopsis*, too. In some lineages, such as *A. halleri*, taxonomic subgrouping has mostly been introduced on a subspecies level, but in *A. arenosa* taxomomic grouping of the entire complex was done with preference for a species-level concept. However, most important is that the taxa are defined, on either a species or a subspecies level, with unambiguous names linked with all information on the respective taxon (Koch *et al.*, 2018)

Arabidopsis halleri*: metals and soils*

Arabidopsis halleri is a perennial, outcrossing, diploid, creeping species and its various subspecies are widely distributed in Europe and Eastern Asia. Subspecies definition is often based on morphology, ecology, and distribution, and a discussion of initial evidence for correlation with genetic data is summarized below. A first draft genome was recently published (Briskine *et al.*, 2017). This species grows on metal-rich soils and exhibits high accumulation of zinc, cadmium, and lead. The species is one among few which are heavy metal hypertolerant (Ernst, 1974) and are able to colonize metalliferous soils. Furthermore, the species also shows the rare trait of metal hyperaccumulation (e.g. Hanikenne *et al.*, 2008, and references therein), and it has been shown that the complex interactions of plants with contaminated soils are not only environment dependent but also geographically structured (Stein *et al.*, 2017). However, the entire distribution range in montane to alpine environments is also characterized by non-metalliferous soils, and large-scale phylogeographic analysis and ecological niche modelling indicate complex post-glacial recolonization scenarios (Wasowicz *et al.*, 2016). Since metallicolous populations have been founded separately all over the distribution range, this trait seems to have arisen multiple times from distinct populations that do not exhibit that trait (Pauwels *et al.*, 2005). Among the other *Arabidopsis* species, initial work on bedrock adaptation has been done on North American *A. lyrata* from serpentine soils (Turner *et al.*, 2008, 2010), or *A. arenosa* from serpentine stands in Eastern Austria (Arnold *et al.*, 2016).

Within *A. halleri*, up to five subspecies have been recognized (for details, refer to Koch *et al.*, 2008) with two of them, *A. halleri* subsp. *gemmifera* and *A. halleri* subsp. *ovirensis*, accepted by some authors as separate species, namely *A. gemmifera* and *A. ovirensis*, respectively (Iljinska *et al.*, 2007; Kadota, 2007). In Central Europe three subspecies can be differentiated (Kolnik and Marhold, 2006). The most widely distributed taxon is *A. halleri* subsp. *halleri* found from Poland to Serbia and from France to Western Ukraine. The second taxon, *A.halleri* subsp. *tatrica*, is a Western Carpathian endemic species. In contrast to these two subspecies, which are substrate indifferent, the third subspecies, *A. halleri* subsp. *dacica*, from the Eastern and Southern Carpathians is an alpine and rarely montane species from acidic bedrock types. The Eastern Asian subspecies *A. halleri* subsp. *gemmifera* is geographically and genetically fully isolated (Koch *et al.*, 2008); and *A. halleri* subsp. *ovirensis* described as endemic to the East Austrian high mountain range at Mount Obir, in Carinthia, might not represent a genetically defined taxon but rather an isolated population from within the *A. halleri* subsp. *halleri* gene pool (Koch and Matschinger, 2007; Koch *et al.*, 2008). There are some first phylogeographic studies, and

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it has been shown that one major centre of genetic diversity is located in the Eastern Austrian Alps (Koch and Matschinger, 2007; Pauwels *et al.*, 2012).

A comprehensive phylogeographic scenario (Pauwels *et al.*, 2012) also demonstrated high levels of genetic diversity found in the eastern region of the European Alps and was explained convincingly by admixture and secondary contact of different European gene pools. The evolutionary scenario of *A. halleri* is best placed among Pleistocene glaciation and deglaciation cycles (Koch and Matschinger, 2007; Wasowicz *et al*, 2016). In a detailed evolutionary study, Roux *et al.* (2011) suggested the onset of radiation within *A. halleri* subsp. halleri to be ~335 000 years ago but, because this study does not consider other subspecies, a much deeper evolutionary split is likely, as indicated more recently (Novikova *et al.*, 2016). Generally, the number of genetic–evolutionary studies centred around *A. halleri* is high (e.g. Van Rossum *et al.*, 2004; Meyer *et al.*, 2009; Heidel *et al.*, 2010), and various ecological studies consider traits such as herbivory (Kawagoe and Kudoh, 2010; Sato and Kudoh, 2017), flowering time (Shimizu *et al.*, 2011), or reproduction (Llaurens *et al.*, 2008).

Arabidopsis lyrata: *breeding system and evolutionary biology*

Arabidopsis lyrata is a perennial and mostly outbreeding (self-incombatible) species with five taxa in total. Its close relationship to *A. thaliana* and a genetically diverse sporophytic self-incompatibility system fostered its early establishment as a model system to study breeding system evolution and its genetic and molecular components (e.g. Nasrallah *et al.*, 2004; Guo *et al.*, 2011; Vekemans *et al.*, 2014). Various aspects of trait evolution in a perennial plant have also been studied intensively, such as thermal stress response (Wos and Willi, 2018), seed biology (Hämälä *et al.*, 2017), or general fitness and survival (Leinonen *et al.*, 2011). More details and earlier ecological work have been summarized by Clauss and Koch (2006). The species is one of the model systems used to study local adaptation in the context of trait evolution. One of those traits is adaptation in response to heavy metal such as nickel, thereby linking this species with *A. halleri* (e.g. Turner *et al.*, 2008, 2010; Veatch-Blohm *et al.*, 2017); other traits are herbivory response (Vergeer and Kunin, 2011), flowering time (Hämälä *et al.*, 2018), or more generally pathogen-mediated selection (Buckley *et al.*, 2018). Studies of molecular evolution have been fostered by the publication of the *A. lyrata* genome (Hu *et al.*, 2011) and have focused on various features including transposons (Bonchev and Willi, 2018), transcriptional changes (Wos and Willi, 2018), or accumulation of mutational load (Willi *et al.*, 2018). Research on populations in North America at the Great Lakes shows that some of them are undergoing a loss of a functional self-incompatible (SI) system (Mable *et al.*, 2005), which allows the study of causes and genomic consequences of mating shifts (e.g. Mable *et al.*, 2005, 2017; Griffin and Willi, 2014) and to compare those with largely inbreeding *A. thaliana*. Artifical interspecific hybrids of *A. lyrata* with Arabidopsis were created to study the expression pattern of transposable elements (TEs) in the hybrid genomic context and showing that TE expression is globally robust (Göbel *et al.*, 2018). An artificial interspecific hybrid of *A. lyrata* with *A. halleri* elucidated the role of *cis*-acting modifications in cold adaption (He *et al.*, 2016)

The rosette-forming plant has a circumpolar distribution. The two main distribution centres are formed by subsp. *petraea* in Central and Northern Europe and subsp. *lyrata* in Northern America. This disjunct distribution is mediated by subsp. *umbrosa* and subsp. *septentrionalis* (Table 1). The fifth taxon, *Arabidopsis arenicola*, was originally described as *Arabis* and later transferred to *Arabidopsis* as a separate species. *Arabidopsis arenicola* is an arctic and self-compatible (MAK, unpublished results) species from Canada and Greenland of very recent and probably post-glacial origin from subsp. *lyrata* (Hohmann *et al.*, 2014). Therefore, it might be best treated in future as another subspecies of *A. lyrata*. The species complex is diploid with two exceptions: *A. lyrata* subsp. *sepentrionalis* probably represents a tetraploid taxon; it might have arisen via secondary contact between the two main subsp. *lyrata* and subsp. *petraea* gene pools and may represent an 'allo'tetraploid (Hohmann *et al.*, 2014). The other exceptions are tetraploid populations from the northeastern limestone Forealps and pannonical dryland regions close to the Danube river in Austria. Those originated from adaptive introgression between two species (*A. lyrata* and *A. arenosa*) and are discussed separately below (Schmickl and Koch, 2011; Hohmann and Koch, 2017).

Studying six populations, Ross-Ibara *et al.* (2008) presented an estimate of the split time between the European and North American distribution ranges of ~35 000 years based on demographic models and assuming a mutation rate of 1.5×10^{-8} (following Koch *et al.*, 2000; see also the section on *A. arenosa* for application of different mutational rates). This was also compared with F_{ST}-based comparisons which result instead in an estimate of ~90 000–170 000 years ago. A recent study estimated a split time between subsp. *petraea* and subsp. *lyrata* at 190 000–310 000 years ago (Mattila *et al.*, 2017). This much better fits presented comprehensive phylogeographic scenarios covering the entire distribution range. It also considers the amphiberingean region (which means that the range is centred on what was formerly Beringia and that the species occurs on both sides of the Bering Strait) as a melting pot of lineages coming into secondary contact during the last glaciation and deglaciation cycles (e.g. Schmickl *et al.*, 2008, 2010; Hohmann *et al.*, 2014).

A phylogeographic study focusing on North American subsp. *lyrata* was not able to show any clear structure of genetic variation (Tedder *et al.*, 2010), tentatively because of a very recent post-glacial biogeography. Similarly, Hämälä *et al.* (2018) demonstrated post-glacial evolutionary demographic scenarios in Scandinavia. Central European populations might have diverged from direct ancestors of Scandinavian populations ~28 000 generations ago. This equals ~56 000 years ago considering the life cycle of this plant which flowers latest in its second year.

Arabidopsis arenosa: *polyploid evolution and interspecies gene flow*

The *A. arenosa* complex is definitely the most complex and diverse group of taxa. Although its overall distribution is

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smaller than that of *A. lyrata* and *A. halleri*, the taxa occupy a wide range of habitats from alpine regions to sandy coastal sites and dune vegetation. The species complex consists of short-lived perennials, and the original rosette often dies after flowering. Daughter rosettes are frequently formed. At the moment, five species with various subspecies (Table 1) are recognized. However, in various cases, the respective names are provisional, such as *A. nitida*. There are tetraploid and diploid taxa, and it was only recently that a single origin of the tetraploids was demonstrated (Arnold *et al.*, 2015). This may be surprising since a large-scale genetic screen using microsatellite variation demonstrated that tetraploids are genetically very diverse and mask the primary centre of diversity of diploids in the Carpathians (Schmickl *et al.*, 2012). One explanation could be that tetraploid *A. arenosa* and its tetraploid subspecies originated from within large populations carrying a substantial amount of genetic variation. Furthermore, at least some inter- and intraspecies level gene flow might have occurred after polyploidization, even crossing ploidy levels (Jørgensen *et al.*, 2011; Arnold *et al.*, 2015) and thereby contributing substantial genetic variation. Intensive genetic interplay of *A. arenosa* has also been demonstrated with *A. lyrata* (Schmickl and Koch, 2011) and *A. halleri* (Hohmann, 2011; Hohmann *et al.*, 2014) (Fig. 2).

Arabidopsis arenosa contributed as paternal hybridization partner to give rise to *A. suecica* (Koch and Matschinger, 2007; Novikova *et al.*, 2017). Meanwhile *A. suecica* served as a model for interspecies *A. thaliana* hybrids (Säll *et al.*, 2003), and studies using artificial hybrids between *A. arenosa* and *Arabidopsis* have been used (Nasrallah *et al.*, 2000) to study gene silencing (e.g. Comai *et al.*, 2000) or post-zygotic hybridization barriers (Bushell *et al.*, 2003).

More recently, with Yant *et al.* (2013) and the overview given by Bomblies and Madlung (2014), *A. arenosa* was introduced as a system to study polyploidization. It also serves as a model system to study the molecular basis and evolution of meiosis in polyploids (e.g. Bomblies *et al.*, 2015; Yant and Bomblies, 2017). This work also hints at interactive effects with important environmental factors such as temperature (Wright *et al.*, 2015; Morgan *et al.*, 2017).

Arabidopsis lyrata as well as *A. arenosa* only rarely occur on metalliferous soils, the exceptions being serpentine (e.g. in Austria), and it has been shown that parallel adaptation of different populations occurred via post-glacial adaptive introgression of genes from populations from the same species but also from *A. lyrata* (Arnold *et al.*, 2016). This is another example of interspecies and interploidal gene flow since in this area *A. arenosa* is exclusively tetraploid and *A. lyrata* is diploid. The species split time between *A. lyrata* and *A. arenosa* was calculated as ~400 000 generations, which corresponds to ~800 000 years ago. This is in line with previous assumptions of a Mid- to Late-Pleistocene species split (Hohmann *et al.*, 2014;

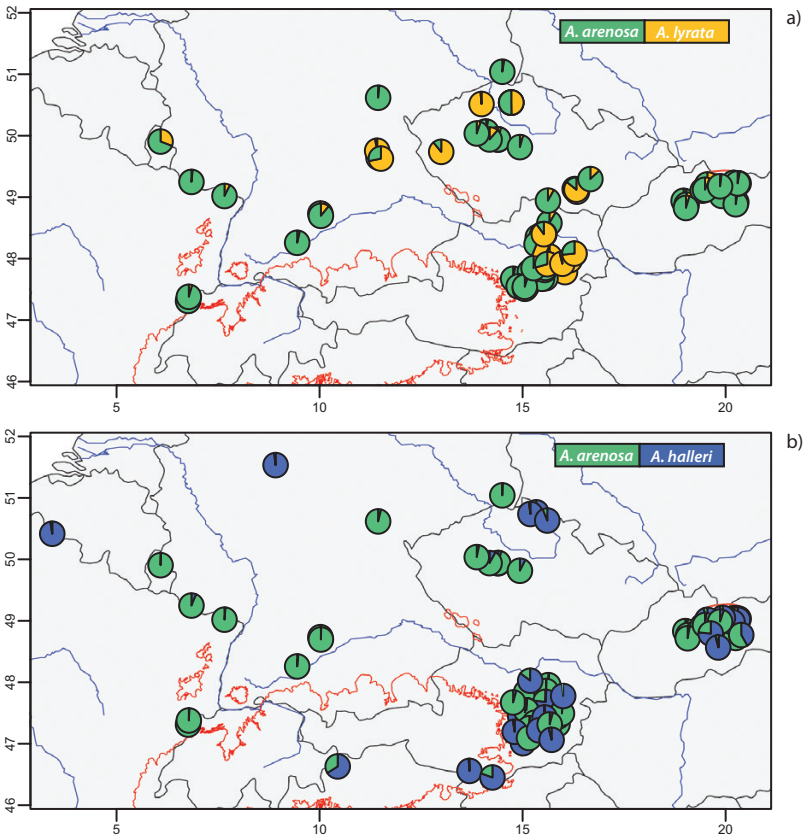

Fig. 2. Examples for genetic admixture between the three more widely distributed species groups in Central Europe. Genetic admixture is shown (a) for *A. lyrata–A. arenosa* and (b) for *A. halleri–A. arenosa*. Genetic admixture data are taken and redrawn as pie charts from earlier published microsatellite data (Hohmann, 2011; Hohmann *et al.*, 2014). (Genetic assignment analysis, number of genetic clusters: *K*=2 each, using Structure; Falush *et al.*, 2007.) Glacial border from the Last Glacial Maximum (~25 000 years ago) are drawn as red lines based on Gibbard (2002) and Zasadni and Klapyta (2014).

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Novikova *et al.*, 2016). However, plastome data indicate a species divergence, which is younger and of ~550 000 years ago (Hohmann and Koch, 2017).

A single origin of all tetraploids in *A. arenosa* (Arnold *et al.*, 2015) was estimated to ~11 000–33 000 generations ago and, considering phylogenetic relationships among tetraploid lineages, the centre of origin is best placed within the Carpathian Mountains. Geographically this matches the centre of species diversity of the *A. arenosa* lineage (Koch and Matschinger, 2007) as well as the distribution centre of diploids within the *A. arenosa* lineage (Kolár *et al.*, 2016*b*). Extensive interglacial, glacial, or post-glacial range expansion of diploids has not been demonstrated (Kolár *et al.*, 2016*a*), but a few diploids have migrated post-glacially towards the North into the Baltic. This also matches spatio-temporally with post-glacial hybrid speciation of Fennoscandinavian *A. suecica* (Novikova *et al.*, 2017). However, it should be mentioned that the age estimate of tetraploid *A. arenosa* (Arnold *et al.*, 2015) was based on a mutation rate of 3.7×10^{-8}. This is five times higher than the rates measured in *A. thaliana* in laboratory-based experiments (Ossowski *et al.*, 2010); and applying those rates for the origin of tetraploid *A. arenosa* would result in a five times higher age estimate of ~110 000–330 000 years ago (compared with 11 000–33 000 generations with the 2 year life cycle equalling 22 000–66 000 years). This does correlate well with a spatio-temporal scenario of introgression of tetraploid *A. arenosa* into *A. lyrata* in Eastern Austria after the Riss glaciation (130 000 years ago) (Hohmann and Koch, 2017).

The diploid and local endemics: A. cebennensis, A. pedemontana, *and* A. croatica—*from the French volcanic Massif Central to the Croatian Karst mountains*

There are three species with a particularly narrow distribution. All of them are also phylogenetically separated from the other major lineages (Fig. 1). *Arabidopsis cebennensis* and *A. pedemontana* represent sister species and have the smallest distribution range in the whole genus (Koch *et al.*, 2008). *Arabidopsis cebennensis* is restricted to the mountainous regions in Southern France at elevations ranging from 900 m to 1500 m above sea level. The highly disjunct populations occur in the Massif Central, the Cevennes, and the Ardeche regions. The outcrossing and perennial species is the tallest among all *Arabidopsis* relatives and can reach a size of up to 1 m. It grows in a narrow ecological niche in riverine systems often close to natural springs and characterized by continuously running cold mineral-rich water.

Arabidopsis pedemontana is restricted to a range of 50 km^2 in the Piedmont region of the north-western Italian Alps, at altitudes ranging from 1300 m to 2200 m above sea level. Also *A. pedemontana* is presumably self-incombatible, with a strong tendency for vegetative reproduction by clonal growth (Hohmann *et al.*, 2014), but it resembles a growth type more similar to *A. halleri* (Fig. 1). Both species demonstrate very strong inter-regional genetic differentiation indicating severe genetic bottlenecks due to past glaciations (Jacquemin *et al.*, 2016, Preprint). Drastic reductions of effective population sizes have been demonstrated and placed those events with a maximum of 4000 and 40 000 years ago for *A. cebennensis* and *A. pedemontana*, respectively (Jacquemin *et al.*, 2016, Preprint). Because the same authors questioned the dimension of the timing results considering their calculated and highly contradictory species split time of 160 000 years ago (see Fig. 1, compared ith 800 000 years ago), it is worth considering five times higher estimates. This would place the drastic bottleneck events for both species close to the glaciation maxima 25 000 years ago (Würm glaciation, *A. cebennensis*) and 130 000 years ago (Riss glaciation, *A. pedemontana*). Both species are genetically isolated from any other *Arabidopsis* species, and they also do not exhibit significant signatures of past gene flow among different species as was demonstrated for the other taxa (Koch and Matchinger, 2007; Hohmann *et al.*, 2014; Novikova *et al.*, 2016). However, ancient gene flow between the common ancestor of *A. pedemontana* and *A. cebennensis* with *A. halleri* from its western distribution range is nonetheless likely (Novikova *et al.*, 2016).

Arabidopsis croatica is distributed along the Dinaric Mountains on rocky outcroppings and fissures in Croatia. The thermophylous diploid species is perennial and self-incompatible, and it is restricted to calcareous bedrock. Phylogenetic analyses placed this taxon as a sister species basal to *A. lyrata* and *A. arenosa* (Novikova *et al.*, 2016; sequence data from re-sequenced nuclear genomes), and maternal signatures from entire plastome sequences even placed this taxon basal to all three species complexes (*A. halleri*, *A. lyrata*, and *A. arenosa*). However, only very few individuals of *A. croatica* have been analysed so far, and a more comprehensive sampling is needed to explain the incongruency which might reflect incomplete lineage sorting, secondary gene flow, or ancestral shared polymorphisms. It is interesting to see that genetic admixture analysis assuming five genetic clusters among perennial *Arabidopsis* relatives shows *A. croatica* sharing substantial genetic variation with *A. cebennensis* and *A. pedemontana* (Novikova *et al.*, 2016), which cannot be explained by (unlikely) gene flow during the last 130 000 years and which may indeed indicate massive shared ancestral genetic variation.

All three species are endangered, and *A. croatica* and *A. pedemontana* are strictly protected according to national law and listed as 'critically endangered' according to the IUCN definition. *Arabidopsis cebennensis* is most often found in protected nature reserve areas, and thereby also receives full protection. Hence, major efforts should be undertaken to cultivate these species and provide germplasm resources, with the scientific community following the regulations of the Convention on Biological Diversity and the Nagoya protocol.

Allopolyploid systems: whole-genome duplications in A. kamchatica *and* A. suecica

There are two contrasting allopolyploid species systems, which have been nicely introduced in a recent review (Novikova *et al.*, 2018), thereby highlighting the origin of these polyploid taxa around recent glaciation maxima. The Brassicaceae family as a whole is characterized by a high percentage of polyploid taxa. More than 43% of the species are neopolyploids (Hohmann

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et al., 2015), and actually 10 mesopolyploidization events predating the evolution of tribes (monophyletic assemblages of genera) have been described (Lysak *et al.*, 2005, 2007; Haudry *et al.*, 2013; Mandákova *et al.*, 2017). A family-wide summary of genome size and ploidy level evolution is provided in Hohmann *et al.* (2015) and indicates tremendous evolutionary dynamics of the genomes in size and structure, and continuous and rapid genome downsizing after polyploidization events (Lysak *et al.*, 2009; Mandákova and Lysak, 2018). Therefore, polyploidization in Brassicaceae can be regarded as one of the driving mechanisms of adaptation to rapidly changing environments and is often able to explain the high speciation rates found (Jordon-Thaden *et al.*, 2013). On the family level, there is also a significant correlation of lower 1 C*x* (monoploid) genome size with annual life cycle in *Arabidopsis* (Hohmann *et al.*, 2015) compared with its perennial wild relatives.

Arabidopsis suecica ($2n=4x=26$) had an origin with *A. thaliana* ($2n=2x=10$) as maternal partner providing an unreduced gamete and tetraploid *A. arenosa* providing the parental $n=16$ gamete. This plastid (i.e. maternally inherited) molecular signature was demonstrated more than two decades ago (Mummenhoff and Hurka, 1995; O'Kane *et al.*, 1996). Chloroplast and nuclear markers suggest that *A. suecica* arose just once (Säll *et al.*, 2003; Jakobsson *et al.*, 2006). An analysis of haplotype variation in the *A. thaliana* portion of the *A. suecica* genome was recently used to argue that there were multiple origins (Novikova *et al.*, 2016). The time of origin was estimated to be ~16 000 years ago in Eastern Europe or Central Eurasia, with subsequent migration into the Fennoscandinavian region while glaciers were retreating (Novikova *et al.*, 2017). Whether it has a single or multiple origins, *A. suecica* is certainly of a more regional origin and carries limited genetic variation.

Showing high levels of genetic diversity compared with *A. suecica*, another allopolyploid, *A. kamchatica* ($2n=4x=32$), originated via hybridization and polyploidization of outcrossing diploid *A. lyrata* and diploid *A. halleri* subsp. *gemmifera* in Eastern Asia, presumably around Japan, north-eastern China, and eastern Siberia (Shimizu-Inatsugi *et al.*, 2009; Schmickl *et al.*, 2010). A post-glacial origin ~20 000 years ago is likely (Tsuchimatsu *et al.*, 2012), but there is still some uncertainty because of different mutation rates applicable to the analyses. Both *A. suecica* and *A. kamchatica* are selfing species. In *A. suecica*, the self-incombatible system seems to have been overcome just once at the beginning of its evolutionary history (Novikova *et al.*, 2017), whereas *A. kamchatica* underwent transitions to selfing several times via degradation of male specificity genes (Tsuchimatsu *et al.*, 2012; Shimizu and Tsuchimatsu, 2015). *Arabidopsis suecica* is an annual plant like its maternal parent, *A. thaliana*, while the amphiberingean *A. kamchatica* subsp. *kamchatica*, which occurs on both sides of the Bering Strait, is a short-lived perennial, though in Japan the subspecies *kawasakiana* is also annual, in association with its adaptation to highly disturbed sandy seashore habitats at Lake Biwa in Japan (Higashi *et al.*, 2012).

The combination of two different genomes in natural allopolyploids attracts research to study various aspects of genomic interactions. Both species allow study of the interplay of genomes which diverged nearly 6 million years ago (*A. suecica*: *A. thaliana* versus *A. arenosa*) and ~600 000 years ago (*A. kamchatica*: *A. lyrata* versus *A. halleri*) with a similar time span of allopolyploid evolutionary history of ~20 000 years. These studies focus on gene expression (e.g. Tian *et al.*, 2014; Miller *et al.*, 2015; Paape *et al.*, 2016), epigenetic regulation (Costa-Nunes *et al.*, 2010; Pontvianne *et al.*, 2012), retention of homologues (Chang *et al.*, 2010; Paape *et al.*, 2018, Preprint), or heterosis effects (Solhaug *et al.*, 2016). Furthermore, ecological aspects of adaptation are addressed, such as cold tolerance (Armstrong *et al.*, 2015), flowering biology (Kenta *et al.*, 2011), trichome production and reproductive trade-off evolution (Steets *et al.*, 2010), and also the ability to cope with heavy metal-rich soils (Paape *et al.*, 2016) by retaining the ability to hyperaccumulate zinc from *A. halleri*.

Arabidopsis thaliana*: evolutionary history beyond the 1001 genomes*

Since the first phylogeographic studies on *A. thaliana* were published more than a decade ago (Sharbel *et al.*, 2000; Beck *et al.*, 2008), the 1001 Arabidopsis genomes consortium provided the first comprehensive insights into *A. thaliana* evolutionary history. These indicate glacial refuge areas on the Iberian Peninsula, the Canary and Cape Verde Islands, Sicily, and the Levant region (1001 Genomes Consortium, 2016). A very dynamic post-glacial spatio-temporal diversification pattern all over Eurasia was shown, with strong footprints of selection correlated with post-glacially changing climate and environment. This study highlighted the importance of the Last Glacial Maximum in structuring the present-day *A. thaliana* populations, and the detected spatio-temporal signature collapsed ~130 000 years ago, which exactly matches the preceding glacial maximum of the Mindel glacial. This highlights again, as shown for wild allopolyploid relatives (Novikova *et al.*, 2018), that diversification processes in space and time are often set into the context of glacial maxima and the subsequent early phase of the generally shorter interglacial intervals. More detailed studies on *A. thaliana* (Brennan *et al.*, 2014; Durvasula *et al.*, 2017; Zou *et al.*, 2017; Fulgione *et al.*, 2018) elucidated multiple colonizations of the Iberian Peninsula via Central Europe and via Africa during the last glaciation (45 000 and 90 000 years ago, respectively) but pre-dating the Last Glacial Maximum, and large-scale range expansions in Africa at ~120 000–90 000 years ago were demonstrated. Africa was shown to be one primary cradle of genetic diversity (Durvasula *et al.*, 2017) of present-day *A. thaliana*, with the transition to selfing occurring in North-western Africa. It was concluded that African populations best represent the early history of the species (Fulgione and Hancock, 2018). However, this conclusion does have some restrictions, because the presented modelling of nuclear genomic data does not reveal deeper evolutionary splits than 130 000 years ago and thereby points to the last common ancestor of present-day *A. thaliana* populations. Furthermore, there are no Eurasian *A. thaliana* populations older than any African lineages. However, there are at least a few indirect hints allowing tracing of even deeper evolutionary trajectories in *A. thaliana*. S-locus haplotype variation suggests a geographic localization of the transition to selfing in Africa

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(Durvasula *et al.*, 2017), and comparative studies among various *Arabidopsis* species estimated this transition to have occurred 413 000 years ago (Bechsgaard *et al.*, 2006) or even ~1 million years ago (Tang *et al.*, 2007). Assuming that these older estimates are reliable, the African history of *A. thaliana* is indeed nearly 1 million years old. However, *A. thaliana* split from its relatives >5 million years ago (e.g. Hohmann *et al.*, 2015; Huang *et al.*, 2016; Guo *et al.*, 2017) and, therefore, more >4 million years of evolutionary history remains unclear.

It is worth mentioning that for several genera of Brassicaceae there is a phylogenetic sister relationship of a species-poor clade of annuals (often with one single species only) and a predominantly perennial clade. Environmental changes (e.g. increasing temperature or drought) led to the realization of two different strategies: (i) transition to an annual life cycle with later transition to selfing, rapid colonization of low-elevation habitats; and (ii) migration to the North and in particular towards higher elevations, thereby favouring niche differentiation, allopatric speciation, and increased speciation (Karl and Koch, 2013; Koch *et al.*, 2016). Accordingly, it may be hypothesized that ~1 million years ago two perennial lineages evolved rapidly and independently. One lineage may have successfully colonized the African continent with a transition towards selfing and an annual life cycle. The other lineage underwent a complex evolutionary history leading to speciation in Eurasia and the amphiberingean region and leaving deep footprints of its development within its plastid genomes (Novikova *et al.*, 2016; Hohmann and Koch, 2017). This scenario is in agreement with the finding of ancient gene flow between *A. thaliana* and *A. lyrata* but not between *A. thaliana* and *A. arenosa* or *A. halleri* (Novikova *et al.*, 2016). However, most probably the detailed biogeographical context will remain a mystery, because we have no data for paleoenvironments from 1 million years ago and present distribution ranges do not allow comparative phylogeographic conclusions in deeper times.

The temporal context might be solved in much more detail in the future. Estimation of a temporally resolved evolutionary scenario largely depends on assumptions on the underlying mutational rate of DNA. Here it is important to distinguish between the mutation rate, which is the rate at which genomes change due to DNA damage, faulty repair, gene conversion, and replication errors, and the substitution rate, which is the rate at which mutations accumulate within a given gene pool (Exposito-Alonso *et al.*, 2018). Therefore, it is important that any rate used is critically chosen, set into the right context, and compared carefully with other studies. The following examples apply for the nuclear genome. Studies spanning hundreds of millions of years and analysing various plant families including Brassicaceae used, for example, synonymous substitution rates of 6–7 × 10^{-9} substitutions per site per year (Lynch, 2010; De la Torre *et al.*, 2017), data sets focusing on the Brassicaceae family and spanning a few million years assumed 3.83–8.56 × 10^{-9} (Huang *et al.*, 2012) or 8.22 × 10^{-9} (Kagale *et al.*, 2014) synonymous mutations per site per year, whereas in a study focusing on *Capsella* and *Arabidopsis*, a substitution rate per site per year of 7 × 10^{-9} was used (Wu *et al.*, 2017). Other studies aiming to resolve time spans of a few hundreds or thousands years have elaborated substitution rates of 2.7 × 10^{-9} substitutions per site and generation for Arabidopsis (Exposito-Alonso *et al.*, 2018), which was translated into 2–5 × 10^{-9} substitutions per site per year as *A. thaliana* is an annual. A mutation rate of *A. thaliana* under 'lab conditions' was estimated and introduced with 7 × 10^{-9} mutations per site per year per generation (Ossowski *et al.*, 2010). Finally, Arnold *et al.* (2015) simulated a rate for their analyses in *A. arenosa* of 3.7 × 10^{-8} substitutions per site per year. In summary, there is a great demand carefully to document and explain the nature of the chosen rates and compare results with those obtained using alternative rates and thereby allow cross-study comparisons.

Summary: bridging *Arabidopsis thaliana* and its relatives

This review highlighted that *A. thaliana* and its relatives do not just share a common ancestor at ~6 million years. After this split, the various species shared a spatio-temporal context to varying degrees. Severe environmental changes, such as via oscillating climate change during the entire Pleistocene, affected some of the lineages. This did not only lead to differing patterns and processes, but some are similar among them. This makes the genus *Arabidopsis* as a whole a suitable system to conduct comparative and across-species studies given that reliable spatio-temporal evolutionary scenarios are available. It is also summarized that secondary genetic contact is often triggered by glaciation maxima and subsequent shorter warming phases, and has affected any lineage including *A. thaliana*. There are many open questions such as the 'deep history' of *A. thaliana* or more detailed analyses differentiating between contemporary and past gene flow among *A. lyrata*, *A. arenosa*, and *A. halleri*. So far, most often comparative studies have involved only two species but, with the knowledge of putative gene flow among all species, future studies might consider multi-species approaches.

Comment on germplasm accessibility

It has to be highlighted that for some of the perennial relatives of *Arabidopsis*, access to natural populations requires not only considering local/regional regulations (e.g. protected areas such as nature reserves or national parks) and international regulations of benefit sharing (Convention of Biological Diversity, Nagoya protocol from 2014), but some species are actually under severe threat and are categorized according to IUCN protection definition categories as 'critically endangered', such as *A. croatica* and *A. pedemontana*. Others are locally endangered, and some populations of *A. lyrata*, in particular in Eastern Austria, are regionally endangered and may even be 'oversampled'.

Acknowledgements

I thank Nora Hohmann for her help with data export and preparation of Fig. 2. Markus Kiefer, Kirsten Bomblies, Angela Hancock, and two anonymous reviewers are greatly acknowledged for their very

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helpful comments. This work was supported by the German Research Foundation (DFG) and DFG grants 2302/5, 2302/14, and 2302/23.

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