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Plant speciation in the Quaternary

Joachim W. Kadereit^a and Richard J. Abbott^b

^aInstitut für Organismische und Molekulare Evolutionsbiologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany; ^bSchool of Biology, Mitchell Building, University of St Andrews, St Andrews, UK

ABSTRACT

Background: There are conflicting views between palaeobotanists and plant systematists/evolutionary biologists regarding the occurrence of plant speciation in the Quaternary. Palaeobotanists advocate that Quaternary speciation was rare despite opposing molecular phylogenetic evidence, the extent of which appears underappreciated.

Aims: To document, describe and discuss evidence for Quaternary plant speciation across different geographical regions based on dated molecular phylogenies and related studies.

Methods: From a search of the literature, we compiled a selection mainly of dated molecular phylogenies from all continents (except Antarctica) and from all major climate zones.

Results: Molecular phylogenetic analyses and related studies show that Quaternary plant speciation and radiations occurred frequently and that in many instances Quaternary climatic oscillations were likely important drivers of them. In all geographical regions studied, Quaternary plant speciation and radiations were particularly evident in mountainous areas and arid regions, and were also prevalent on all major oceanic archipelagos.

Conclusions: Based on our survey of the molecular phylogenetic and related literature we propose there is now overwhelming evidence that plant speciation and radiations were ubiquitous during the Quaternary. We therefore reject the view of palaeobotanists that plant speciation was rare during this period and briefly discuss possible reasons for this discrepancy.

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Introduction

There is a continuing debate over whether plant speciation was frequent during the Quaternary period (the last 2.6 million years), with opposing evidence offered by some palaeobotanists on the one hand and plant systematists/evolutionary biologists on the other hand. In his monumental review of ‘Contributions of Quaternary botany to modern ecology and biogeography’, Birks (2019) examined, as one of his four major topics, biotic responses to Quaternary environmental change, which he considered to include distributional range shifts, extinctions, and persistence and adaptation. Speciation, although an evolutionary response as much as adaptation, is touched upon, but with only one fossil-based example given of possibly allopatric speciation (Kienast et al. 2018). The examination of Quaternary speciation clearly was not among the major aims of the review by Birks (2019). For a discussion of the interface between Quaternary botany and evolution, Birks (2019) referred to Bennett (1997). In his book ‘Evolution and ecology—the pace of life’, Bennett (1997) concluded that ‘given the overall low frequency of any evolutionary response, it must be concluded that, for most

species, most of the time, stasis is the rule through climatic oscillations of Milankovitch time-scales’. This was re-iterated by Bennett (2004) in his concluding paper of a Royal Society Discussion Meeting on ‘The evolutionary legacy of the ice ages’, where he wrote that ‘The Quaternary [...] does not appear to be associated particularly with the origination of new species’, and again in a later article (Bennett 2013) in which he emphasised that in response to Quaternary climate changes ‘both speciation and extinction are rare consequences.’ Views similar to Bennett’s (Bennett 1997, 2004, 2013) have been expressed also by Lang (1994) and Willis and Niklas (2004).

Such assessment of the frequency of Quaternary speciation, more by Bennett (1997, 2004, 2013) than by Birks (2019), in our opinion overlooks a vast number of dated molecular phylogenies of various plant groups that have shown massive plant speciation in the Quaternary. This omission is even more surprising as Birks (2019) clearly appreciated the potential of DNA analysis in palaeogenetic, palaeogenomic, and phylogeographic studies. Just as radiocarbon dating freed, as pointed out by Birks (2019), pollen analysis from being a relative

CONTACT Richard J. Abbott  rja@st-andrews.ac.uk
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chronological tool, application of a molecular clock made it possible to date molecular phylogenies, potentially providing the opportunity to recognise (and test) correlations between diversification events and environmental change. Ideally, dating of molecular phylogenies relies on correctly identified and correctly dated fossils for the calibration of correctly chosen nodes in a molecular phylogeny, thus illustrating the dependence of molecular dating on palaeobotanical evidence and expertise. In plant groups where fossils are lacking, dating of molecular phylogenies relies on the results of fossil-calibrated molecular clocks mostly from more comprehensive groups (secondary calibration), or more rarely, on the use of molecular rates (Hipsley and Müller 2014).

It seems to us that the high frequency of Quaternary plant speciation is underappreciated by some. On this background we here provide evidence of Quaternary plant speciation. From a search of the literature we have compiled a selection mainly of dated molecular phylogenies from all continents (except Antarctica), several islands and archipelagos and from all major climate zones in order to show that plant speciation in the Quaternary was ubiquitous. Relevant literature was identified by searching the ISI Web of Knowledge using the search terms 'Quaternary speciation' and 'Pleistocene speciation', by examining a range of journals expected to publish articles on the topic, and from information provided by fellow-botanists. In this way, we identified examples of Quaternary speciation in 202 plant genera and 64 families (Tables 1–8, Table S1). Further examples of Quaternary speciation have been provided by Lu et al. (2018) for the Qinghai-Tibet Plateau flora, representing 184 additional genera and 10 additional families (Table S2), and by Maurin et al. (2022) for the New Zealand flora, representing 14 additional genera and six additional families. Therefore, in total, examples of Quaternary speciation have been obtained for 400 plant genera and 80 families. Below, we briefly describe episodes of Quaternary speciation that have taken place in different geographical regions, highlighting that rapid plant radiations have been frequent in divergent biomes and genera throughout this period.

Europe

In Europe (Table 1), Quaternary speciation has been detected particularly in the Mediterranean region and in high mountain areas across the European

Alpine System (EAS), ranging from the Pyrenees in the west across the Alps to the Carpathians, Dinarids and Balkans in the east. Examples of Quaternary speciation of Mediterranean lineages include *Senecio* (Comes and Abbott 2001; for family assignment of genera throughout this paper see Table 1), *Anthemis* (Lo Presti and Oberprieler 2009), *Reseda* sect. *Glaucoseseda* (Martín-Bravo et al. 2010), *Lathyrus*, *Pisum* and *Vicia* (Schaefer et al. 2012), *Centaurium* (Jiménez-Lobato et al. 2019), *Limonium* (Koutroumpa et al. 2021) and *Antirrhinum* (Figure 1; Vargas et al. 2009; Otero et al. 2021). Quaternary speciation in these and other Mediterranean lineages is often considered to have resulted from climate-related vicariance, either with or without accompanying habitat divergence (Nieto Feliner 2014; Rundel et al. 2016). It is thought that during Pleistocene glacial periods populations of species often became isolated from each other in different refugia south of the EAS, e.g. in the Iberian, Apennine and Balkan peninsulas (Hewitt 1996). Recurrent allopatry of these populations occurring over several glacial periods, each lasting for ca. 100,000 years, is deemed to have resulted in genetic divergence and eventually speciation, thus acting as a 'species pump' *sensu* Haffer (1969). A variant form of this model is suggested for the *Nigella arvensis* species complex in which Quaternary speciation is related to Late Quaternary changes in climate and sea level in the Aegean archipelago with diversification caused by genetic drift (Bittkau and Comes 2009). Changes in sea-level are also considered important (along with apomixis) in diversification of *Limonium* (Koutroumpa et al. 2021). In contrast, in *Cistus* Pleistocene speciation is believed to have resulted from adaptation to different habitats following establishment of the Mediterranean climate prior to the Quaternary (Guzman et al. 2009), while for two species of *Senecio* (*S. aethnensis* and *S. chrysanthemifolius*) occupying different elevations on Mt. Etna (Sicily), speciation with gene flow was dated to ca. 150,000 yrs ago and linked to the increase in elevation of Mt. Etna at this time rather than to changes of climate (Osborne et al. 2013).

Climatic oscillations causing recurrent glacial and interglacial cycles are also viewed as a driver of Quaternary speciation in the EAS with notable examples reported in *Gentiana*, *Primula* sect. *Auricula* (Figure 1) and *Soldanella* (Hungerer and Kadereit 1998; Zhang et al. 2001, 2004). A traditional belief is that such speciation was brought about by isolation of populations on

Table 1. Studies reporting Quaternary speciation (QS) in plant genera in Europe and North Africa based on dated molecular phylogenies or other molecular evidence (*Radiations).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
EUROPE/N AFRICA					
<i>Aconitum</i> (Ranunculaceae)	Mediterranean region	pDNA/nrITS	Not specified	One example of species diversification (BEAST analysis)	Jabbour and Renner (2012)
<i>Anthemis</i> (Asteraceae)	Mediterranean region	nrITS	Climatic oscillations	<2 Mya (PL analysis)	Lo Presti and Oberprieler (2009)
* <i>Antirrhinum</i> (Plantaginaceae)	Mediterranean region	pDNA/nrITS; ~4000 nr loci	Terrain complexity and eco-climatic novelty	Considerable speciation (PL implemented in TreePL)	Vargas et al. (2009); Otero et al. (2021)
* <i>Aquilegia</i> (Ranunculaceae)	Mediterranean region and European mountains	pDNA/nr ITS	Climatic oscillations, geographical isolation and habitat divergence	All 13 European species originated from ~2.54 Mya (BEAST analysis)	Bastida et al. (2010)
<i>Callianthemum</i> (Ranunculaceae)	Europe (QS occurred after colonisation by ancestral forms from Asia)	pDNA	Climatic niche differentiation in Europe	Three European species originated (BEAST analysis)	Kadereit et al. (2019)
<i>Campanula</i> (Campanulaceae)	Eurasia and Azores	pDNA	Diverse	Some speciation (PL analysis)	Mansion et al. (2012)
<i>Carthamus</i> (Asteraceae), <i>C. tinctorius</i> group	Turkey	nrITS	Habitat divergence accompanying climatic oscillations	Divergence occurred within sections <i>Atractylis</i> and <i>Carthamus</i> (BEAST analysis)	Tarikahya-Hacıoğlu et al. (2014)
* <i>Centaureum</i> (Gentianaceae)	Mediterranean region	pDNA/nrDNA	Climatic oscillations and geographic isolation	Considerable speciation (BEAST analysis)	Jiménez-Lobato et al. (2019)
* <i>Cistus</i> (Cistaceae)	Mediterranean region	pDNA/nrDNA	Habitat divergence following establishment of Mediterranean climate	Diversification from ~1.04 Mya onwards (PL analysis)	Guzman et al. (2009)
<i>Delphinium</i> (Ranunculaceae)	Mainly Mediterranean	pDNA/nrITS	Not specified	Some speciation (BEAST analysis)	Jabbour and Renner (2012)
* <i>Dianthus</i> (Caryophyllaceae)	Eurasia and Africa	pDNA/nrITS	Topographic diversity triggered geographical isolation and allopatric speciation	Nearly all Eurasian species (>200) originated from early to late Pleistocene (BEAST and NPRS analysis)	Valente et al. (2010b)
* <i>Erysimum</i> (Brassicaceae)	East and West Europe	nrITS	Not specified	Considerable speciation (BEAST analysis)	Moazzeni et al. (2014)
* <i>Festuca</i> (Poaceae)	Widespread	pDNA/nrITS	Climatic oscillation, polyploidy	Considerable speciation (estimated using <i>MultiDivtimeA</i>)	Inda et al. (2008)
* <i>Gentiana</i> (Gentianaceae)	Mountain Ranges	nrITS	Climatic oscillations causing cycles of geographical spread and isolation	Considerable speciation from ~1.8 to 0.6 Mya (clock calibration based on LGM glaciation events)	Hungerer and Kadereit (1998)
<i>Ilex</i> (Aquifoliaceae)	Widespread	pDNA/nrDNA	Divergence after dispersal to mesic environments	Some speciation (BEAST analysis)	Yao et al. (2021)
* <i>Lathyrus</i> , <i>Pisum</i> , <i>Vicia</i> (Fabaceae: Fabeae)	Mediterranean, Macaronesia, West/Central Europe	pDNA/nrDNA	Not specified	Considerable speciation (BEAST analysis)	Schaefer et al. (2012)
* <i>Limonium</i> (Plumbaginaceae)	Mediterranean region	pDNA/nrITS	Climatic and sea-level oscillations, facultative apomixis	Considerable speciation (ML in RAxML, Bayesian Inference in MrBayes)	Koutroumpa et al. (2021)
* <i>Linaria</i> subsect. <i>Versicolores</i> (Plantaginaceae)	Iberian Peninsula	pDNA/nrITS	Pollinator shifts linked to floral divergence, edaphic divergence	All 8 species diverged since ~0.43 Mya (relaxed molecular-clock in BEAST)	Fernández-Mazuecos et al. (2013); Fernández-Mazuecos and Vargas (2015)
<i>Lolium</i> (Poaceae)	Mediterranean region, N Europe	pDNA/nrITS	Climatic oscillations	Some speciation (Bayesian relaxed clock method in <i>Baseml</i> , <i>Estbranches</i> and <i>MultiDivtime</i>)	Inda et al. (2008)
* <i>Nigella</i> (Ranunculaceae), <i>N. arvensis</i> group	Aegean archipelago, Mediterranean Basin	nrITS	Climate and sea level oscillations favoured allopatric speciation	All species originated from ~0.78 to 0.16 Mya onwards (Log-lineages through time analysis)	Bittkau and Comes (2009)
<i>Petasites</i> (Asteraceae)	Central and East Europe	pDNA/nrITS	Possible ecological divergence	Some speciation (Bayesian relaxed molecular clock of ITS variation)	Steffen et al. (2016)
* <i>Picris</i> (Asteraceae)	Mediterranean, N Africa	pDNA/nrITS	Shifts in intrinsic/extrinsic traits, climate oscillations	Considerable speciation throughout distribution (relaxed molecular clock in MCMCTree)	Slovák et al. (2018)

(Continued)

Table 1. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
* <i>Poa</i> and related genera (Poaceae)	Widespread	nrITS	Pliocene cooling enabled adaptation to different habitats in Pleistocene	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
* <i>Primula</i> sect. <i>Auricula</i> (Primulaceae)	Europe Mountain Ranges	nrITS	Climatic oscillations causing cycles of geographical spread and isolation	All 25 species originated from ~2.4 Mya onwards (Log-lineages through time analysis)	Zhang et al. (2004); Kadereit et al. (2004)
<i>Ranunculus</i> (Ranunculaceae), <i>R. auricomus</i> complex	Europe Mountain Ranges	nrDNA	Climatic oscillations causing geographical isolation	All 5 species originated between ~0.83 and 0.58 Mya (BEAST analysis)	Tomasello et al. (2020)
<i>Reseda</i> sect. <i>Glaucosceda</i> (Resedaceae)	Mountains of Iberia and Morocco	pDNA/nrITS	Climatic oscillations and long-distance dispersal causing geographical isolation	Species originated from ~0.73–0.60 Mya onwards (PL analysis)	Martín-Bravo et al. (2010)
<i>Saxifraga</i> (Saxifragaceae)	Widespread at high elevations and northern regions	pDNA/nrITS	Climate change and oscillations, niche divergence, geographical isolation, hybridisation and polyploidy	Some speciation (BEAST analysis)	Ebersbach et al. (2017)
* <i>Senecio</i> (Asteraceae)	Mediterranean region	pDNA/nrITS	Climatic oscillations causing geographical isolation and habitat divergence	Considerable speciation from ~2.13 Mya onwards (K2P distances)	Comes and Abbott (2001)
<i>Senecio aethnensis</i> / <i>S. chrysanthemifolius</i>	Mount Etna, Sicily	nrSNPs; transcriptome sequences	Increased elevation of Mt Etna and habitat divergence	Species diverged ~0.108 Mya (<i>Impre</i> in <i>dadl</i>) or 0.153 Mya (3s program of Yang, 2002)	Chapman et al. (2013); Osborne et al. (2013)
* <i>Soldanella</i> (Primulaceae)	European high mountain ranges	nrITS/AFLPs	Climatic oscillations, geographic isolation, habitat divergence	Speciation from ~0.62–0.14 Mya onwards (ITS K2P distances)	Zhang et al. (2001)
<i>Vulpia</i> (Poaceae)	Mediterranean region	pDNA/nrDNA	Climatic oscillations	Some speciation (<i>MultiDivtimeA</i>)	Inda et al. (2008)

Key for Tables 1–8:

Computer programs: *Baseml*, *Estbranches*, *MultiDivtime* (Rutschmann (2004); BEAST = Bayesian evolutionary Analysis by Sampling Trees (Drummond and Rambaut (2007); **ada*i = Diffusion Approximations for Demographic Inference (Gutenkunst et al. 2009); *fastsimcoal2* = continuous-time coalescent simulator of genomic diversity (Excoffier and Foll 2011); IM = Isolation with Migration (Hey and Nielsen 2004); K2P distance = Kimura two-parameter distances (Kimura 1980); MCMCTree = Markov chain Monte Carlo algorithm in PAML; MrBayes (Ronquist 1997); PAML = Phylogenetic analysis using maximum likelihood (Yang 2007); PL = Penalized Likelihood (Sanderson 2002); PSMC = Pairwise Sequentially Markovian Coalescent (Li and Durbin 2011); r8s program (Sanderson 1997); NPRS = Nonparametric rate smoothing (Bremer et al. 2004); RAxML (Stamatakis 2014); RelTime (Tamura et al. 2012); RevBayes (Höhna et al. 2014). **Abbreviations:** AFLPs = Amplified Fragment Length Polymorphisms; ddRADseq = double digest RAD sequencing; ETS = External Transcribed Spacer regions of 18S-26S nuclear ribosomal DNA; GBS = Genotype by Sequencing; HMR = Hengduan Mountain Region; ITS = Internal Transcribed Spacer regions of 18S-26S nuclear ribosomal DNA; pDNA = plastid DNA; QTP = Qinghai-Tibetan Plateau; SSR = Simple Sequence Repeat.

different mountains (sky islands) during interglacial periods (see Ortego and Knowles 2021, for supporting evidence from animal studies). However, for *Primula* sect. *Auricula* (Primulaceae), a lineage of ca. 25 species endemic to the EAS and with a crown group age of 2.4 my (Zhang et al. 2004), Kadereit et al. (2004) found a negative correlation between temperature and diversification, and interpreted this to imply speciation in geographically isolated low-elevation glacial refugia instead of in geographically isolated interglacial high-elevation refugia. In the *Senecio carniolicus* (= *Jacobaea c.*) complex, now regarded to comprise four distinct species (Flatscher et al. 2015), the divergence of the two diploid species clearly has a geographical component, and persistence of both species in both peripheral and interior refugia was indicated (Escobar García et al. 2012).

Other factors, acting either independently or in addition to climate oscillations, have also triggered Quaternary speciation in some lineages in the EAS.

For example, *Androsace brigantiaca* (Dixon et al. 2009) originated by allopolyploid speciation, and in the *Doronicum clusii* aggregate (Pachschwöll et al. 2015) the tetraploid *D. stiriaticum* may have originated through either auto- or allopolyploidy, while for five species comprising the *Ranunculus alpestris* clade (Hörandl and Emadzade 2011), and for a sister species pair of *Campanula* (Park et al. 2006), substrate preference, calcicole vs. calcifuge, is likely to have been a key factor in diversification.

Climate-induced range changes, creating opportunities for divergence, secondary contact, hybridisation and re-colonisation, have further been linked to the origin of apomictic lineages in the EAS (Hörandl 2011; Pegoraro et al. 2020). Thus, the origin of *Ranunculus carpaticola*, an allohexaploid apomictic species, has been dated to maximally 40,000 yrs ago (Paun et al. 2006), and the (repeated) origin of tetraploid *Ranunculus kuepferi*, where apomixis appears to have followed autopolyploidy, took place in the last glacial or even in the Holocene (Cosendai et al.



Figure 1. Species of two genera in which Quaternary speciation occurred in Europe. Left: *Antirrhinum sempervirens* (Photographic credit: Pablo Vargas); right: *Primula latifolia* (Photographic credit: Gudrun Kadereit).

2011a, 2011b; Kirchheimer et al. 2018). In addition, diversification of sexual species of the otherwise apomictic *Ranunculus auricomus* species complex was dated to the mid-Pleistocene Transition (1.2–0.8 Mya) by Tomasello et al. (2020), implying an even younger age for all apomictic species of the complex.

For genera widely distributed in Europe (and partly beyond), comparative studies by Affenzeller et al. (2018) and Wagner et al. (2019) have illustrated different processes of Quaternary diversification within closely related lineages having different latitudinal distributions. Thus, a comparison of *Globularia*, most diverse in the Mediterranean region, and *Campylanthus*, most diverse in the Eritreo-Arabian region, revealed similar rates of diversification (Affenzeller et al. 2018). However, it was hypothesised that diversification in the more northern *Globularia*, related to glacial cycles, was adaptive, whereas diversification in the more southern *Campylanthus*, related to aridity cycles, was geographical. Different processes of diversification have also been inferred for *Rhodanthemum*, a genus centred in north-west African mountain areas, and *Leucanthemum*, a largely European genus (Wagner et al. 2019). Whereas diversification in *Rhodanthemum* took place at the diploid level, much allopolyploid speciation occurred in *Leucanthemum*. This striking difference is believed to have resulted from different responses to Quaternary climatic oscillations. While *Rhodanthemum* responded by elevational migration without much interspecific contact, changes in latitudinal distribution in *Leucanthemum* likely resulted in much secondary contact, hybridisation and allopolyploidisation (Wagner et al. 2019). Interestingly, for *Linaria* sect. *Supinae*, Blanco-Pastor and Vargas (2013) reported how diversification in response to Quaternary climatic oscillations is associated with mating system. Whereas self-fertility was found to

be associated with a species-poor lineage of species with wide geographical distributions, without much intraspecific differentiation and tolerant of different substrates, self-sterility was associated with a species-rich lineage of narrowly endemic and ecologically more specialised species.

Among the examples of Quaternary speciation in Europe (Table 1) many include radiations (here defined as involving the origin of >5 species), reflecting bursts of speciation that took place during the Quaternary. The most notable of these is in the widespread genus *Dianthus* comprising >200 European species that originated in the Pleistocene, most probably triggered by recurrent cycles of geographical spread and isolation resulting from climatic oscillations (Valente et al. 2010b). In contrast, there are other genera in which significant radiation has occurred, but with most speciation events in Europe occurring before the Quaternary. This is the case for *Saxifraga*, a large genus that extends beyond Europe to North America and Asia, containing up to 500 species (Tkach et al. 2015). However, even in this genus some notable Quaternary speciation events in Europe have been detected, resulting in the allopolyploid *S. osloensis* (Brochmann et al. 1996; Tkach et al. 2019) and the homoploid hybrid *S. opdalensis* (Steen et al. 2000) in southern Scandinavia, and several alpine species in the EAS and other mountain ranges of southern Europe (Ebersbach et al. 2017; Tkach et al. 2019).

Asia

Evidence of Quaternary plant speciation in Asia largely comes from studies of the Chinese flora (Table 2; Table S2). A recent phylogenetic analysis of the evolutionary history of the angiosperm flora of China, which included 92% (2,665 of 2,884) of native angiosperm genera and 5,864 native species,

Table 2. Studies reporting Quaternary speciation (QS) in plant genera in Asia (*Radiations). Not included in this table are examples of QS in the Qinghai-Tibet Plateau reported by Lu et al. (2018). These are listed in Supplementary Table S2.

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
ASIA					
* <i>Abies</i> (Pinaceae)	QTP/Himalayas	mtDNA/pDNA	Range expansion during glaciation period	Considerable speciation ~0.293–190 Mya (Mismatch distribution); ~0.900 Mya (Bayesian skyline plot, BSP)	Peng et al. (2015)
* <i>Acantholimon</i> (Plumbaginaceae)	Central and SW Asia	pDNA/nrITS	Colonization of mountain habitats, geographic isolation, climatic oscillations	Considerable speciation (BEAST analysis)	Moharrek et al. (2019)
* <i>Acanthophyllum</i> (Caryophyllaceae)	Central and SW Asia	pDNA/nrITS	Not specified	Considerable speciation (BEAST analysis)	Pirani et al. (2014)
<i>Aconitum</i> (Ranunculaceae)	QTP/HMR	pDNA/nrITS	Not specified	Some speciation (BEAST analysis)	Jabbour and Renner (2012)
<i>Actaea</i> (Ranunculaceae)	North China	pDNA/nrSNPs	Pollinator shifts linked to floral divergence	Three species diverged: ~0.63 Mya (pDNA); ~0.127 Mya (nrSNPs, * <i>daði</i> analysis)	Chang et al. (2020)
<i>Allium</i> (Amaryllidaceae)	QTP/HMR	pDNA/nrITS/nrAt103	Aridification causing vicariance; allopolyploidy during interglacial	Some speciation: ~2 Mya to ~0.38 Mya (BEAST analysis on pDNA)	Li et al. (2016)
<i>Angelica</i> (Apiaceae)	Eastern Himalayas	pDNA/nrITS/nrETS	Climate change causing range fragmentation and population isolation	Some speciation (BEAST analysis)	Liao et al. (2012)
* <i>Asarum</i> (Aristolochiaceae)	China, Taiwan, Japan and neighbouring islands	pDNA/nrITS	Geographic isolation and habitat divergence	Considerable speciation (BEAST analysis)	Takahashi and Setoguchi (2018)
* <i>Astragalus</i> sect. <i>Hymenostegis</i> (Fabaceae)	SW Asia	pDNA/nrITS	Climatic oscillations causing repeated cycles of dry and more humid conditions	All species originated (BEAST analysis)	Bagheri et al. (2017)
* <i>Begonia</i> (Begoniaceae)	SE Asia/Malesia	pDNA	Topographic heterogeneity, cyclic vicariance due to climatic and sea-level oscillations	Considerable speciation (BEAST analysis)	Thomas et al. (2012)
<i>Calligonum</i> (Polygonaceae)	NW China	pDNA	Climate change, aridification and habitat divergence	Much speciation from ~1.97 Mya (BEAST analysis)	Wen et al. (2016)
<i>Cardamine</i> (Brassicaceae)	Arctic-Alpine distribution, including Japan	nrITS/nr genes	Climatic oscillations causing alternating population extinctions and contact	Two species originated ~0.21 Mya (IM analysis)	Ikeda et al. (2012)
* <i>Carex</i> sect. <i>Confertiflorae</i> (Cyperaceae)	East Asia	pDNA/nrITS/nrETS	Climatic oscillations causing allopatric divergence	Considerable speciation (BEAST analysis)	Lu et al. (2021)
<i>Clematis</i> (Ranunculaceae)	SE/SW China	pDNA/nrITS	Climate change	Some speciation (BEAST analysis)	Xie et al. (2011)
<i>Delphinium</i> (Ranunculaceae)	Widespread	pDNA/nrITS	Not specified	Some speciation (BEAST analysis)	Jabbour and Renner (2012)
<i>Dipelta</i> (Caprifoliaceae)	West China	pDNA/nrDNA	Glaciation and complex topography induced divergent range shifts	Two species diverged ~0.43 Mya (BEAST analysis of pDNA) or ~0.63 to 1.02 Mya (ABC analysis of nr and pDNA)	Tian et al. (2020)
<i>Dyosma</i> (Berberidaceae)	Subtropical China	pDNA/nrSSR loci	Climate change followed by recurrent cycles of range contractions/expansions	Four species diverged ~0.92 to 0.59 Mya (ABC analysis)	Wang et al. (2017)
* <i>Epimedium</i> sect. <i>Diphyllon</i> (Berberidaceae)	Montane areas of China	pDNA/nrITS	Climatic oscillation and range shifts	44 species originated from ~0.52 to 0.4 Mya (PL in r8s)	Zhang et al. (2007)
* <i>Erysimum</i> (Brassicaceae)	Central Asia	nrITS	Not specified	Considerable speciation (BEAST analysis)	Moazzeni et al. (2014)
<i>Eutrema</i> (Brassicaceae)	QTP/Himalayas; Central Asia	pDNA/nrITS	Climatic oscillations causing allopatric divergence	Some speciation: ~1.9 to 0.53 Mya (BEAST analysis of pDNA)	Gao et al. (2017)

(Continued)

Table 2. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
* <i>Lathyrus, Vavilova, Vicia</i> (Fabaceae: Fabeae)	Western/Central Asia	pDNA/nrDNA	Not specified	Considerable speciation (BEAST analysis)	Schaefer et al. (2012)
* <i>Festuca</i> (Poaceae)	Widespread	pDNA/nrITS	Climatic oscillation	Some speciation (<i>MultiDivTimeA</i>)	Inda et al. (2008)
<i>Ilex</i> (Aquifoliaceae)	Widespread	pDNA/nrDNA	Divergence after dispersal to mesic environments	Some speciation (BEAST analysis)	Yao et al. (2021)
* <i>Juglans</i> (Juglandaceae)	East and Central Asia /North America	nr genome sequences	Climatic oscillations and coevolutionary interactions with pathogens	11 species diverged since ~1 Mya (PMSC analysis)	Bai et al. (2018)
<i>Leucomeris/Nouelia</i> (Asteraceae)	SW China	pDNA/nrDNA	Climatic oscillations causing allopatric divergence	Two species diverged ~2.07 Mya (IM analysis) to ~2.63 Mya (DIYABC analysis)	Zhao et al. (2018)
* <i>Myricaria</i> (Tamaricaceae)	Western China	pDNA	Geological and climate change	All species originated ~2.30 to 1.46 Mya (Bayesian relaxed clock method)	Liu et al. (2009)
* <i>Oxytropis</i> (Fabaceae)	SW and Central Asia	pDNA/nrDNA	Mountain uplift, geographic isolation, habitat divergence, climatic oscillations	Considerable speciation (BEAST analysis)	Shavvon et al. (2017)
<i>Paeonia</i> subsect. <i>Delavayanae</i> (Paeoniaceae)	Himalayas/HMR	pDNA/nrDNA	Geographic isolation due to geological and climate change	Two species diverged ~0.026 Mya (IMA analysis of pDNA and nrDNA)	Zhao et al. (2021)
<i>Paeonia</i> subsect. <i>Vaginatae</i> (Paeoniaceae)	Qinling-Daba Mountains, central China	pDNA/nrSSR variation	Geographic isolation due to climatic oscillation and ecological divergence	Three species diverged ~0.050–0.024 Mya (DIYABC analysis of nrSSR variation)	Xu et al. (2019c)
* <i>Phyllolobium</i> (Fabaceae)	QTP	nrITS	QTP uplift and climatic oscillations	Considerable speciation (r8s and BEAST analyses)	Zhang et al. (2012)
* <i>Picris</i> (Asteraceae)	Widespread	pDNA/nrITS	Shifts in intrinsic/extrinsic traits; climate oscillations	Considerable speciation (relaxed molecular clock in MCMCTree)	Slovák et al. (2018)
* <i>Poa</i> (Poaceae) and related genera	Widespread	nrITS	Pliocene cooling enabled adaptation to different habitats	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
<i>Populus</i> sect. <i>Turanga</i> (Salicaceae)	NW China	nrDNA	Climatic oscillation and aridification causing habitat divergence	Two species diverged ~1.37–0.66 Mya (IM analysis)	Wang et al. (2014)
<i>Populus</i> sect. <i>Populus</i> (Salicaceae)	QTP/SWt to NE China	nrSNPs	Climatic oscillation and habitat divergence	Two species diverged ~0.878 Mya (<i>fastsimcoal2</i>)	Li et al. (2021)
<i>Pugionium</i> (Brassicaceae)	NW China	pDNA/nrDNA	Aridification and habitat divergence	Two species diverged ~0.23–0.09 Mya (IM analysis of nrDNA)	Wang et al. (2013)
<i>Quercus</i> sect. <i>Quercus</i> (Fagaceae)	North China	pDNA/nrDNA	Geological and climatic oscillations causing isolation and niche divergence	Two species diverged ~2.15–0.92 Mya (IM analysis of pDNA and nrDNA)	Yang et al. (2016)
<i>Rhodiola</i> (Crassulaceae)	QTP/NE China	pDNA/nrITS	Geographical isolation, climate oscillations	Much speciation (BEAST analysis)	Zhang et al. (2014)
<i>Roscoea</i> (Zingiberaceae)	HMR, SW China	pDNA/nrITS	Niche divergence accompanying climatic oscillations	Speciation occurred ~1.48–0.01 Mya (IM analysis)	Zhao et al. (2016)
<i>Saussurea</i> (Asteraceae)	QTP and neighbouring areas	pDNA	Topographic heterogeneity and climate oscillation	Some speciation (treePL analysis)	Xu et al. (2019b)
<i>Saxifraga</i> (Saxifragaceae)	Widespread at high elevations and northern regions	pDNA/nrITS	Climate change and oscillations, niche divergence, geographic isolation, hybridisation and polyploidy	Some speciation (BEAST analysis)	Ebersbach et al. (2017)
<i>Sinallaria</i> (Brassicaceae)	Eastern China	nrSSR/nrDNA; nrSNPs	Niche divergence accompanying climatic oscillations	Two species diverged: ~0.53 Mya (IM analysis of nrDNA); or ~0.22 Mya (estimated by <i>fastsimcoal2</i>)	Zhang et al. (2018); Wang et al. (2019)

(Continued)

Table 2. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
* <i>Trigonostemon</i> sect. <i>Trigonostemon</i> (Euphorbiaceae)	SW China and Indonesia	pDNA/nrITS	Fluctuating sea levels allowing migration from SE Asia and isolation on Indonesian islands	Much speciation (BEAST analysis)	Yu and Van Welzen (2020)
Mangrove: <i>Aegiceras</i> (Primulaceae); <i>Avicennia</i> (Acanthaceae); <i>Ceriops</i> , <i>Kandelia</i> , <i>Rhizophora</i> (Rhizophoraceae); <i>Sonneratia</i> (Lythraceae); <i>Xylocarpus</i> (Meliaceae)	Indo-Western Pacific	nr gene DNA	Sea-level oscillations causing cycles of isolation and migration	Speciation in these genera dated to ~2.23–0.97 Mya (using HKY85 + gamma model in PAML)	He et al. (2019)



Figure 2. Species of two genera in which Quaternary speciation occurred in Asia. Left: *Acanthophyllum laxiusculum* (Photographic credit: Atefeh Pirani); Right: *Paeonia jishanensis* (Photographic credit: Fangyun Chen).



Figure 3. *Pugionium cornutum* (left) and *P. dolabratum* (right), native to the deserts of northwest China, estimated to have diverged 0.09–0.23 Mya (Photographic credit: Jianquan Liu).

showed that the flora of western China is younger than that of eastern China with species in many genera originating during and since the Miocene (Lu et al. 2018, 2020). The dated phylogeny, constructed from sequences of four plastid genes and one mitochondrial gene, further revealed that for 192 genera (ca. 7% of the genera analysed) Chinese species originated during the Pleistocene with stem dates ranging from 0.045 to 2.569 Mya (Supplementary Table S2). Quaternary origins were particularly evident for herbaceous plants, with species in many of the youngest herbaceous

genera shown to have originated during the Pleistocene, especially in the Qinghai-Tibet Plateau (QTP).

Considering Asia more broadly, Quaternary radiations have been detected in both woody and herbaceous genera throughout the continent (Table 2). For woody genera, these include radiations in *Abies* (Peng et al. 2015) in the QTP and in the Himalayas, *Juglans* (Bai et al. 2018) in east and central Asia, and *Trigonostemon* in the lowland ever-wet forests along rivers and coastlines of mainland south-east Asia and Malesia (Yu and Van Welzen 2020).

For herbaceous genera, Quaternary radiations have been reported in *Epimedium* from temperate to subtropical eastern China (Zhang et al. 2007), *Carex* from eastern Asia (Lu et al. 2021), *Asarum* sect. *Heterotropa* ranging from the Ryukyu Islands to Korea (Takahashi and Setoguchi 2018), *Begonia* from Malesia (Thomas et al. 2012), *Phyllobium* from the QTP (Zhang et al. 2012), and in several genera in arid areas of south-west (to central) Asia: *Erysimum* (Moazzeni et al. 2014), *Acanthophyllum* (Figure 2; Pirani et al. 2014), *Astragalus* sect. *Hymenostegis* (Bagheri et al. 2017), *Oxytropis* (Shavvon et al. 2017) and *Acantholimon* (Moharrek et al. 2019). Quaternary speciation has also been detected in the woody genera *Juniperus* (Xu et al. 2019) in the QTP, *Populus* in the QTP and Central Asia (Wang et al. 2014; Li et al. 2021), in *Quercus* in northeast China (Yang et al. 2016), plus several mangrove genera from the coasts of Indo-Malaysia (He et al. 2019). It has further resulted in pairs of herbaceous species originating in *Pugionium* (Figure 3; Wang et al. 2013) and *Sinalliaria* (Wang et al. 2019) in northwestern and eastern China, respectively.

It has been frequently proposed that Quaternary speciation in the QTP was triggered by recent uplifts of the plateau (during the Miocene, Pliocene and Quaternary periods) and the increased topographic heterogeneity resulting from this (e.g. Wen et al. 2014). Such

topographic heterogeneity could isolate populations, thus increasing the likelihood of local adaptation and allopatric speciation. Renner (2016) and Spicer et al. (2021), however, have pointed out that the most recent geological and palaeontological evidence shows that the QTP reached its present elevation of ca. 4–5 km long before the Miocene, and that there is no evidence, therefore, that recent uplifts occurred and triggered Quaternary speciation in the QTP. Nonetheless, Spicer et al. (2021) have emphasised that the orography of the QTP offers high levels of niche heterogeneity and together with climatic changes that occurred in the Miocene will have favoured increased speciation during that period. Similarly, climatic oscillations during the Quaternary are likely to have triggered further bouts of speciation related to ecological niche shifts and repeated fragmentation of species distributions and isolation of populations across the diverse and heterogeneous QTP landscape (Muellner-Riehl 2019; Chen et al. 2019; Feng et al. 2020). In this regard, a possible causal link between rapid (and partly also Quaternary) speciation in the QTP and levels of UV-B has been suggested by Willis et al. (2009).

Climatic oscillations during the Pleistocene are known to have caused fluctuations in sea-levels resulting in cycles of geographical isolation and

Table 3. Studies reporting Quaternary speciation (QS) in plant genera in the Arctic (*Radiations). Examples of cryptic speciation within genera are mentioned in the text.

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
ARCTIC					
* <i>Androsace</i> sect. <i>Douglasia</i> (Primulaceae)	NW America and NE Asia (Beringia)	pDNA/nrITS	Not specified	All speciation in section occurred in late Pliocene and Pleistocene	Schneeweiss et al. (2004)
<i>Artemisia</i> (Asteraceae)	Arctic lineages widespread	nrITS/nrETS	Not specified	Some speciation (BEAST analysis of combined data)	Tkach et al. (2008b)
* <i>Carex</i> sect. <i>Phacocystis</i> (Cyperaceae)	Widespread	pDNA/nrITS/nrETS	Ecophysiological differentiation	'Northern' and 'Mixed' clades of species originated (r8s analysis)	Dragon and Barrington (2009); Gebauer et al. (2014)
<i>Cerastium</i> (Caryophyllaceae)	Widespread arctic-alpine clade	pDNA	Not specified	Speciation occurred ~1.48–0.44 Mya (molecular clock calibration based on opening of Bering Strait)	Scheen et al. (2004)
<i>Ranunculus</i> , <i>R. acris</i> complex (Ranunculaceae)	Widespread in Arctic	pDNA/nrITS	Not specified	All 'species' originated in Pleistocene (r8s analysis)	Hoffmann et al. (2010)
<i>Saxifraga</i> (Saxifragaceae)	Widespread	pDNA/nrITS	Climate change and oscillations, niche divergence, geographic isolation, hybridisation and polyploidy	Some speciation (BEAST analysis)	Ebersbach et al. (2017)



Figure 4. Species of two genera in which Quaternary speciation occurred in the Arctic. Left: *Androsace constancei* (Photographic credit: Jacob W. Frank; CC BY 2.0); right: *Draba nivalis* (Photographic credit: Geir Arnesen; courtesy svalbardflora.no).

renewed contact of species populations along the coastlines of Asia. Recently, strong evidence has been obtained that such cycles caused mangrove speciation across the Strait of Malacca (He et al. 2019) where sea level fell during glacial periods producing a land barrier isolating populations to the East and West of the Strait. It is also proposed that sea-level fluctuations were important in causing Quaternary radiation in *Trigonostemon* (Yu and Van Welzen 2020).

The increasing use of ecological niche and species distribution modelling (and projection of such models into the past) has provided greater insights into the potential impact of Quaternary climate oscillations on speciation processes in Asia (as well as elsewhere). For example, in the analysis of two species of *Quercus* in China, Yang et al. (2016), using species distribution modelling, found that the two species, which have overlapping ranges today, are likely to have been almost allopatric in the Last Interglacial (LIG) and concluded this was important in their initial divergence. Also, for the homoploid hybrid species *Ostryopsis intermedia* in the QTP, estimated to have originated ca. 1.8 Mya (Wang et al. 2021), species distribution modelling indicated that the parental species, now distributed allopatrically, could have come into contact in the Last Glacial Maximum (LGM; Liu et al. 2014). As suitable climate projections are not available for periods earlier than the LIG, and even the climate of the LIG remains controversial, preventing the projection of species distribution models into earlier periods, Liu et al. (2014) could only postulate that such contact may also have occurred in earlier glacials. For two species of *Dipelta*, distributed on the edges of the Sichuan Basin, Tian et al. (2020) concluded that their extant allopatric distribution originated much later than species divergence. Equally, Wang et al. (2017), investigating two species of *Dysosma* in East China,

concluded that the currently abutting ranges of the two species are secondary, and that their initial divergence took place at the extreme edges of the range of the ancestral species. Xu et al. (2019c) further showed that for *Paeonia* (Figure 2) from the Qinling-Daba Mountains, two of the three species investigated had wider ranges during the LGM, and the range of the third species was not much altered in comparison to its extant range. All of these studies illustrate that extant distribution ranges need not be reliable indicators of the geographical setting of speciation.

The Arctic

Considering the young geological age of the Arctic biome, i.e. 2 to 3 my old (Brochmann and Brysting 2008), it is not surprising that immigration played a large role in the assembly of its plant diversity. Analyses of a number of large genera that are species-rich in the Arctic have revealed multiple immigration (Hoffmann and Röser 2009): 13 to 18 times in *Artemisia* (Tkach et al. 2008a, 2008b), at least 3 times in *Cardamine* (Carlsen et al. 2009), at least 7 times in *Ranunculus* (Hoffmann et al. 2010), and 48 times in *Carex* (Hoffmann et al. 2017). However, the Arctic clearly is not an ‘evolutionary freezer’ (Brochmann and Brysting 2008), and Arctic radiations of Quaternary age have been identified in three of these four genera (for *Carex*, also see Dragon and Barrington 2009; Gebauer et al. 2014) as well as in *Douglasia* (as a subgroup of *Androsace*, Figure 4; Schneeweiss et al. 2004), *Cerastium* (Scheen et al. 2004; Brysting et al. 2007) and *Draba* (Grundt et al. 2004) (Table 3).

As noted by Abbott and Brochmann (2003), complex reticulation and chromosome doubling driven by successive cycles of divergent evolution and hybridisation in areas of secondary contact is

Table 4. Studies reporting Quaternary speciation (QS) in plant genera in North America (*Radiations).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
NORTH AMERICA					
<i>Achlys</i> (Berberidaceae), <i>A. triphylla</i> vs. <i>A. japonica</i>	Western N America (and E Asia)	pDNA	Geographic isolation following dispersal from East Asia	Species diverged from East Asian species ~1.0 +/- 0.7 Mya (PL analysis)	Wang et al. (2007)
* <i>Aphyllon</i> (Orobanchaceae) / * <i>Grindelia</i> (Asteraceae)	Eastern and Western N America	nrDNA	Diversification of <i>Aphyllon</i> (parasite) dependent on that in <i>Grindelia</i> (host); glacial cycles also could have contributed to speciation	Considerable speciation in both genera in N America (RevBayes)	Schneider & Moore (2017)
* <i>Aquilegia</i> (Ranunculaceae)	N America and Asia	pDNA/nrITS	Habitat and pollinator specialisation	Considerable speciation (BEAST analysis)	Bastida et al. (2010)
<i>Arabis</i> (Brassicaceae)	N America, especially west and northwest	pDNA/nrITS	Climatic oscillations, range expansions and contractions, hybridisation and polyploidy	All species diverged in late Pliocene and Pleistocene (BEAST analysis)	Koch et al. (2010)
<i>Astragalus</i> (Fabaceae)	Utah, N America	nrSNPs	Climatic oscillations and habitat divergence	All three taxa diverged in Pleistocene (ðaði analysis)	Jones et al. (2021)
* <i>Campanula</i> , Cordilleran group (Campanulaceae)	Western N America	nrDNA	Climatic oscillations, isolation and habitat divergence	All seven taxa originated from ~2.18 to 0.51 Mya (BEAST analysis)	De Chaîne et al. (2014)
<i>Carex</i> (Cyperaceae)	Eastern N America	nrITS; nrSSR variation	Climatic oscillation causing geographic isolation	Speciation occurred: 0.47 Mya (BEAST analysis of nrITS); 0.05 Mya (IM analysis of SSR)	Hipp et al. (2010); Escudero et al. (2019)
<i>Ceanothus</i> (Rhamnaceae)	California	pDNA/nrITS	Not specified	Some speciation (BEAST analysis of combined data)	Ornstein et al. (2015)
<i>Clematis</i> (Ranunculaceae)	East, West, South USA	pDNA/nrITS	Climate change	Some speciation (BEAST analysis)	Xie et al. (2011)
<i>Cunila</i> (Lamiaceae), <i>C. lythrifolia</i> vs. <i>C. pycnantha</i>	Mexico	pDNA	Not specified	Species diverged in mid-Pleistocene (BEAST analysis)	Drew & Sytsma (2012)
<i>Delphinium</i> (Ranunculaceae)	Western N America	pDNA/nrITS	Not specified	Some speciation (BEAST analysis)	Jabbour & Renner (2012)
* <i>Dioon</i> (Zamiaceae)	Mexico / Honduras	nr genes	Climatic oscillation, cycles of isolation and contact	All 14 species originated from ~2.41 to 0.32 Mya (starBEAST)	Dorsey et al. (2018)
<i>Drymocalis</i> (Rosaceae)	Western USA	pDNA	Not specified	Some speciation (BEAST analysis)	Dobes & Paule (2010)
* <i>Encelia</i> (Asteraceae)	SW N America, Baja California (11 species) / Western S America (1 species)	nrDNA (ddRAD-seq)	Aridification, climatic oscillation and habitat divergence	All 12 species originated from mid-Pleistocene onwards (R package APE)	Singhal et al. (2021)
<i>Ephedra</i> (Ephedraceae)	Arid parts of USA and Mexico	pDNA/nrITS	Aridification and habitat divergence (particularly edaphic)	One pair of sister species diverged (BEAST analysis)	Loera et al. (2012)
* <i>Eryngium</i> (Apiaceae)	Western N America	pDNA/nrITS	Aridification and polyploidy	Considerable speciation (PL in r8s)	Kaderleit et al. (2008)
* <i>Erysimum</i> (Brassicaceae)	Mainly Western N America	nrITS	Not specified	Considerable speciation (BEAST analysis)	Moazzeni et al. (2014)
* <i>Festuca</i> (Poaceae)	Widespread	pDNA/nrITS	Climatic oscillation, polyploidy	Considerable speciation (<i>MultiDivTimeA</i>)	Inda et al. (2008)
<i>Ilex</i> (Aquifoliaceae)	Eastern and SE N America	pDNA/nrDNA	Divergence after dispersal to mesic environments	Some speciation (BEAST analysis)	Yao et al. (2021)
* <i>Lathyrus</i> , <i>Vicia</i> (Fabaceae: Fabeae)	USA	pDNA/nrDNA	Not specified	Considerable speciation (BEAST analysis)	Schaefer et al. (2012)
<i>Mentzelia</i> (Loasaceae)	Western N America	pDNA	Not specified	Some speciation	Schenk & Hufford (2010)
<i>Mimulus</i> (Phrymaceae)	California	14,000 nrSNPs	Outcrossing to selfing transition	Budding of <i>M. nasutus</i> from <i>M. guttatus</i> occurred ~ 0.5-0.2 Mya (PSMC analysis)	Brandvain et al. (2014)

(Continued)

Table 4. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
<i>Opuntia</i> (Cactaceae)	Western and SW N America	pDNA/nrDNA	Aridification, range expansion, hybridization, allopolyploidy	Some speciation (NPRS)	Majure et al. (2012)
* <i>Pediomelum</i> , <i>Rupertia</i> , <i>Psoralidium</i> , <i>Orbexilum</i> , <i>Hoita</i> (Fabaceae: Psoraleeae)	Widespread in USA	pDNA/nrDNA	Glaciation-induced climate change	Considerable speciation (BEAST analysis)	Egan & Crandall (2008)
* <i>Penstemon</i> (Plantaginaceae)	Widespread in N America	nrDNA (43 loci)	Climate oscillation and glacial cycles; founder-events important	Bulk of 285 species originated ~1.0-0.5 Mya (BEAST and treePL)	Wolfe et al. (2021)
* <i>Poa</i> and related genera (Poaceae)	Widespread	nrITS	Pliocene cooling enabled adaptation to different habitats in Pleistocene	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
<i>Populus</i> (Salicaceae), <i>P. balsamifera</i> vs <i>P. trichocarpa</i>	Boreal and Pacific temperate forests of N America	nrDNA	Climatic oscillation causing geographical isolation	~0.075 Mya (IM analysis)	Levens et al. (2012)
<i>Saxifraga</i> (Saxifragaceae)	Widespread at high elevations and northern regions	pDNA/nrITS	Climate change and oscillations, niche divergence, geographical isolation, hybridization and polyploidy	Some speciation (BEAST analysis)	Ebersbach et al. (2017)
<i>Stachys</i> (Lamiaceae)	Widespread in N America	pDNA/nrDNA	Not specified	Much speciation (BEAST analysis)	Roy et al. (2013)
<i>Viola</i> (Violaceae)	N and Central America	pDNA/nrDNA	Not specified	Some speciation (BEAST analysis)	Marcussen et al. (2012)
<i>Yucca</i> (Asparagaceae)	Arid parts of N and Central America	pDNA/AFLPs	Not specified	Some speciation (BEAST analysis)	Smith et al. (2008)
<i>Zeltnera</i> (Gentianaceae)	Western and SW N America	pDNA nrITS	Aridification range expansion and geographical isolation	Some speciation (NPRS analysis)	Mansion & Zeltner (2004)

a prominent feature of Arctic plant evolution. The complexity of these processes has been reconstructed in considerable detail for 8x and 10x *Cerastium* (Brysting et al. 2007) and for 2x to 14x *Primula* sect. *Aleuritia* subsect. *Aleuritia* (Guggisberg et al. 2009), and led to an allotetraploid origin of *Arabidopsis kamchatica* in the amphiberingian area (Schmickl et al. 2010). In all three instances the evolution of these groups was assumed (but not shown with a molecular clock approach) to have taken place in the Quaternary. A Quaternary origin has similarly been postulated (in this case

during the Holocene) for the homoploid hybrid *Saxifraga svalbardensis* which reproduces mainly asexually (Brochmann et al. 1998).

Examples for divergent evolution in the Quaternary without changes in ploidy level include tetraploid *Euphrasia wettsteinii*, where two at least partly sympatric amphiatlantic lineages were identified by Gussarova et al. (2012). As these have never been recognised taxonomically, they represent an instance of cryptic speciation (Abbott 2008). Such cryptic speciation without changes in ploidy level has also been demonstrated for three diploid Arctic



Figure 5. Species of two genera in which Quaternary speciation occurred in North America. Left: *Penstemon pumilus* (Photographic credit: Matt Lavin; CC BY-SA 2.0); right: *Grindelia ciliata* (Photographic credit: Abigail J. Moore).

species of *Draba* (Grundt et al. 2006), and more recently within *Cardamine bellidifolia*, *Cochlearia groenlandica*, *Saxifraga hyperborea*, *Ranunculus pygmaeus* and *Silene uralensis* (Gustafsson et al. 2021), based on observations of low levels of seed set and/or pollen fertility in hybrids between conspecific individuals from different geographical regions. In one of the *Draba* species, *D. nivalis* (Figure 4), QTL studies designed to understand the genetic basis of hybrid sterility (Skrede et al. 2008; Gustafsson et al. 2014) concluded that multiple genetic mechanisms resulted in the rapid evolution of reproductive reproductive isolation. In *Cardamine bellidifolia* hybrid incompatibilities were confirmed to have originated during and since the LGM based on molecular phylogenetic analysis (Gustafsson et al. 2021).

In *Ranunculus*, Hoffmann et al. (2010) observed mainly one Arctic radiation of 10 species. These 10 species had been subsumed in one variable species by other authors, so that this radiation could also be considered cryptic. In explanation, Hoffmann et al. (2010) suggested that the ubiquitous availability of habitat, in this case wetland, over vast areas, might prevent or slow phenotypic divergence of genetic lineages. This explanation for the lack of phenotypic divergence might also apply to other groups of cryptic species in the Arctic.

North America

A number of large plant radiations in North America, particularly in arid areas, have been dated to the Quaternary (Table 4). Most remarkably, the bulk of diversification in *Penstemon* (Figure 5), a genus of ca. 285 species distributed in most biogeographical regions of North America, though with most species adapted to xeric conditions, is reported to have taken place from 0.5–1.0 Mya (Wolfe et al. 2021). The authors linked this radiation to the oscillating climate of the Quaternary and hypothesised that much speciation resulted from founder-events in newly available niches during interglacial periods. Similarly, for Fabaceae tribe Psoraleae, a lineage of five genera and 47 species in North America, Egan and Crandall (2008) reported that essentially all speciation took place in the Quaternary, and that the origin of each genus was not much older. Other Quaternary radiations mainly in arid areas have been detected in *Grindelia* (Figure 5) and its flowering plant parasite *Aphyllon*, also evident in South America (Schneider and Moore 2017), *Encelia*

(Singhal et al. 2021), *Opuntia* (Majure et al. 2012) and *Dioon* (Dorsey et al. 2018). In *Dioon*, a genus of cycads distributed mainly in Mexico, all 14 species originated in the Quaternary, emphasising that Quaternary speciation is not limited to short-lived herbaceous lineages but has also occurred in ancient woody lineages (Dorsey et al. 2018).

Remarkably young species ages have also been recorded for several species pairs across North America. Thus, divergence between *Mimulus guttatus* and *M. nasutus*, which show high hybrid sterility (Sweigart et al. 2006), is estimated to have occurred 200,000–500,000 years ago (Brandvain et al. 2014), that between *Populus balsamifera* and *P. trichocarpa* ca. 75,000 years ago (Levsen et al. 2012), that between *Astragalus iselyi* and *A. sabulosus* var. *sabulosus* and var. *vehiculus* near the beginning of the last glacial (Jones et al. 2021), and that between *Carex scoparia* and *C. waponahkikensis* after the LGM (Escudero et al. 2019). In addition, some of the sky-island endemics of the desert flora of California are hypothesised to have originated in the Holocene (Kraft et al. 2010), while the remarkable radiation of *Aquilegia* in North America, clearly linked to pollinator shifts (Whittall and Hodges 2007), was shown to have taken place largely in the Quaternary (Bastida et al. 2010). As *Aquilegia* colonised America in the late Pliocene when a rich pollinator fauna including hummingbirds already existed there, the genus is considered an example of diversification resulting from an encounter with a new and diverse pollinator fauna (Bastida et al. 2010).

South and Central America

Quaternary speciation in South America (Table 5) is probably best documented for lineages occurring at high altitude sites (páramos) in the northern Andes which only became available for colonisation after the most recent uplift of the northern Andes 2–4 Mya (Luebert and Weigend 2014). In a review of the evolution of 73 páramo lineages, Madriñán et al. (2013) found that 144 of 177 speciation events occurred in the Quaternary, and postulated that these resulted largely from range expansion and contraction in response to Quaternary climatic oscillations. More specifically, elevation range shifts and shifts between adjacent Cordilleras were considered responsible for Quaternary speciation in *Puya* (Jabaily and Sytsma 2013; Figure 6) and also in Andean *Lupinus* (Hughes and Eastwood 2006;

Table 5. Studies reporting Quaternary speciation (QS) in plant genera in South and Central America (*Radiations).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
SOUTH & CENTRAL AMERICA					
* <i>Abrotanella</i> (Asteraceae)	Chile, Tierra del Fuego, Falkland Islands	pDNA/nrITS	Climate oscillation (glacial/interglacial cycles)	Considerable speciation (NPRS in r8s)	Wagstaff et al. (2006)
* <i>Burmeistera</i> , <i>Centropogon</i> , <i>Lobelia</i> , <i>Lysipomia</i> , <i>Siphocampylus</i> (Campanulaceae)	Andes	pDNA	New habitats after mountain uplift and climate cooling; changes in pollination syndrome and fruit type	Many species originated from early to late Pleistocene (PL and BEAST analysis)	Lagomarsino et al. (2016)
* <i>Andira</i> , <i>Lupinus</i> , <i>Mimosa</i> (Fabaceae), <i>Microllicieae</i> (Melastomataceae)	Cerrado, Brazil	pDNA and/or nrDNA	Climatic oscillations, divergent adaptation to fire disturbance	Many species originated from early to late Pleistocene (BEAST analysis)	Simon et al. (2009)
<i>Aphyllon</i> (Orobanchaceae)/ <i>Grindelia</i> (Asteraceae)	Eastern and Western S America	nrDNA	Diversification of <i>Aphyllon</i> (parasite) dependent on that in <i>Grindelia</i> (host)	Some speciation in <i>Aphyllon</i> , much more in <i>Grindelia</i> (RevBayes)	Schneider and Moore (2017)
* <i>Aragoa</i> (Plantaginaceae)/ <i>Arcytophyllum</i> (Rubiaceae)/ <i>Berberis</i> (Berberidaceae)/ <i>Calceolaria</i> (Calceolariaceae) / <i>Draba</i> (Brassicaceae)/ <i>Espeletiinae</i> (Asteraceae)/ <i>Festuca</i> (Poaceae)/ <i>Lysipomia</i> (Campanulaceae)/ <i>Oreobolus</i> (Cyperaceae)	Andes (páramo)	DNA	Climatic oscillations, range expansions and contractions	Many species of these genera originated (BEAST analysis)	Madriñán et al. (2013)
* <i>Astragalus</i> (Fabaceae)	Andes (Ecuador to S Argentina)	pDNA/nrITS	Not specified	Two S American clades diversified from ~1.89 and ~0.98 Mya, respectively (r8s program)	Scherson et al. (2008)
* <i>Bartsia</i> (<i>Neobartsia</i>) (Orobanchaceae)	Andes	pDNA/ITS/ETS	Range expansions and ecological divergence	Majority of species diverged since ~2.59 Mya (BEAST analysis)	Uribe-Convers and Tank (2015)
<i>Brownea</i> clade (Fabaceae) <i>Brachycylis</i> , <i>Brownea</i> , <i>Ecuadendron</i> , <i>Elizabetha</i> , <i>Macrolobium</i>	Central America and northern and central South America	pDNA/nrITS	Founder events after orogeny; dispersal and habitat divergence	Some speciation within each of these 5 genera (BEAST analysis)	Schley et al. (2018)
<i>Conanthera</i> (Tecophilaeaceae)	Mediterranean region of Chile	pDNA	Divergence following establishment of Mediterranean climate in Chile	Some speciation (BEAST analysis)	Buerki et al. (2013)
* <i>Costus</i> (Costaceae)	Central America, parts of S America (some species in Mexico)	nrITS/ETS; 853 nr genes	Climatic oscillations, geographic isolation and floral adaptation to different pollinators	Many neotropical species originated from early to late Pleistocene (BEAST analysis)	Kay et al. (2005); Vargas et al. (2020)
* <i>Diplostephium</i> (Asteraceae)	Costa Rica and N and central Andes	pDNA/mtDNA, nr ribosomal DNA, nrDNA (ddRAD seq)	Emphasizes importance of hybridisation and reticulate evolution in species diversification	Considerable speciation from ~2.4 Mya onwards (BEAST analysis)	Vargas et al. (2017)
* <i>Epidendrum</i> (Orchidaceae)	Amazonian and Atlantic forests	pDNA, nrITS, nr genes	Climate shifts causing niche divergence, vicariance and peripheral isolation	All 7 species in <i>E. latilabre</i> complex originated (BEAST analysis)	Pessoa et al. (2021)
* <i>Eryngium</i> (Apiaceae)	Widespread in S America (some species in Mexico)	pDNA/nrITS	Aridification and polyploidy	Considerable speciation (PL in r8s)	Kadereit et al. (2008)
* <i>Espeletia</i> (Asteraceae)	Northern Andes (Venezuela to Ecuador)	pDNA/nr SNPs	Geographic isolation, adaptive divergence	All speciation occurred in Pleistocene (PL in r8s)	Pouchon et al. (2018, 2021)
* <i>Eulychnia</i> (Cactaceae)	Atacama and Peruvian deserts	pDNA and nuclear sequence variation (GBS)	Aridification oscillation, range fragmentation resulting in geographic isolation	All 11 species originated between early to mid-Pleistocene (BEAST analysis of pDNA, PL of GBS tree)	Merklinger et al. (2021)
<i>Lathyrus</i> , <i>Vicia</i> (Fabaceae: Fabeae)	Argentina, Chile, Paraguay	pDNA/nrDNA	Not specified	Considerable speciation (BEAST analysis)	Schaefer et al. (2012)

(Continued)

Table 5. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
* <i>Festuca</i> (Poaceae)	Widespread	pDNA/nrITS	Climatic oscillation, polyploidy	Considerable speciation (<i>MultiDivtimeA</i>)	Inda et al. (2008)
* <i>Gentianella</i> (Gentianaceae)	Andes	nrITS	Availability of newly formed alpine area for colonization	Considerable speciation (K2P distances)	Von Hagen and Kadereit (2001)
<i>Guarea</i> , <i>Heckeldora</i> , <i>Leploea</i> , <i>Aglaia</i> , <i>Chisocheton</i> , <i>Trichillia</i> (Meliaceae)	Rainforest	pDNA/nrITS	Climate change possibly	Some speciation in each genus originated (BEAST analysis)	Koenen et al. (2015)
* <i>Halenia</i> (Gentianaceae)	Paramo and temperate habitats	nrITS	Changes in floral form in response to new and diverse pollinators	Considerable speciation in mid-Pleistocene: 0.95–0.83 Mya (K2Pdistances)	Von Hagen and Kadereit (2003)
* <i>Hordeum</i> (Poaceae)	Mainly Argentina to Chile	pDNA/nrDNA	Climate oscillations and ecological diversification	American originated from ~1.5 to 0.43 Mya (BEAST analysis)	Brassac and Blattner (2015)
* <i>Hypericum</i> (Hypericaceae)	N Andes	nrITS	Colonisation and adaptive divergence in new páramohabitats	Many páramo species originated since ~2.4 Mya (BEAST analysis)	Nürk et al. (2013)
* <i>Hypochaeris</i> (Asteraceae)	Mainly Andes	nrITS	Habitat divergence after long-distance dispersal	All S American species (~40) originated since ~1.00–0.25 Mya (PL in r8s)	Tremetsberger et al. (2005)
<i>Ilex</i> (Aquifoliaceae)	Widespread	pDNA/nrDNA	Divergence after dispersal to mesic environments	Some speciation (BEAST analysis)	Yao et al. (2021)
* <i>Inga</i> (Fabaceae)	Rainforests in Central America/N and central parts of S America	pDNA/nrITS	Climatic oscillations	~30% of species originated since ~2 Mya (calibration based on time of bridging of Isthmus of Panama)	Richardson et al. (2001)
<i>Ipomoea</i> (Convolvulaceae)	Caribbean, Central America, north and central S America	pDNA/nrDNA	Not specified, but numerous shifts in growth habit noted	Some speciation (PL analysis)	Muñoz-Rodríguez et al. (2019)
* <i>Lachemilla</i> (Rosaceae)	Central America cordillera and Andes of S America	pDNA/nrITS	Habitat divergence; hybridisation and polyploidy	Considerable speciation (BEAST analysis)	Morales-Briones et al. (2018)
* <i>Loricaria</i> (Asteraceae)	N Andes (Ecuador and Columbia)	pDNA	Climatic oscillations, range expansions, ecological divergence across environmental gradients	Speciation between ~0.148–0.108 Mya (BEAST analysis)	Kolař et al. (2016)
* <i>Lupinus</i> (Fabaceae)	High-altitude flora of Andes (Venezuela to Argentina)	pDNA/nrITS/~6000 genes	Habitat divergence during climate oscillation and emergence of island-like habitats	Considerable speciation (PL in r8s and demographic modelling)	Hughes and Eastwood (2006); Drummond (2008); Nevado et al. (2018)
* <i>Oreobolus</i> (Cyperaceae)	Andes	pDNA/nrITS	Isolation and habitat divergence as genus migrated northwards along Andes	All 5 species comprising N Andean clade originated (BEAST analysis of combined data)	Gómez-Gutiérrez et al. (2017)
<i>Petunia</i> (Solanaceae), <i>P. integrifolia</i> ssp. <i>integrifolia</i> vs. ssp. <i>depauperata</i>	Southern Brazil	pDNA/nrITS	Climatic oscillations causing marine transgression / regression cycles	Sub-speciation began ~1 Mya (mismatch analysis pDNA); or ~0.635 Mya (BEAST analysis)	Longo et al. (2014); Ramos-Fregonezi et al. (2015)
* <i>Poa</i> and related genera (Poaceae)	Widespread	nrITS	Pliocene cooling enabled adaptation to different habitats in Pleistocene	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
* <i>Puya</i> (Bromeliaceae)	Andes from sea level to >4500 m	pDNA/nrAFLPs	Climatic oscillations causing cycles of elevational change	Chile radiation began ~2.5 Mya (PL in r8s)	Givnish et al. (2011); Jabaily and Sytsma (2013)

(Continued)

Table 5. (Continued).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
<i>Ruprechtia</i> (Polygonaceae), <i>Chaetocalyx</i> , <i>Coursetia</i> , <i>Nissolia</i> (Fabaceae) <i>Loxopterygium</i> (Anacardiaceae)	Seasonally dry forests in Central America and N and central parts of S America	nrITS	Climatic oscillations	Some speciation in Central America (PL in r8s)	Pennington et al. (2004)
<i>Saxifraga</i> (Saxifragaceae)	Widespread at high elevations	pDNA/nrITS	Climate change and oscillations, niche divergence, geographic isolation, hybridization and polyploidy	Some speciation (BEAST analysis)	Ebersbach et al. (2017)
* <i>Solanum</i> sect. <i>Lycopersicon</i> (Solanaceae)	Andes and Galapagos Islands	Whole trans-cryptome sequences	New habitats created after climate change and Andean uplift	All 13 species originated (r8s)	Pease et al. (2016)
* <i>Stachys</i> (Lamiaceae)	Mainly Andes and mountains in Central America	pDNA/nrDNA	Not specified	Much speciation (BEAST analysis)	Roy et al. (2013)
* <i>Tetraglochin</i> (Rosaceae)	Central and S Andes to Patagonian steppe	pDNA/nrITS	Climate oscillations causing periods of geographic isolation	All 6 species originated from ~2.23 Mya onwards (BEAST analysis)	Salariato et al. (2019)



Figure 6. Species of two genera in which Quaternary speciation occurred in South and Central America. Left: *Puya raimondii* (Photographic credit: Urrola; CC BY-SA 4.0); Right: *Costus wilsonii* (Photographic credit: Pedro Juarez).

Nevado et al. 2018) where adaptive divergence was further viewed as important (Nevado et al. 2016). However, in a clade of Andean bellflowers (including various genera of Campanulaceae), Lagomarsino et al. (2016) postulated that Quaternary diversification was related to changes in pollination syndrome (resulting in floral isolation) and fruit type (resulting in long-distance dispersal), with no link evident between climatic oscillations and biotic changes. Furthermore, in a neotropical clade of *Costus* (Figure 6), in which considerable speciation was detected in the Quaternary (Vargas et al. 2020), changes from bee to hummingbird pollination were linked to changes in geographical distribution by Kay et al. (2005) who postulated that these changes took place in geographically isolated populations. However, a somewhat different view of the role of biotic interactions in Quaternary speciation was

taken by Von Hagen and Kadereit (2003). They hypothesised that for South American *Halenia*, a genus with spurred flowers which colonised South America from Asia via North America probably within the last 1 my, significantly increased diversification in South America might have resulted from the encounter with a new and diverse pollinator fauna, similar to that postulated for *Aquilegia* in North America (Bastida et al. 2010).

Away from the Andes, substantial Quaternary speciation has been demonstrated across various ecological settings. Thus, Koenen et al. (2015; see also Pennington et al. 2015) demonstrated Quaternary speciation for subclades of two genera, *Guarea* and *Trichilia*, most diverse as understory trees in primary evergreen rainforests. Interestingly, these two radiations were ecologically and phenotypically convergent, and also convergent in location, timing and



Figure 7. Species of genera in which Quaternary speciation occurred in Africa. Left: *Erica abietina* (Photographic credit: Michael D. Pirie); Right: *Impatiens niarniamensis* (Photographic credit: Cbaile 19; CC0 1.0).

speciation rates. It was concluded that such similarities imply a common underlying factor, though the authors did not advocate Haffer's (1969) 'Pleistocene refuge hypothesis' which has been questioned by many (Colinvaux et al. 2001) since first advanced (for review see Dick and Pennington 2019). For seasonally dry forests, the analysis of four different lineages of flowering plants (*Ruprechtia*, *Chaetocalyx*, *Nissolia*, *Loxopterygium*) by Pennington et al. (2004) showed Quaternary speciation in Central but not in South America and was linked to Central American seasonally dry forests having been colonised from South America by older stocks of these lineages. More recently, Pessoa et al. (2021) have shown that a clade of *Epidendrum*, comprising seven species of epiphytic orchids present in the Amazon and Atlantic rain forests, diverged in the Pleistocene, probably as a result of climatic shifts causing niche divergence.

Other studies in South America have been more specific in proposing possible causes of Quaternary speciation. Thus, investigations of subspecific differentiation in *Petunia integrifolia* in the South Atlantic Coastal Plain concluded that this differentiation resulted from marine transgression/regression cycles during the Quaternary (Longo et al. 2014; Ramos-Fregonezi et al. 2015), while from a study of the temporal assembly of the Cerrado, a savanna area in Brazil, Bolivia and Paraguay, Simon et al. (2009) postulated that Quaternary speciation as found in, e.g., *Andira*, may have resulted from changes in the spatial extent of the Cerrado, which was likely to have been more extensive in dry glacial periods. Also, for the diversification of the largely Chilean desert genus *Eulychnia*, found to have taken place mostly in the Quaternary, Merklinger et al. (2021) hypothesised range fragmentation and allopatric speciation in periods of hyperaridity. In addition, for southern South American species of *Hordeum*, Brassac and Blattner

(2015) identified three speciation events within the last 1 my, and the entire American clade of the genus was estimated to be ca. 1.5 my old. It was further postulated that a pair of Patagonian sister species, *H. patagonicum* and *H. pubiflorum*, originated by vicariance without, however, retreat into isolated glacial refugia harbouring only small populations (Jakob et al. 2009). Finally, a modelling approach used by Rangel et al. (2018) to understand the evolution of biodiversity in South America implicated the Late Quaternary (last 800,000 years) glacial-interglacial cycles again as important drivers of both diversification and extinction on a continental scale.

Africa and Madagascar

There are fewer dated molecular phylogenies available for species groups distributed in Africa (Table 6) compared to those with distributions in Asia and the Americas (Table 2–5, Supplementary Tables S1 and S2). Nonetheless, there is evidence from these phylogenies that Quaternary speciation occurred throughout Africa. In a comparison of the evolutionary dynamics of plant lineages distributed in both the Mediterranean area of Europe and North Africa and the Cape Floristic Region (CFR) of South Africa, Valente and Vargas (2013) concluded that high species richness in the Cape is linked to long-term lineage persistence in a heterogeneous but stable environment, while the climatically unstable Mediterranean Basin provided fewer opportunities for diversity accumulation but is a centre of recent rapid speciation. This again illustrates that the evolutionary effects of the climatic oscillations of the Quaternary depend on the general environmental context, and indeed Quaternary climatic oscillations were small in the Cape (Linder and Bouchenak-Khelladi 2015). However, Quaternary speciation has been recorded in the CFR, with examples including

Table 6. Studies reporting Quaternary speciation (QS) in plant genera in Africa (not including North Africa) and Madagascar (*Radiations).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
AFRICA/MADAGASCAR					
* <i>Alchemilla</i> (Rosaceae)	E African high mountains	pDNA/ nrDNA	Climatic oscillations causing aridification and niche space expansion	Dwarf shrub speciation occurred ~1.9–0.5 Mya (RelTime analysis of pDNA)	Gehrke et al. (2016)
<i>Annikia</i> (Annonaceae)	West/Central and E Africa rainforests	nrDNA	Possibly climatic oscillations	Some speciation (BEAST analysis)	Brée et al. (2020)
* <i>Babiana</i> (Iridaceae)	Greater Cape Floristic Region	pDNA/ nrDNA	Soil type shifts	Considerable speciation (BEAST analysis)	Schnitzler et al. (2011)
<i>Begonia</i> (Begoniaceae)	Africa /Madagascar	pDNA/ nrITS	Not specified	Some speciation (NPRS analysis)	Plana et al. (2004)
* <i>Bulbophyllum</i> (Orchidaceae)	Madagascar	pDNA/ nrDNA	Quaternary vegetational shifts promoted niche transitions	Considerable speciation ~2.4 Mya to late Pleistocene (BEAST analysis)	Gamisch et al. (2015); Gamisch et al. (2016)
<i>Clematis</i> (Ranunculaceae)	S Africa/Madagascar	pDNA/ nrITS	Climate change	Some speciation (BEAST analysis)	Xie et al. (2011)
<i>Coffea</i> and related genera (Rubiaceae)	Madagascar and smaller West Indian Ocean islands	pDNA	Not specified	Considerable speciation in some clades (BEAST analysis)	Kainulainen et al. (2017)
<i>Dianthus</i> (Caryophyllaceae)	Not specified	pDNA/ nrITS	None suggested	All African species examined originated from early to late Pleistocene (BEAST and NPRS analysis)	Valente et al. (2010b)
* <i>Erica</i> (Ericaceae)	S Africa: Cape Floristic Region	pDNA/ nrITS	Formation of multiple new niches	Considerable speciation (BEAST and RelTime analyses)	Pirie et al. (2016)
<i>Heliophila</i> (Brassicaceae)	Cape Region	pDNA/ nrITS	Aridification, habitat divergence	Speciation from ~5–2 Mya (r8s analysis of ITS)	Mummenhoff et al. (2005)
* <i>Impatiens</i> (Balsaminaceae)	Tropical/subtropical Africa and Madagascar	pDNA/ nrDNA	Climatic oscillations causing spatial isolation	Considerable speciation (PL in r8s)	Janssens et al. (2009)
<i>Isolana</i> (Annonaceae)	African tropical rain forests	pDNA	Spatial isolation	Some speciation (relaxed molecular clock in BEAST)	Couvreur et al. (2011)
* <i>Ixora</i> (Rubiaceae)	Evergreen humid forests in Madagascar	pDNA/ITS/ ETS	Climatic oscillations causing spatial isolation; local adaptation and pollinator specialisation	Considerable speciation in one Madagascan clade (relaxed molecular clock in BEAST)	Tosh et al. (2013)
<i>Lychnis</i> (Caryophyllaceae)	E African high mountains	pDNA/ nrDNA	Aridification, habitat fragmentation, isolation and allopatric speciation	Some speciation (BEAST analysis of combined data)	Gizaw et al. (2016)
<i>Monodora</i> (Annonaceae)	African tropical rain forests	pDNA	Climatic oscillations causing spatial isolation	Some speciation (relaxed molecular clock in BEAST)	Couvreur et al. (2011)
<i>Moraea</i> (Iridaceae)	Greater Cape Floristic Region	pDNA/ nrDNA	Soil type shifts	Some speciation (BEAST analysis)	Schnitzler et al. (2011)
* <i>Phyllica</i> (Rhamnaceae)	S Africa/Madagascar/ neighbouring Atlantic, S Atlantic and Indian Ocean Islands	pDNA/ nrITS	Dispersal to and allopatric divergence on islands	Speciation from 2 Mya (NPRS of combined data)	Richardson et al. (2001)
* <i>Picris</i> (Asteraceae)	E Africa, Arabian Peninsula	pDNA/ nrITS	Shifts in intrinsic/extrinsic traits; climatic oscillations	Considerable speciation (relaxed molecular clock using MCMCTree)	Slovák et al. (2018)
* <i>Piptostigma</i> (Annonaceae)	West/Central and E Africa rainforests	nrDNA	Not specified, possibly due to climatic oscillations	Considerable speciation (BEAST analysis)	Brée et al. (2020)
* <i>Poa</i> and related genera (Poaceae)	Widespread	nrITS	Pliocene cooling followed by habitat divergence	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
<i>Podalyria</i> , <i>Liparia</i> , <i>Amphithalea</i> , <i>Virgilia</i> , <i>Calpurnia</i> (Fabaceae: Podalyrieae)	Cape Floristic Region	pDNA/ nrDNA	Shifts in fire-survival ability	Some speciation (BEAST analysis)	Schnitzler et al. (2011)
<i>Protea</i> (Proteaceae)	Cape Region and other parts of Africa	pDNA/ nrDNA	Left open	Some speciation within and outside Cape Region (BEAST analysis)	Valente et al. (2010)
* <i>Psiadia</i> (Asteraceae)	Madagascar	pDNA/ nrITS	Climatic oscillations, geographic isolation, habitat divergence	Considerable speciation (PL in R8s and BEAST analysis)	Strijk et al. (2012)
* <i>Senecio</i> (Asteraceae)	Northern and Western Cape, Namibia	nrITS	Climatic oscillation and habitat divergence	Speciation from 1.67 to 0.15 Mya (Based on ITS substitution rates)	Coleman et al. (2003)
<i>Senecio</i> (Asteraceae)	E African tropical high mountains	nrITS/ nrETS	Geographical isolation across different mountains	Some speciation (BEAST analysis of combined data)	Kandziora et al. (2016)
<i>Senecio</i> (Asteraceae)	N Africa	AFLPs	Hybridisation	Two polyploid species originated	Kadereit et al. (2006)

Protea (Valente et al. 2010a) and the megadiverse genus *Erica* (Figure 7), which contains 690 species endemic to the CFR (Pirie et al. 2016, 2017). Some of this diversification appears to be related to pollinator shifts (Pirie et al. 2011), as also advocated for the evolution of Cruciferae tribe Heliophleae in southern Africa (Mummenhoff et al. 2005). For *Babiana*, Schnitzler et al. (2011, 2012) linked Quaternary speciation to shifts in soil and climatic niches, and in *Protea* sect. *Exsertae* speciation was suggested to have been allopatric (Prunier and Holsinger 2010).

In their review of diversification of the tropical African fauna and flora, Couvreur et al. (2021) concluded that although many animal groups show Quaternary speciation best explained as having taken place in lowland forest refugia, few examples for this are known in plants. Exceptions, however, occur for the herbaceous plant genera *Begonia* (Plana et al. 2004) and *Impatiens* (Figure 7; Janssens et al. 2009), both showing substantial Quaternary speciation, and for woody groups, including *Monodora*, in which a minority of speciation events is dated to the Quaternary (Couvreur et al. 2011), and *Piptostigma*, in which the Quaternary origin of most of its 13 species has been tentatively explained to result from allopatric speciation in lowland forest refugia (Brée et al. 2020). Quaternary speciation has also been detected in Madagascar for the Coffeae alliance (Kainulainen et al. 2017), *Impatiens* (Janssens et al. 2009), *Ixora* (Tosh et al. 2013) and *Psiadia* (Strijk et al. 2012), and in a Madagascar clade of the pantropical orchid genus *Bulbophyllum* has been linked to Quaternary climatic changes causing niche transitions (Gamisch et al. 2016).

Some Quaternary speciation but few Quaternary radiations have been reported in the afroalpine flora of the East African high mountains. Radiations in

this flora, which originated mostly through long-distance dispersal from Eurasia of lineages pre-adapted to seasonally cold climates (Brochmann et al. 2021), include *Alchemilla* (Gehrke et al. 2016), the fresenii clade of *Senecio* (Kandziora et al. 2016) and *Lychnis* (Gizaw et al. 2016). In the case of *Anthoxanthum*, with two species of late Pliocene/early Quaternary origin, Tusiime et al. (2017) obtained evidence that part of *A. nivale* had hybridised with a widely allopatric South African species of the genus. This suggests that plant movement in the Quaternary sometimes covered vast distances, as further indicated by the Quaternary origin of North African *Senecio mohavensis* ssp. *breviflorus* and *S. hoggariensis* through hybridization between *S. glaucus* and *S. flavus* (Kadereit et al. 2006). Whereas *S. glaucus* is native to the Mediterranean, *S. flavus* has clear southern African relationships and is postulated to have reached North Africa only in the Quaternary (Coleman et al. 2003).

Australia/New Zealand

Similar to what was found for North America, some large Quaternary plant radiations have been detected in semi-arid and arid areas of Australia (Table 7). This is particularly notable for *Eucalyptus* subg. *Symphomyrtus*, which contains more than 300 species distributed in semi-arid open woodland and forests (Thornhill et al. 2019), and is also postulated for *Acacia* (Figure 8) comprising ca. 1000 species (Miller et al. 2003; Murphy et al. 2010). For the southwest Australian flora, Hopper (1979) emphasised that based on palynological and geomorphological evidence, Quaternary climatic oscillations caused recurrent cycles of aridity interspersed by pluvial stages



Figure 8. Species of two genera in which Quaternary speciation occurred in Australia and New Zealand. Left: *Acacia daphnifolia* (Photographic credit: Bruce Maslin, Western Australian Herbarium); right: *Myosotis glabrescens* (photographic credit: Heidi Meudt; CC BY 4.0. Te Papa (WELT SP108859)).

Table 7. Studies reporting Quaternary speciation (QS) in plant genera in Australia and New Zealand (*Radiations). Additional examples of QS related to the origin of divaricate species in 15 plant genera and families within New Zealand are given in Maurin et al. (2022).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
AUSTRALIA/NEW ZEALAND					
* <i>Abrotanella</i> (Asteraceae)	New Zealand/Tasmania	pDNA/nrITS	Climate oscillations (glacial/interglacial cycles)	Considerable speciation in New Zealand (NPRS in r8s)	Wagstaff et al. (2006)
* <i>Brachyglottis</i> (Asteraceae) and related genera	New Zealand/Tasmania	pDNA/nrITS	Habitat divergence	Considerable speciation in New Zealand	Wagstaff and Breitwieser (2004)
<i>Cardamine</i> (Brassicaceae)	Australia/New Zealand	pDNA/nrITS	Not specified	Some speciation (based on low sequence diversity)	Bleeker et al. (2022a)
* <i>Dracophyllum</i> (Ericaceae)	New Zealand/New Caledonia	pDNA	Climate oscillations (glacial/interglacial cycles)	Considerable speciation in New Zealand (PL in r8s and BEAST analyses)	Wagstaff et al. (2010)
<i>Eryngium</i> (Apiaceae)	Australia/New Zealand	pDNA/nrITS	Aridification	Some speciation (PL in r8s)	Kadereit et al. (2008)
* <i>Eucalyptus/Corymbia/Angophora</i> (Myrtaceae)	Widespread in Australia	pDNA/nrITS/nrETS	Aridification and habitat divergence	Much speciation (PL in r8s on combined data)	Thornhill et al. (2019)
<i>Festuca</i> (Poaceae)	New Zealand	pDNA/nrITS	Climatic oscillation, polyploidy	Some speciation (<i>MultiDivTimeA</i>)	Inda et al. (2008)
* <i>Gentianella</i> (Gentianaceae)	New Zealand	nrITS	Availability of newly formed large alpine area for colonization	Considerable speciation (K2P distances)	Von Hagen and Kadereit (2001)
* <i>Gossypium</i> sect. <i>Grandicalyx</i> (Malvaceae)	Australia	pDNA, nrITS/nrADHD	Range fragmentation during aridification	Considerable speciation (time since divergence calculated by dividing Jukes-Cantor distances by twice rate of nucleotide substitution)	Seelanan et al. (1999)
* <i>Lepidium</i> (Brassicaceae)	Australia/New Zealand	pDNA/nrITS	Climate/geological changes causing diversification in habitat preference	All species originated (fossil-based substitution rates)	Mummenhoff et al. (2004)
* <i>Myosotis</i> (Boraginaceae)	New Zealand	nrITS/AFLPs	Climate oscillations (glacial/interglacial cycles)	Considerable speciation (Maximum Likelihood analysis)	Winkworth et al. (2002); Meudt et al. (2015)
* <i>Ourisia</i> (Plantaginaceae)	New Zealand	nrITS	Climate oscillations, habitat divergence	Considerable speciation from ~0.8 Mya (BEAST analysis)	Meudt et al. (2009)
* <i>Pachycladon</i> (Brassicaceae)	New Zealand	nrDNA	Allopolyploidy	All 10 NZ species originated (BEAST analysis)	Joly et al. (2009)
* <i>Picris</i> (Asteraceae)	E, S and SW Australia	pDNA/nrITS	Shifts in intrinsic/extrinsic traits; climate oscillations	Considerable speciation (relaxed molecular clock method using MCMCTree)	Slovák et al. (2018)
* <i>Plantago</i> (Plantaginaceae)	New Zealand	nrITS	Multiple introductions, mountain uplift, isolation and habitat divergence	All 10 NZ species originated from ~2.29 to 0.50 Mya (BEAST analysis)	Tay et al. (2010)
* <i>Poa</i> (Poaceae) and related genera	Australia/New Zealand	nrITS	Pliocene cooling followed by habitat divergence	Considerable speciation (relaxed clock in BEAST)	Hoffmann et al. (2013)
* <i>Ranunculus</i> (Ranunculaceae)	New Zealand	nrITS	Climate oscillations in Pleistocene	Considerable speciation	Lockhart et al. (2001)
<i>Rorippa</i> (Brassicaceae)	Australia/New Zealand	pDNA	Not specified	Most species originated (determined from Jukes-Cantor distances and fossil-based nucleotide substitution rate)	Bleeker et al. (2002b)
* <i>Triodia</i> (Poaceae)	Australia (arid zone)	pDNA/nrSNPs	Diversification in substrate preference	Nine species in <i>T. basedowii</i> complex originated (BEAST analysis)	Anderson et al. (2019)
* <i>Wahlenbergia</i> (Campanulaceae)	New Zealand	pDNA/nrITS	Not specified	All 10 NZ species originated (BEAST analysis)	Prebble et al. (2011)

that were an important trigger of speciation across a landscape characterised by landform dissection and edaphic complexity.

Quaternary speciation has further been reported in the *Triodia basedowii* species complex (Anderson et al. 2019), and in *Gossypium* sect. *Grandicalyx* in

north-east Australia (Seelanan et al. 1999), and been linked to diversification in substrate (sandy, gravelly, rocky) preference, and conditions of annual monsoon rains and dry season fire, respectively. A radiation of *Brachyglottis* and related genera (*Bedfordia*, *Dolichoglottis*, *Haastia*, *Traversia*;

Table 8. Studies reporting Quaternary speciation (QS) in plant genera on Oceanic Islands and New Caledonia (*Radiations).

Taxa	Region	Molecular variation	Drivers of QS	Occurrence in Quaternary (dating method in brackets)	References
OCEANIC ISLANDS/NEW CALEDONIA					
<i>Aeonium</i> alliance (Crassulaceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	pDNA/nrITS	Divergence on different islands and habitat divergence	Some speciation (<i>MultiDivTime</i> analysis)	Kim et al. (2008)
* <i>Argyranthemum</i> (Asteraceae)	Macaronesia (Canary Islands, Madeira, Salvagem Pequena)	nrSNPs	Geographic isolation, habitat shifts and hybridisation	All 24 species originated (MCMCTree in PAML)	White et al. (2020)
* <i>Argyroxiphium/Dubautia/Wilkesia</i> (Asteraceae)	Hawaiian Islands	nrITS	Divergence on different islands and habitat divergence	All species originated (based on biogeographic modelling)	Landis et al. (2018)
* <i>Artemisia</i> (Asteraceae)	Hawaiian Islands	pDNA/nrITS/nrETS	Habitat divergence	Speciation began ~1.45 Mya (BEAST analysis of nrDNA)	Hobbs and Baldwin (2013)
* <i>Bidens</i> (Asteraceae)	Polynesia (Hawaiian, Marquesan, Society, Austral Islands)	pDNA/nrITS/nrETS	Divergence on different islands and habitat divergence	All 41 species originated (BEAST analysis)	Knape et al. (2020)
<i>Azorina, Campanula, Musschia</i> (Campanulaceae)	Macaronesia (Azores, Cape Verde, Madeira)	pDNA/nrITS	Divergence on different islands and habitat divergence	Some speciation (BEAST analysis)	Menezes et al. (2017)
* <i>Cheirolophus</i> (Asteraceae)	Macaronesia (Canary Islands)	pDNA/nrITS/nrETS	Divergence on different islands and habitat divergence	All species originated (Based on BEAST analysis)	Vitales et al. (2014)
<i>Crambe</i> (Brassicaceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	nrITS	Divergence on different islands and habitat divergence	Some speciation (<i>MultiDivTime</i> analysis)	Kim et al. (2008)
<i>Echium</i> (Boraginaceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	pDNA/nrITS	Divergence on different islands and habitat divergence	Some speciation (<i>MultiDivTime</i> analysis)	Kim et al. (2008)
<i>Festuca</i> (Poaceae)	Macaronesia (Canary Islands, Azores)	pDNA/nrITS	Climatic oscillation, polyploidy	Some speciation (<i>MultiDivTimeA</i>)	Inda et al. (2008)
<i>Gesnouinia</i> (Urticaceae)	Macaronesia (Canary Islands)	pDNA/nrITS	Climatic oscillations	Two endemic species diverged in Pleistocene (BEAST analysis)	Schüßler et al. (2019)
* <i>Limonium</i> (Plumbaginaceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	pDNA/nrITS	Divergence on different islands and habitat divergence	Considerable speciation (ML in RAXML, Bayesian Inference in MrBayes)	Koutroumpa et al. (2021)
* <i>Lotus</i> (Fabaceae)	Macaronesia (Canary Islands, Azores, Madeira, Cape Verde)	pDNA/nrITS	Divergence on different islands and habitat divergence	Considerable (BEAST analysis)	Jaén-Molina et al. (2021)
* <i>Melicope</i> (Rutaceae)	Indian/Pacific Ocean: Mascarene Islands, Polynesia (especially Hawaiian Islands)	pDNA/nrDNA	Wider ecological niches, bird-dispersal, geographic isolation	Considerable speciation (BEAST analysis)	Appelhans et al. (2018)
* <i>Metrosideros</i> (Myrtaceae)	Hawaiian Islands	nrITS/nrETS	Not specified	All species originated since ~1 Mya (based on age of sub-fossils and islands)	Wright et al. (2001)
* <i>Oxera</i> (Lamiaceae)	New Caledonia	pDNA/nrDNA	Habitat isolation and divergence	Considerable speciation (BEAST analyses)	Barrabé et al. (2019)
* <i>Pericallis</i> (Asteraceae)	Macaronesia (Canary Islands, Azores, Madeira)	pDNA/nrITS	Divergence on different islands and habitat divergence	Considerable speciation (BEAST analyses)	Jones et al. (2014)
* <i>Psiadia</i> (Asteraceae)	Mascarene Islands (Mauritius, Reunion, Rodrigues)	pDNA/nrITS	Geographic isolation and habitat divergence	Considerable speciation (PL in r8s and BEAST analysis)	Strijk et al. (2012)
* <i>Psychotria</i> (Rubiaceae)	New Caledonia	pDNA/nrITS	Spatial isolation	Considerable speciation (BEAST analysis)	Barrabé et al. (2014)
* <i>Scalesia</i> (Asteraceae)	Galapagos Islands	pDNA/nrDNA	Habitat divergence within islands and some divergence between islands	All 15 species originated since ~0.74–0.63 Mya (BEAST analysis)	Fernández-Mazuecos et al. (2020)
<i>Sideritis</i> (Lamiaceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	nrITS	Divergence on different islands and habitat divergence	Some speciation (<i>MultiDivTime</i> analysis)	Kim et al. (2008)
<i>Sonchus</i> (Asteraceae)	Macaronesia (Canary Islands, Madeira, Cape Verde)	nrITS	Divergence on different islands and habitat divergence	Some speciation (<i>MultiDivTime</i> analysis)	Kim et al. (2008)
* <i>Haplostachys, Phyllostegia, Stenogyne</i> (Lamiaceae: Stachydeae)	Hawaiian Islands	pDNA/nrDNA	Hybridisation and polyploidy	Considerable speciation occurred in these genera (BEAST analysis)	Roy et al. (2013)

Wagstaff and Breitwieser 2004), distributed mostly in New Zealand, is also dated to the Quaternary (Pelsner et al. 2010).

In both Australia and New Zealand, Quaternary radiations have been reported for a number of lineages that colonised these areas mostly in the Pliocene.

These include radiations in *Cardamine* (Bleeker et al. 2022a) and *Rorippa* (Bleeker et al. 2022b) in Australia, and in *Lepidium* (Mummenhoff et al. 2004) in both Australia and New Zealand. Interestingly, *Lepidium* in Australia (19 species) and New Zealand (7 species) has been shown to have a hybrid origin involving Californian and South African parental lineages (Mummenhoff et al. 2004).

Several instances of Quaternary radiations of Pliocene/Pleistocene immigrants have been detected in the New Zealand Alps (Winkworth et al. 2005), where alpine habitats became available only about 1.9 Mya through orogeny (Heenan and McGlone 2013). These include: *Gentianella* (Von Hagen and Kadereit 2001; Glenny 2004) and *Ourisia* (Meudt et al. 2009), which both appear to have colonised New Zealand from South America; *Myosotis* (Figure 8; Meudt et al. 2015), a morphologically and ecologically diverse lineage with ca. 40 species that entered New Zealand from the northern hemisphere; and *Plantago*, which entered New Zealand most likely from Australia at least three times independently (Tay et al. 2010). The genus *Pachycladon* with 8 species, is reported to have diversified as an adaptive radiation in the New Zealand Alps during the Quaternary (Joly et al. 2014), having originated as a result of allopolyploid hybridisation between two

distinct northern hemisphere lineages of Brassicaceae (Joly et al. 2009). Of considerable interest is the recent finding by Maurin et al. (2022) that many woody species in New Zealand which exhibit a divaricately branching ‘cage’ architecture, diverged from non-divaricate, woody sister species during the Pleistocene. This was evident in 15 genera representing 15 different families. A divaricate cage architecture has been demonstrated to serve as a defence against browsing birds (Bond et al. 2004), although is also thought to be an adaptation to cold and dry conditions (Lusk et al. 2018). Maurin et al. (2022) propose that their results (based on a dated phylogeny constructed from 45 protein-coding sequences from plastid genomes) support a combined hypothesis that a divaricate cage architecture was selected as a defence mechanism in many New Zealand plant genera during the Pliocene and Pleistocene periods when low temperatures prevented woody plants from growing rapidly out of the reach of large, flightless browsing birds, such as moas (Dinornithiformes, which remained extant until historical times). Global cooling during these periods combined with the rise of the Southern Alps would have created frosty and wind-swept environments in New Zealand, negatively impacting the rapid growth of woody plants within them.



Figure 9. Species of two genera in which Quaternary speciation occurred in Oceanic islands. Left: *Argyranthemum teneriffae* (Photographic credit: Oliver White); Right: *Argyroxiphium sandwicense* (Photographic credit: Donald W. Kyhos).

Oceanic islands and New Caledonia

Oceanic islands have long been recognised as natural theatres for animal and plant radiations (Darwin 1905; Wagner and Funk 1995), with Quaternary plant speciation reported in all major oceanic island archipelagos and also on New Caledonia (Table 8). Lineages with considerable Pleistocene speciation or Pleistocene crown group ages include *Argyranthemum* (Figure 9; White et al. 2020), *Cheirolophus* (Vitales et al. 2014), *Limonium* (Koutroumpa et al. 2021) and *Lotus* (Jaén-Molina et al. 2021) in Macaronesia (including the Canary Islands), the silversword alliance – *Argyroxiphium/Dubautia/Wilkesia* (Figure 9; Landis et al. 2018), *Metrosideros* (Wright et al. 2001) and *Melicope* (Appelhans et al. 2018) in the Hawaiian Islands (the last lineage also contains several species of Quaternary age on other Polynesian islands and in the Mascarene Islands), *Bidens* (Knope et al. 2020) in Polynesia, *Scalesia* (Fernández-Mazuecos et al. 2020) in the Galapagos Islands, *Psiadia* (Strijk et al. 2012) in the Mascarene Islands and one clade each of *Psychotria* (Barrabé et al. 2014) and *Oxera* (Barrabé et al. 2019) on New Caledonia.

Much in contrast to Quaternary speciation in continental settings, Quaternary climatic oscillations have only rarely been advocated as drivers of speciation in islands. Instead, inter-island dispersal and intra-island adaptive divergence have been considered to be major causes of speciation in such settings. However, a direct influence of Quaternary climatic oscillations on island speciation has been advocated in the following three different ways. First, Carine (2005), investigating the evolution of *Convolvulus* in Macaronesia, in his ‘colonization window hypothesis’ suggested that the early Pleistocene as a time of profound climatic changes (but also of active volcanism in the Canaries) would have been a plausible window of opportunity (though clearly not the only one) for the colonisation of Macaronesia. In support, early Pleistocene colonisation of Macaronesia has also been detected for *Aeonium* (Kim et al. 2008) and *Lotus* (Jaén-Molina et al. 2021). Second, changes in island configuration through Pleistocene alterations in sea level have been advocated as drivers of speciation in *Psiadia* in the Mascarene Islands (Strijk et al. 2012) where the existence in the Quaternary of large numbers of islands along the Nazareth and Saya de Malha banks has been documented. Also, for the Hawaiian Islands, it is known that Lana’i, Maui and Moloka’i formed the ancient island of Maui Nui in Quaternary times, with

its maximal areal extent around 1.2 Mya (Price and Elliott-Fisk 2004). However, fragmentation of this island through rises in sea level has, to our knowledge, never been considered as a driver of speciation or has been viewed unlikely to have affected speciation in the case of *Tetramolopium* (Lowrey 1995). Third, as in continental settings, the direct influence of Quaternary climatic oscillations on speciation through changes in distribution range and the origin of new habitats has been advocated. For New Caledonia, Barrabé et al. (2019) concluded that ‘Pliocene and Pleistocene climatic fluctuations considerably affected the dynamic of New Caledonian biotas, leading to the origination of new habitats such as the unique shrubby sclerophyllous vegetation’. Pintaud et al. (2001) further hypothesised that the distribution of the 36 palm species on New Caledonia reflects the distribution of Pleistocene lowland rain forest refugia where range fragmentation resulted in speciation. A non-adaptive radiation through range fragmentation was hypothesised for a New Caledonian lineage of *Psychotria* (Barrabé et al. 2019), while in the Canary Islands, Schüßler et al. (2019) hypothesised that differentiation of the laurel forest species *Gesnouinia arborea* and the rupicolous and more xeric *G. filamentosa* was related to range shifts during Pleistocene climatic changes, and similar hypotheses have been proposed for *Cheirolophus* (Vitales et al. 2014) and *Pericallis* (Jones et al. 2014).

Quaternary climatic oscillations as a possible driver of the pronounced intra-island ecological shifts that have often been found in oceanic islands (e.g., Baldwin 2003), are clearly worth further exploration. For the Hawaiian Islands, the large majority of colonisers is of temperate or boreal North American origin and accordingly established at high elevations (Baldwin and Wagner 2010). Diversification there and along an elevational gradient may well have been driven by elevational shifts in the Quaternary. This may also apply to Hawaiian *Artemisia* which unusually evolved from coastal habitats into drier and colder subalpine habitats (Hobbs and Baldwin 2013).

Taken overall, it does seem probable that Quaternary cycles of climate change were a contributory cause of Quaternary plant speciation on oceanic islands and consequently greater note should be taken of the words of Whittaker et al. (2010) that ‘for those oceanic islands that do conform to the simple ontogenetic model, perhaps one of the

most important omissions from the framework is the role of Pleistocene climate change and accompanying variation in the configuration of islands.’

Discussion

As evident from our compilation of examples above and in [Tables 1–8](#) and [Table S2](#), many plant speciation events and radiations across the globe and in all climates have been dated to the Quaternary. We do not claim that the Quaternary was a period with increased speciation rates, although this has been shown in some studies. Neither do we propose that all Quaternary speciation was related to the climatic oscillations of that period, although many studies have concluded this. We do conclude, however, that according to the plant phylogeny literature speciation occurred frequently in the Quaternary. We are well aware that despite molecular clock methods having developed greatly over the last ca. 20 years, the dating of divergence times with a molecular clock rests on numerous assumptions ([Donoghue and Benton 2007](#); [Donoghue and Yang 2016](#); [Bromham et al. 2018](#)) and at times may be incorrect. For example, in deep geological time molecular clock dating appears to greatly overestimate the age of angiosperm diversification ([Coiro et al. 2019](#)), while the use of secondary calibrations, commonly used in studies of young lineages because of lack of fossils, often results in younger ages and narrower age ranges than primary estimates ([Schenk 2016](#)). That said, explorations of the performance of molecular clocks in shallow phylogenies, using both simulated and real data sets (e.g., [Brown and Yang 2010](#); [Van Tuinen and Torres 2015](#)), have shown that divergence times are not consistently underestimated in young lineages.

Most dated plant phylogenies are constructed from variation in either a few plastid (chloroplast) or nuclear DNA sequences or a combination of both, with the Internal Transcribed Spacer (ITS) regions of 18S–26S nuclear ribosomal DNA being by far the most commonly used nuclear DNA sequence ([Tables 1–8](#)). Because DNA sequences can vary in mutation rate and be differentially affected in divergence by factors such as incomplete lineage sorting and historical gene flow, phylogenies based on one or a few DNA sequences, rather than many, may provide a poor indication of species relationships and dates of divergence. The latter was recently emphasised with regard to dates of divergence for pairs of European butterfly sister species ([Ebdon et al. 2021](#)). Whereas estimates of

divergence based on mitochondrial DNA sequence and allozyme data previously indicated that such species pairs diverged in the Pleistocene, estimates based on genome-wide transcriptome data showed that divergence for 10 of 18 sister species pairs occurred before the Pleistocene (2.6 Mya) and for a further six pairs before the mid-Pleistocene transition (0.8–1.2 Mya), i.e. the onset of the major Pleistocene glacial cycles ([Ebdon et al. 2021](#)). Clearly, this suggests that estimates of species divergence based on few DNA sequences should be treated with caution. For plants, however, a recent phylogenetic analysis of neotropical *Costus* based on 756 nuclear gene sequences ([Vargas et al. 2020](#)) generated a phylogeny with a crown date of ca. 3 Mya similar to that estimated previously from ITS and ETS sequences (1.1–5.4 Mya, [Kay et al. 2005](#)). Furthermore, the analysis showed that all 31 sister species pairs examined diverged during the Pleistocene ([Vargas et al. 2020](#)). Similarly, a phylogenetic analysis based on variation across ca. 4000 loci confirmed that many European *Antirrhinum* species originated in the Pleistocene ([Otero et al. 2021](#)) as indicated earlier by a dated phylogeny based on two pDNA sequences ([Vargas et al. 2009](#)). In addition, a growing number of recent studies utilising large numbers of nuclear DNA sequences and coalescent simulation methods to estimate dates of divergence from summary population genetic statistics, have reported Quaternary divergence times for speciation and some radiations ([Tables 1–8](#)). One of these studies conducted by [Nevado et al. \(2018\)](#), utilised variation in 6013 orthologous genes and showed that two sister species pairs within an Andean clade of *Lupinus* in South America diverged in the late Pleistocene, in line with the Pleistocene origin of this clade previously indicated by dated phylogenies constructed from two nuclear DNA ([Hughes and Eastwood 2006](#)) and three plastid DNA sequences ([Drummond 2008](#)). Thus, though conclusions of Quaternary plant speciation based on phylogenies constructed from a few plant DNA sequences might need to be treated with caution, new evidence from using much more sequence data indicates they often likely identified the correct age range.

The primary effect of Quaternary climatic oscillations on species has been to change their geographical distributions (latitudinal, elevational, and also longitudinal) caused by changes in temperature, precipitation, or sea level. Changes in geographical distribution often may have resulted in the fragmentation of distribution ranges, providing

the opportunity for divergence and speciation in geographical isolation. While it has been argued that periods of isolation may not have been long enough for speciation to be completed (Willis and Niklas 2004), there is growing evidence that this is incorrect. For example, He et al. (2019) showed that Quaternary mangrove divergence and speciation along the Indo-Malayan coasts on either side of the Strait of Malacca was driven by cycles of isolation and mixing (gene flow) resulting from Quaternary fluctuations in sea level and the repeated closing and opening of the Strait to ocean currents. Also, Ortego and Knowles (2021) have shown that isolation on different mountain tops (sky islands) in the Iberian Peninsula during Pleistocene interglacial periods resulted in speciation within the flightless grasshopper genus *Podisma*, despite evidence of limited gene flow during glacial periods. Most remarkably, perhaps, there is now strong evidence that geographical isolation during glacial periods caused Pleistocene speciation in open-ocean, widely dispersing phytoplankton of the genus *Gephyrocapsa* (Filatov et al. 2021).

Renewed contact between transiently separated lineages (the ‘secondary contact’ of Stebbins 1984), may on occasion have been the starting point for hybrid speciation, both homoploid and allopolyploid, as reported in some of the studies compiled above. In this regard, climatic oscillations may not only have led to a sequence of geographical isolation and secondary contact providing opportunity for hybridisation, but may have, in the next cycle, resulted in the geographical segregation of parental and hybrid lineages, the latter with ecological properties different from those of the parents, permitting hybrid speciation to complete in allopatry (Kadereit 2015). Changes in geographical distribution may also have exposed populations to novel abiotic and biotic environments. This often may have added an adaptive component to Quaternary speciation and led to changes in, e.g., soil preference, while exposure to new pollinator faunas may have resulted in floral ecological diversification. In the latter instances, the role of Quaternary climatic oscillations as the primary cause of diversification may be limited to the facilitation of migration over large distances. For example, connectivity by stepping-stone migration between the northern and southern hemispheres for plant lineages from temperate climates may have been better in glacial times through the lowering of vegetation belts or the lowering of sea levels (North America – South America: Luebert

and Weigend 2014; western Eurasia – southern Africa: Galley et al. 2007; Bragg et al. 2013; Eurasia – Australasia: Raven 1973; Binney et al. 2017). Also, establishment after migration or dispersal may have been easier in rapidly changing and somewhat disturbed environments in which inter-specific competition may have been weakened.

Conclusions

We consider that there is now overwhelming evidence that Quaternary plant speciation occurred frequently. The perception of the Quaternary as a period of little or no speciation by at least some palaeobotanists (e.g., Lang 1994; Bennett 1997, 2004, 2013; Willis and Niklas 2004) probably reflects the palaeobotanical evidence available. Fossil pollen is the most commonly used material in palaeobotany for detecting divergent taxa but cannot in most cases resolve differences at species level and often not even at genus level (Lang 1994). Accordingly, the ‘species’ of Quaternary palaeobotanists in most cases do not correlate with those recognised by systematists or evolutionary biologists (Birks and Birks 1980). With such data at hand, recent speciation, resulting in morphologically very similar (but morphologically and molecularly distinguishable) species, cannot be seen in the fossil record in most cases.

Climatic oscillations are recognised as a primary driver of Quaternary speciation in many instances. Even in settings such as oceanic archipelagos where Quaternary speciation is thought to have been mainly triggered by inter-island dispersal and intra-island divergence across topographically and ecologically diverse landscapes, Quaternary climatic oscillations are now considered to have often played a supplementary role by causing ecological niche shifts and cycles of fragmentation and isolation in species distributions. Similarly, in parts of the world where alpine habitats became available only in the Pliocene and/or Quaternary through orogeny (e.g., in the northern Andes and New Zealand Alps), environmental change and geographical isolation brought about by both orogeny and climatic change are likely to have been major drivers of Quaternary speciation (Flantua et al. 2019).

Quaternary plant speciation continues unabated into the present time with examples of both allopolyploid and homoploid hybrid speciation occurring within the past 250 years (Vallejo-Marin and Hiscock 2016; Abbott and Rieseberg 2021). In these instances, the proximity of previously isolated parental species as the result of human induced

habitat disturbance and alteration of species distributions, sometimes as a consequence of climate warming (e.g., Gramlich et al. 2018), is recognised as an important extant driver of speciation.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

Joachim W. Kadereit is emeritus professor. His current research interests are in plant evolution in the European Alpine System and in the geographical and ecological settings of hybrid speciation.

Richard J. Abbott is emeritus professor. His research interests are in diverse aspects of plant evolution, especially plant speciation and the evolutionary consequences of hybridisation.

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