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Plant speciation in the Quaternary
Joachim W. Kadereit\textsuperscript{a} and Richard J. Abbott\textsuperscript{b}

\textsuperscript{a}Institut für Organismische und Molekulare Evolutionsbiologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany; \textsuperscript{b}School 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.

**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
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. *Glaucocreseda* (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 Haeff (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
| Taxa | Region | Molecular variation | Drivers of QS | Occurrence in Quaternary (dating method in brackets) | References |
|------|--------|---------------------|---------------|----------------------------------------------------|------------|
| **EUROPE/N AFRICA** | | | | | |
| *Aconitum* (Ranunculaceae) | Mediterranean region | pDNA/nrITS; ~4000 nr loci | Climatic oscillations | Considerable speciation (PL implemented in TreePL); All 13 European species originated from ~2.54 Ma (BEAST analysis) | Vargas et al. (2009); Otero et al. (2021) Bastida et al. (2010) |
| *Anthemis* (Asteraceae) | Mediterranean region | nrITS | Climate complexity and eco-climatic novelty | Considerable speciation (PL) | Lo Presti and Oterminier (2009) |
| *Antirrhinum* (Plantaginaceae) | Mediterranean region and European mountains | pDNA/nr ITS | Climatic oscillations, geographical isolation and habitat divergence | Considerable speciation (PL); Tetrane (TreePL); All European species originated from ~2.54 Ma (BEAST analysis) | Vargas et al. (2009); Otero et al. (2021) Bastida et al. (2010) |
| *Aquilegia* (Ranunculaceae) | Europe (QS occurred after colonisation by ancestral forms from Asia) | pDNA | Climatic niche differentiation in Europe | Three European species originated (BEAST analysis) | Kaderiet et al. (2019) |
| *Campanula* (Campanulaceae) | Eurasia and Azores | pDNA | Diverse | Some speciation (PL analysis) | Mansion et al. (2012) Tankahaya-Hacoglu et al. (2014) |
| *Carthamus* (Asteraceae), *C. tinctorius* group | Turkey | nrITS | Habitat divergence accompanying climatic oscillations | Divergence occurred within sections | Atractylis and Carthamus (BEAST analysis) |
| *Centaurium* (Gentianaceae) | Mediterranean region | pDNA/nrDNA | Climatic oscillations and geographic isolation | Considerable speciation (BEAST analysis) | Jiménez-Lobato et al. (2019) Gonzan et al. (2009) |
| *Cistus* (Cistaceae) | Mediterranean region | pDNA/nrDNA | Habitat divergence following establishment of Mediterranean climate | Diversification from ~1.04 Ma onwards (PL analysis) | Jabbour et al. (2012) Valente et al. (2010b) |
| *Delphinium* (Ranunculaceae) | Mainly Mediterranean | pDNA/nrITS | Not specified | Some speciation (BEAST analysis) | Jabbour and Renner (2012) |
| *Dianthus* (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 NPP analysis) | Jabbour et al. (2012) |
| *Erysimum* (Brassicaceae) | East and West Europe | nrITS | Not specified | Considerable speciation (BEAST analysis) | Moazzeni et al. (2014) |
| *Festuca* (Poaceae) | Widespread | pDNA/nrITS | Climatic oscillation, polyplody | Considerable speciation (estimated using MultiDivitime) | Inda et al. (2008) |
| *Gentiana* (Gentianaceae) | Mountain Ranges | nrITS | Climatic oscillations causing cycles of geographical spread and isolation | Considerable speciation from ~1.6 to 0.6 Ma (clock calibration based on LGM glaciation events) | Hungerer and Kaderiet (1998) |
| *Ilex* (Aquifoliaceae) | Widespread | pDNA/nrDNA | Divergence after dispersal to mesic environments | Some speciation (BEAST analysis) | Yao et al. (2021) |
| *Lathyrus, Pisum, Vicia* (Fabaceae: Fabaeae) | Mediterranean, Macaronesia, West/Central Europe | pDNA/nrDNA | Not specified | Considerable speciation (BEAST analysis) | Schaefer et al. (2012) |
| *Limonium* (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) Ferrández-Mazuecos et al. (2013); Ferrández-Mazuecos and Vargas (2015) |
| *Linaria* subsect. *Versicolores* (Plantaginaceae) | Iberian Peninsula | pDNA/nrITS | Pollinator shifts linked to floral divergence, edaphic divergence | All 8 species diverged since ~0.43 Ma (relaxed molecular-clock in BEAST) | Fernández-Mazuecos et al. (2013); Ferrández-Mazuecos and Vargas (2015) |
| *Lolium* (Poaceae) | Mediterranean region, N Europe | pDNA/nrITS | Climatic oscillations | Some speciation (Bayesian relaxed clock method in BEAST, Estrobranches and MultiDivitime) | Inda et al. (2008) |
| *Nigella* (Ranunculaceae), *N. arvensis* group | Aegean archipelago, Mediterranean Basin | nrITS | Climate and sea level oscillations favoured allopatric speciation | All species originated from ~0.78 to 0.16 Ma onwards (Log-lineages through time analysis) | Bitkau and Comes (2009) |
| *Petasites* (Asteraceae) | Central and East Europe | pDNA/nrITS | Possible ecological divergence | Some speciation (Bayesian relaxed molecular clock of ITS variation) | Steffen et al. (2016) |
| *Picris* (Asteraceae) | Mediterranean, N Africa | pDNA/nrITS | Shifts in intrinsic/extrinsic traits, climate oscillations | Considerable speciation throughout distribution (relaxed molecular clock in ABCMTree) | Slovak et al. (2018) |

(Continued)
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 carneolius (= 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 brigiatica* (Dixon et al. 2009) originated by allopolyploid speciation, and in the *Doronicum clusii* aggregate (Pachschwöll et al. 2015) the tetraploid *D. stiriacum* 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 kueperi*, where apomixis appears to have followed autopolyploidy, took place in the last glacial or even in the Holocene (Cosendai et al. 2021).
Rhodanthemum (credit: Pablo Vargas). Quaternary (dinal ence) place Whereas diversification is 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 Rhodanthennum, a genus centred in north-west African mountain areas, and Leucanthemum, a largely European genus (Wagner et al. 2019). Whereas diversification in Rhodanthennum 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 Rhodanthennum 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**        |                         |                     |                                                                               |                                                      |            |
| *Abies* (Pinaceae) | QTP/Himalayas          | mtDNA/pDNA          | Range expansion during glaciation period                                       | Considerable speciation (~0.293–190 Mya (MMP))       | Peng et al. (2015) |
| *Acantoholimon* (Plumbaginaceae) | Central and SW Asia   | pDNA/nrITS          | Colonization of mountain habitats, geographic isolation, climatic oscillations | Considerable speciation (BEAST analysis)             | Moharrek et al. (2019) |
| *Acanthophyllum* (Caryophyllaceae) | Central and SW Asia | pDNA/nrITS          | Not specified                                                                 | Considerable speciation (BEAST analysis)             | Pirani et al. (2014) |
| Aconitum (Ranunculaceae) | QTP/HMR             | pDNA/nrITS          | Not specified                                                                 | Some speciation (BEAST analysis)                     | Jabbour and Renner (2012) |
| Actaea (Ranunculaceae) | North China           | pDNA/nrSNPs         | Pollinator shifts linked to floral divergence                                  | Three species diverged: ~0.63 Mya (pDNA); ~0.127 Mya (nrSNPs, *θ̂*̂ analysis) | Li et al. (2016) |
| Allium (Amaryllidaceae) | QTP/HMR              | pDNA/nrITS/ nrAt103 | Aridification causing vicariance; allopolyploidy during interglacial           | Some speciation; ~2 Mya to ~0.38 Mya (BEAST analysis on pDNA) | Liao et al. (2012) |
| Angelica (Apiaceae) | Eastern Himalayas     | pDNA/nrITS/nrETS    | Climate change causing range fragmentation and population isolation          | Some speciation (BEAST analysis)                     | Takahashi and Setoguchi (2018) |
| *Asarum* (Aristolochiaceae) | China, Taiwan, Japan and neighbouring islands | pDNA/nrITS          | Geographic isolation and habitat divergence                                  | Considerable speciation (BEAST analysis)             | Bagheri et al. (2017) |
| *Astragalus sect. Hymenostegis* (Fabaceae) | SW Asia              | pDNA/nrITS          | Cimatic oscillations causing repeated cycles of dry and more humid conditions | All species originated (BEAST analysis)               | Thomas et al. (2012) |
| *Begonia* (Begoniaceae) | SE Asia/Malesia       | pDNA                | Topographic heterogeneity, cyclic vicariance due to climatic and sea-level oscillations | Considerable speciation (BEAST analysis)             | Wen et al. (2016) |
| Calligonum (Polygonaceae) | NW China             | pDNA                | Climate change, aridification and habitat divergence                         | Much speciation from ~1.97 Mya (BEAST analysis)      | Ikeda et al. (2012) |
| Cardamine (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)       |          |
| *Carex sect. Confortiflorae* (Cyperaceae) | East Asia            | pDNA/nrITS/nrETS    | Climatic oscillations causing allopatric divergence                           | Considerable speciation (BEAST analysis)             | Lu et al. (2021) |
| Clematis (Ranunculaceae) | SE/SW China           | pDNA/nrITS          | Climate change                                                                | Some speciation (BEAST analysis)                     | Xie et al. (2011) |
| Delphinium (Ranunculaceae) | Widespread            | pDNA/nrITS          | Not specified                                                                 | Some speciation (BEAST analysis)                     | Jabbour and Renner (2012) |
| Dipelta (Caprifoliaceae) | West China            | pDNA/nrDNA          | Glaciatic 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) |
| Dysosma (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)) | Zhang et al. (2007) |
| *Epimedium sect. Diphyllon* (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) | Moazzeni et al. (2014) |
| *Erysimum* (Brassicaceae) | Central Asia          | nrITS               | Not specified                                                                 | Considerable speciation (BEAST analysis)             | Gao et al. (2017) |
| *Extrema* (Brassicaceae) | QTP/Himalayas; Central Asia | pDNA/nrITS          | Climatic oscillations causing allopatric divergence                           | Some speciation;  ~1.9 to 0.53 Mya (BEAST analysis of pDNA) |          |

(Continued)
| Taxa                                      | Region                        | Molecular variation | Drivers of QS                                      | Occurrence in Quaternary (dating method in brackets)                     | References                          |
|-------------------------------------------|-------------------------------|---------------------|---------------------------------------------------|--------------------------------------------------------------------------|-------------------------------------|
| *Lathyrus, Vavilova, Vicia* (Fabaceae)    | Western/Central Asia          | pDNA/nrDNA          | Not specified                                     | Considerable speciation (BEAST analysis)                                  | Schaefer et al. (2012)              |
| *Festuca* (Poaceae)                       | Widespread                    | pDNA/nrITS          | Climatic oscillation                              | Some speciation (MultDivtimeA)                                           | Inda et al. (2008)                  |
| *Ilex* (Aquifoliaceae)                    | Widespread                    | pDNA/nrDNA          | Divergence after dispersal to mesic environments  | Some speciation (BEAST analysis)                                          | Yao et al. (2021)                   |
| *Juglans* (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)                   |
| Leucomeris/Nouelia (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)                  |
| *Myrcaria* (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)                   |
| *Oxytropis* (Fabaceae)                    | SW and Central Asia           | pDNA/nrDNA          | Mountain uplift, geographic isolation, habitat divergence, climatic oscillations due to geological and climate change | Two species diverged ~0.026 Mya (MAA analysis of pDNA and nrDNA)          | Shavvon et al. (2017)              |
| *Picris* (Asteraceae)                     | Himalayas/HMR                 | pDNA/nrDNA          | Geographic isolation due to geological and climate change | Two species diverged ~0.050–0.024 Mya (DIYABC analysis of nrSSR variation) | Zhao et al. (2021)                  |
| *Paeonia* subsect. Delavayanae (Paeoniaceae) | QTP                           | nrSSR variation     | Geographic isolation and ecological divergence      | Three species diverged ~0.050–0.024 Mya (DIYABC analysis of nrSSR variation) | Xu et al. (2019c)                   |
| *Phyllobium* (Fabaceae)                   | QTP                           | nrITS               | QTP uplift and climatic oscillations               | Considerable speciation (rds and BEAST analyses)                         | Zhang et al. (2012)                |
| *Picris* (Asteraceae)                     | Widespread                    | pDNA/nrITS          | Shifts in intrinsic/extrinsic traits; climate oscillations and habitat divergence | Considerable speciation (relaxed molecular clock in MCMCtree)           | Slovak et al. (2018)               |
| *Poa* (Poaceae) and related genera        | Widespread                    | nrITS               | Pliocene cooling enabled adaptation to different habitats | Considerable speciation (relaxed clock in BEAST)                        | Hoffmann et al. (2013)             |
| *Populus* sect. Turanga (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)                 |
| *Populus* sect. Populus (Salicaceae)      | QTP/SWt to NE China           | nrSNPs              | Climatic oscillation and habitat divergence        | Two species diverged ~0.878 Mya (fastsimcoal2)                          | Li et al. (2021)                    |
| Pugionium (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)                 |
| Quercus sect. Quercus (Fagaceae)          | North China                   | pDNA/nrDNA          | Geological and climatic oscillations causing niche divergence | Two species diverged ~2.15–0.92 Mya (IM analysis of pDNA and nrDNA)       | Yang et al. (2016)                 |
| *Rhodiola* (Crassulaceae)                 | QTP/NE China                  | pDNA/nrITS          | Geographical isolation, climate oscillations       | Much speciation (BEAST analysis)                                        | Zhang et al. (2014)                |
| *Roscoea* (Zingiberaceae)                 | HMR, SW China                 | pDNA/nrITS          | Niche divergence accompanying climatic oscillations | Speciation occurred ~1.48–0.01 Mya (IM analysis)                        | Zhao et al. (2016)                 |
| *Saussurea* (Asteraceae)                  | QTP and neighbouring areas    | pDNA                | Topographic heterogeneity and climate oscillation  | Some speciation (treePL analysis)                                      | Xu et al. (2019b)                   |
| *Saxifraga* (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)            |
| *Sinallaria* (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 fastsimcoal2) | Zhang et al. (2018); Wang et al. (2019) |
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 southeast 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 *Sinallaria* (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 |
|------|--------|---------------------|---------------|-----------------------------------------------------|------------|
| *Androsace* sect. *Douglasia* (Primulaceae) | NW America and NE Asia (Beringia) | pDNA/ nrITS, nrITS/nrETS | Not specified | All speciation in section occurred in late Pliocene and Pleistocene | Schneeweiss et al. (2004) |
| *Artemisia* (Asteraceae) | Arctic lineages widespread | pDNA | Not specified | Some speciation (BEAST analysis of combined data) | Dragon and Barrington (2009); Gebauer et al. (2014) |
| *Carex* sect. *Phacocystis* (Cyperaceae) | Widespread | pDNA/ nrITS/nrETS | Ecophysiological differentiation | ‘Northern’ and ‘Mixed’ clades of species originated (r8s analysis) | Scheen et al. (2004) |
| *Cerastium* (Caryophyllaceae) | Widespread arctic-alpine clade | pDNA | Not specified | Speciation occurred ~1.48–0.44 Mya (molecular clock calibration based on opening of Bering Strait) | Hoffmann et al. (2010) |
| *Ranunculus, R. acris* complex (Ranunculaceae) | Widespread in Arctic | pDNA/ nrITS | Not specified | All ‘species’ originated in Pleistocene (r8s analysis) | Ebersbach et al. (2017) |
| *Saxifraga* (Saxifragaceae) | Widespread | pDNA/ nrITS | Climate change and oscillations, niche divergence, geographic isolation, hybridisation and polyploidy | Some speciation (BEAST analysis) | Ebersbach et al. (2017) |
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 Ma (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 Dyosoma 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 (Sheen 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** | | | | | |
| Achlys (Berberidaceae), A. triphylla vs. A. japonica | 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) |
| *Aphylion (Orobanchaceae) / *Grindelia (Asteraceae) | Eastern and Western N America | nrDNA | Diversification of Aphylion (parasite) dependent on that in Grindelia (host); glacial cycles also could have contributed to speciation | Considerable speciation in both genera in N America (RevBayes) | Schneider & Moore (2017) |
| *Aquilegia (Ranunculaceae) | N America and Asia | pDNA/nrITS | Habitat and pollinator specialisation | Considerable speciation (BEAST analysis) | Bastida et al. (2010) |
| Ardis (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) |
| Astragalus (Fabaceae) | Utah, N America | nrSNPs | Climatic oscillations and habitat divergence | All three taxa diverged in Pleistocene (Bayeux analysis) | Jones et al. (2021) |
| *Campanula, 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 Chaine et al. (2014) |
| Corex (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) |
| Ceanothus (Rhamnaceae) | California | pDNA/nrITS | Not specified | Some speciation (BEAST analysis combined data) | Orstein et al. (2015) |
| Clematis (Ranunculaceae) | East, West, South USA | pDNA/nrITS | Climate change | Some speciation (BEAST analysis) | Xie et al. (2011) |
| Conilis (Lamiaceae), C. lythritolia vs. C. pycnantha | Mexico | pDNA | Not specified | Species diverged in mid-Pleistocene (BEAST analysis) | Drew & Sytsma (2012) |
| Delphinium (Ranunculaceae) | Western N America | pDNA/nrITS | Not specified | Some speciation (BEAST analysis) | Jabbour & Renner (2012) |
| *Dioon (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); Dobes & Paule (2010) |
| Drymocallis (Rosaceae) | Western USA | pDNA | Not specified | Some speciation (BEAST analysis) | Orstein et al. (2015) |
| *Encelia (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) |
| Ephedra (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); Kaderete et al. (2008) |
| *Eryngium (Apiaceae) | Western N America | pDNA/nrITS | Aridification and polyploidy | Considerable speciation (PL in r8s) | Moazzeni et al. (2014) |
| *Erysimum (Brassicaceae) | Mainly Western N America | nrITS | Not specified | Considerable speciation (BEAST analysis) | Inda et al. (2008) |
| *Festuca (Poaceae) | Widespread | pDNA/nrITS | Climatic oscillation, polyploidy | Considerable speciation (MultiDivineA) | Yao et al. (2021); Schaefer et al. (2012) |
| *Ilex (Aquifoliaceae) | Eastern and SE N America | pDNA/nrDNA | Divergence after dispersal to mesic environments | Some speciation (BEAST analysis) | Brandvain et al. (2014) |
| *Lathyrus, Vicia (Fabaceae: Fabaeae) | USA | pDNA/nrDNA | Not specified | Considerable speciation (BEAST analysis) | Brandvain et al. (2014) |
| Mentzelia (Loasaceae) | Western N America | pDNA | Not specified | Some speciation | Schenk & Hufford (2010) |
| *Mimulus (Phrymaceae) | California | 14,000 nrSNPs | Outcrossing to selfing transition | Budding of M. nasutus from M. guttatus 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 |
|------|--------|---------------------|---------------|----------------------------------------------------|------------|
| Opuntia (Cactaceae) | Western and SW N America | pDNA/nrDNA | Aridification, range expansion, hybridization, allopolyploidy | Some speciation (NPRS) | Majure et al. (2012) |
| *Pediomelum, Rupertia, Pseudastrum, Orbexilum, Hoita (Fabaceae: Pseudastraceae) | Widespread in USA | pDNA/nrDNA | Glaciation-induced climate change | Considerable speciation (BEAST analysis) | Egan & Crandall (2008) |
| *Penstemon (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) |
| *Poa 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) |
| *Populus (Salicaceae), P. balsamifera vs. P. trichocarpa | Boreal and Pacific temperate forests of N America | nrDNA | Climatic oscillation causing geographical isolation | ~0.075 Mya (IM analysis) | Levesen et al. (2012) |
| Saxifraga (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) |
| Stachys (Lamiaceae) | Widespread in N America | pDNA/nrDNA | Not specified | Much speciation (BEAST analysis) | Roy et al. (2013) |
| Viola (Violaceae) | N and Central America | pDNA/nrDNA | Not specified | Some speciation (BEAST analysis) | Marcussen et al. (2012) |
| Yucca (Asparagaceae) | Arid parts of N and Central America | pDNA/AFLPs | Not specified | Some speciation (BEAST analysis) | Smith et al. (2008) |
| Zeltnera (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 kamchatcica in the amphi-Beringian 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 amphi-Atlantic 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 con-
specific 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 evolu-
tion 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 bioge-
ographical 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 oscil-
lating climate of the Quaternary and hypothesised
that much speciation resulted from founder-events
in newly available niches during interglacial periods.
Similarly, for Fabaceae tribe Psoraleeae, a lineage of
five genera and 47 species in North America, Egan
and Crandall (2008) reported that essentially all spec-
ation 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 flower-
ing plant parasite *Aphylion*, also evident in South
America (Schneider and Moore 2017), *Encelia
(Singhal et al. 2021), Opuntia* (Majure et al. 2012)
and *Dion* (Dorsey et al. 2018). In *Dion*, 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 gutta-
tus* 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 (Levens et al. 2012), that
between *Astragalus iselyi* and *A. sabulosus var. sabu-
losus* and var. *vehiculos* near the beginning of the
last glacial (Jones et al. 2021), and that between
*Carex scaparia* 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 remark-
able radiation of *Aquilegia* in North America,
clearly linked to pollinator shifts (Whittall and Hodges
2007), was shown to have taken place lar-
gely in the Quaternary (Bastida et al. 2010). As
*Aquilegia* colonised America in the late Pliocene
when a rich pollinator fauna including humming-
birds 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, Madrínán et al.
(2013) found that 144 of 177 speciation events
occurred in the Quaternary, and postulated that
these resulted largely from range expansion and con-
traction in response to Quaternary climatic oscilla-
tions. 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;
| Taxa | Region | Molecular variation | Drivers of QS | Occurrence in Quaternary (dating method in brackets) | References |
|------|--------|---------------------|---------------|---------------------------------------------------|------------|
| **SOUTH & CENTRAL AMERICA** | | | | | |
| *Abrotanella* (Asteraceae) | Chile, Tierra del Fuego, Falkland Islands | pDNA/ITS | Climate oscillation (glacial/interglacial cycles) | Considerable speciation (NPRS in r8s) | Wagstaff et al. (2006) |
| *Burmeistera, Centropogon, Lobelia, Lysipomia, Siphocamylus* (Craniumaceae) | 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) | Lagomasino et al. (2016) |
| *Andira, Lupinus, Mimosa* (Fabaceae), *Micrololium* (Melastomataceae) | Cerrado, Brazil | pDNA and/or ndDNA | Climatic oscillations, divergent adaptation to fire disturbance | Many species originated from early to late Pleistocene (BEAST analysis) | Simon et al. (2009) |
| Aphyllon (Orobanchaceae)/Grindelia ( Asteraceae) | Eastern and Western South America | nrDNA | Diversification of Aphyllon (parasite) dependent on that in Grindelia (host) | Some speciation in Aphyllon, much more in Grindelia (RevBayes) | Schneider and Moore (2017) |
| *Arapoa* (Plantaginaceae)/Arcytophyllum (Rubiaceae)/Berberis (Berberidaceae)/Calceolaria (Calceolariaeeae)/Draba (Brassicaceae)/Espeletiinae ( Asteraceae)/Festuca (Poaceae)/Lysipomia (Campanulaceae)/Orobanchus (Cyperaceae) | Andes (páramo) | DNA | Climatic oscillations, range expansions and contractions | Many species of these genera originated (BEAST analysis) | Madrínán et al. (2013) |
| *Astralagus* (Fabaceae) | Andes (Ecuador to S Argentina) | pDNA/ndITS | Not specified | Two S American clades diversified from ~1.89 and ~0.98 Mya, respectively (r8s program) | Scherson et al. (2008) |
| *Bartsia* (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) |
| Brownea clade ( Fabaceae)/Brachycylic, Brownea, Ecuadendron, Elizabetha, Macrolobium | Central America and Northern and central South America | pDNA/ndITS | Founder events after orogeny; dispersal and habitat South America | Some speciation within each of these 5 genera (BEAST analysis) | Schley et al. (2018) |
| Conantha (Tecophilaceae) | Mediterranean region of Chile | pDNA | Divergence following establishment of Mediterranean climate in Chile | Some speciation (BEAST analysis) | Buerki et al. (2013) |
| *Costus* (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) |
| *Diplostethium* (Asteraceae) | Costa Rica and N and central Andes | pDNA/mtDNA, nr ribosomal DNA, ndDNA (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) |
| *Epidendrum* (Orchidaceae) | Amazonian and Atlantic forests | pDNA, nrITS, nr genes | Climate shifts causing niche divergence, vicariance and peripheral isolation | All 7 species in *E. latilabre* complex originated (BEAST analysis) | Pessoa et al. (2021) |
| *Eryngium* (Apiaceae) | Widespread in S America (some species in Mexico) | pDNA/ndITS | Aridification and polyploidy | Considerable speciation (PL in r8s) | Kadereit et al. (2008) |
| *Espeletia* (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) |
| *Erythrina* (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) |
| Lathyrus, Vicia (Fabaceae: Fabaeae) | Argentina, Chile, Paraguay | pDNA/nrDNA | Not specified | Considerable speciation (BEAST analysis) | Schaefer et al. (2012) |

(Continued)
| Taxa | Region | Molecular variation | Drivers of QS | Occurrence in Quaternary (dating method in brackets) | References |
|------|--------|---------------------|---------------|------------------------------------------------------|------------|
| *Festuca* (Poaceae) | Widespread | pDNA/nrITS | Climatic oscillation, polyploidy | Considerable speciation (MultidivtimeA) | Inda et al. (2008) |
| *Gentianella* (Gentianaceae) | Andes | nrITS | Availability of newly formed alpine area for colonization | Considerable speciation (K2P distances) | Von Hagen and Kadereit (2001) |
| *Guarea, Heckeldora, Leptolea, Aglaia, Chisocheton, Trichilia* (Meliaceae) | Rainforest | pDNA/nrITS | Climate change possibly | Some speciation in each genus originated (BEAST analysis) | Koenen et al. (2015) |
| *Halenia* (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) |
| *Hordeum* (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) |
| *Hypericum* (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) |
| *Hypochoeris* (Asteraceae) | Mainly Andes | nrITS | Habitat divergence after long-distance dispersal | All 5 American species (~40) originated since ~1.00–0.25 Mya (PL in r8s) | Tremetsberger et al. (2005) |
| *Ilex* (Aquifoliaceae) | Widespread | pDNA/nrDNA | Divergence after dispersal to mesic environments | Some speciation (BEAST analysis) | Yao et al. (2021) |
| *Inga* (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) |
| *Ipomoea* (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) |
| *Lachemilla* (Rosaceae) | Central America cordillera and Andes of S America | pDNA/nrITS | Habitat divergence; hybridisation and polyploidy | Considerable speciation (BEAST analysis) | Morales-Briñes et al. (2018) |
| *Loricaria* (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) | Köål et al. (2016) |
| *Lupinus* (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); Gómez-Gutiérrez et al. (2017) |
| *Oreoibolus* (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) | Longo et al. (2014); Ramos- Fregonezi et al. (2015); Hoffmann et al. (2013) |
| *Petunia* (Solanaceae), *P. integrifolia* ssp. integrifolia vs. ssp. depauperata | 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) | |
| *Poa* and related genera (Poaceae) | Widespread | nrITS | Pliocene cooling enabled adaptation to different habitats in Pleistocene | Considerable speciation (relaxed clock in BEAST) | |
| *Puya* (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) |
Table 5. (Continued).

| Taxa                        | Region                  | Molecular variation | Drivers of QS                                      | Occurrence in Quaternary (dating method in brackets) | References            |
|-----------------------------|-------------------------|---------------------|---------------------------------------------------|-----------------------------------------------------|-----------------------|
| *Ruprechtia* (Polygonaceae), Chaetocalyx, Coursetia, Nissolia (Fabaceae) | 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) |
| Saxifraga (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) |
| *Solanum sect. Lycopersicon* (Solanaceae) | Andes and Galapagos Islands | Whole trans-criptome sequences | New habitats created after climate change and Andean uplift | All 13 species originated (r8s)                         | Roy et al. (2018)      |
| *Stachys* (Lamiaceae)       | Mainly Andes and mountains in Central America | pDNA/nrDNA       | Not specified                                      | Much speciation (BEAST analysis)                      | Roy et al. (2018)      |
| *Tetraglochin* (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) | Salariao 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
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**                     |                               |                    |                                                                                |                                                      |                                |
| *Alchemilla* (Rosaceae)                   | E African high mountains     | pDNA/ nrDNA        | Climatic oscillations causing aridification and niche space expansion           | Dwarf shrub speciation occurred ~1.9–0.5 Mya (RetTime analysis of pDNA) | Gehre et al. (2016)            |
| **Annikia** (Annonaceae)                  | West/Central and E Africa    | nrDNA              | Possibly climatic oscillations                                                 | Some speciation (BEAST analysis)                     | Brée et al. (2020)             |
| **Babiana** (Iridaceae)                   | Greater Cape Floristic Region| pDNA/ nrDNA        | Soil type shifts                                                                | Considerable speciation (BEAST analysis)             | Schnitzler et al. (2011)       |
| **Begonia** (Begoniaceae)                 | Africa /Madagascar           | pDNA/ nrDNA        | Not specified                                                                   | Some speciation (NPRS analysis)                      | Plana et al. (2004)            |
| **Bulbophyllum** (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) |
| **Clematis** (Ranunculaceae)              | S Africa/Madagascar          | pDNA/ nrITS        | Climate change                                                                  | Some speciation (BEAST analysis)                     | Xie et al. (2011)              |
| **Coffee and related genera** (Rubiacae)   | Madagascan and smaller West | pDNA/ nrITS        | Not specified                                                                   | Considerable speciation in some clades (BEAST analysis) | Kainulainen et al. (2017)     |
| **Dianthus** (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)         |
| **Erica** (Ericaceae)                      | S Africa/Cape Floristic Region| pDNA/ nrITS        | Formation of multiple new niches                                               | Considerable speciation (BEAST and RetTime analyses) | Pirie et al.                  |
| **Heliplata** (Brassicaceae)               | Cape Region                   | pDNA/ nrITS        | Aridification, habitat divergence                                              | Speciation from ~5–2 Mya (r8s analysis of ITS)       | Mummenhoff et al. (2005)       |
| **Impatiens** (Balsaminaceae)              | Tropical/subtropical Africa   | pDNA/ nrDNA        | Climatic oscillations causing spatial isolation                                | Considerable speciation (PL in r8s)                   | Janssens et al. (2009)         |
| **Isolana** (Annonaceae)                   | African tropical rain forests | pDNA                | Spatial isolation                                                               | Some speciation (relaxed molecular clock in BEAST)   | Couvreur et al. (2011)         |
| **Ixora** (Rubiacae)                       | Evergreen humid forests in    | 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)             |
| **Lychnis** (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)            |
| **Monodora** (Annonaceae)                  | African tropical rain forests | pDNA                | Climatic oscillations causing spatial isolation                                | Some speciation (relaxed molecular clock in BEAST)   | Couvreur et al. (2011)         |
| **Moraea** (Iridaceae)                     | Greater Cape Floristic Region| pDNA/ nrDNA        | Soil type shifts                                                                | Some speciation (BEAST analysis)                     | Schnitzler et al. (2011)       |
| **Phylaca** (Rhamnaceae)                   | S Africa/Madagascan/         | pDNA/ nrDNA        | Dispersal to and allopatric divergence on islands                               | Speciation from 2 Mya (NPRS of combined data)        | Richardson et al. (2001)       |
| **Picris** (Asteraceae)                    | E Africa, Arabian Peninsula  | pDNA/ nrITS        | Shifts in intrinsic/extrinsic traits; climatic oscillations                     | Considerable speciation (relaxed molecular clock using MCMCTree) | Slovak et al. (2018)           |
| **Piptostigma** (Annonaceae)               | West/Central and E Africa    | nrDNA              | Not specified, possibly due to climatic oscillations                           | Considerable speciation (BEAST analysis)             | Brée et al. (2020)             |
| **Poa** and related genera (Poaceae)       | Widespread                   | nrITS              | Pliocene cooling followed by habitat divergence                                | Considerable speciation (relaxed clock in BEAST)     | Hoffmann et al. (2013)         |
| **Podalyra, Liparia, Amphithasea, Virgilia, Caloprunis** (Fabaceae: Podalyriaceae) | Cape Floristic Region       | pDNA/ nrDNA        | Shifts in fire-survival ability                                                 | Some speciation (BEAST analysis)                     | Schnitzler et al. (2011)       |
| **Protea** (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)         |
| **Psidia** (Asteraceae)                    | Madagascar                    | pDNA/ nrITS        | Climatic oscillations, geographic isolation, habitat divergence                | Considerable speciation (PL in r8s and BEAST analysis) | Strijk et al. (2012)           |
| **Senecio** (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)         |
| **Senecio** (Asteraceae)                   | E African tropical high mountains | nrITS/ nrETS  | Geographical isolation across different mountains                              | Some speciation (BEAST analysis of combined data)    | Kandziora et al. (2016)        |
| **Senecio** (Asteraceae)                   | N Africa                      | AFLPs              | Hybridisation                                                                  | Two polyploid species originated                      | Kaderente 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 Heliphileae 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 Psidia (Strijk et al. 2012), and in a Madagascan 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. brevilflorus 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
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** |        |                     |               |                                                     |            |
| *Abrotanella* (Asteraceae) | New Zealand/ Tasmania | pDNA/ nrITS | Climate oscillations (glacial/interglacial cycles) | Considerable speciation in New Zealand (NPRS in r8s) | Wagstaff et al. (2006) |
| *Brachyglossis* (Asteraceae) and related genera | New Zealand/ Tasmania | pDNA/ nrITS | Habitat divergence | Considerable speciation in New Zealand | Wagstaff and Breitwieser (2004) |
| Cardamine (Brassicaceae) | Australia/ New Zealand | pDNA/ nrITS | Not specified | Some speciation (based on low sequence diversity) | Bleeker et al. (2022a) |
| *Dracophyllum* (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) |
| Eryngium (Apiaceae) | Australia/ New Zealand | pDNA/ nrITS | Aridification | Some speciation (PL in r8s) | Kadereit et al. (2008) |
| *Eucalyptus* | Widespread in Australia | pDNA/ nrITS | Aridification and habitat divergence | Much speciation (PL in r8s on combined data) | Thornhill et al. (2019) |
| *Corymenia* | New Zealand | pDNA/ nrITS | Climate oscillation, polyploidy | Some speciation (MultiDivtimeA) | Inda et al. (2008) |
| *Gentianella* (Gentianaceae) | New Zealand | pDNA/ nrITS | Availability of newly formed large alpine area for colonization | Considerable speciation (K2P distances) | Von Hagen and Kadereit (2001) |
| *Gossypium* sect. Grandicalyx (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) | Seelan et al. (1999) |
| *Lepidium* (Brassicaceae) | Australia/ New Zealand | pDNA/ nrITS | Climate/geological changes causing diversification in habitat preference | All species originated (fossil-based substitution rates) | Mummennhoff et al. (2004) |
| *Myosotis* (Boraginaceae) | New Zealand | nrITS/ AFLPs | Climate oscillations (glacial/interglacial cycles) | Considerable speciation (Maximum Likelihood analysis) | Winkworth et al. (2002), Meudt et al. (2015) |
| *Ourisia* (Plantaginaceae) | New Zealand | nrITS | Climate oscillations, habitat divergence | Considerable speciation from ~0.8 Mya (BEAST analysis) | Meudt et al. (2009) |
| *Pachylodon* (Brassicaceae) | New Zealand | nrDNA | Allopolyploidy | All 10 NZ species originated (BEAST analysis) | Joly et al. (2009) |
| *Picis* (Asteraceae) | E, S and SW Australia | pDNA/ nrITS | Shifts in intrins/ extrinsic traits; climate oscillations | Considerable speciation (relaxed molecular clock method using MCMCTree) | Slovak et al. (2018) |
| *Plantago* (Plantaginaceae) | New Zealand | nrITS | Multiple introductions, mountain uplift, isolation and habitat divergence | All 10 NZ species originated from ~2.29 to 0.30 Mya (BEAST analysis) | Tay et al. (2010) |
| *Poa* (Poaceae) and related genera | Australia/ New Zealand | nrITS | Ploience cooling followed by habitat divergence | Considerable speciation (relaxed clock in BEAST) | Hoffmann et al. (2013) |
| *Ranunculus* (Ranunculaceae) | New Zealand | nrITS | Climate oscillations in Pleistocene | Considerable speciation | Lockhart et al. (2001) |
| *Rorippa* (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) |
| *Triodia* (Poaceae) | Australia/ New Zealand | pDNA/ nrSNPs | Diversification in substrate preference | Nine species in T. basedowii complex originated (BEAST analysis) | Anderson et al. (2019) |
| *Wahlenbergia* (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 (Seelan 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 *Brachyglossis* 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 |                                             |                     |                                                                               |                                                       |                   |
| *Aeonium* alliance (Crassulaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | pDNA/           | Divergence on different islands and habitat divergence                        | Some speciation (MultiDivTime analysis)                | Kim et al. (2008)  |
| *Haplostachys*, *Sideritis*, *Psychotria*, *Lotus*, *Gesnouinia*, *Festuca*, *Cheirolophus*, *Azorina*, *Bidens* (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) |
| *Haplostachys*, *Sideritis*, *Psychotria*, *Lotus*, *Gesnouinia*, *Festuca*, *Cheirolophus*, *Azorina*, *Bidens* (Asteraceae) | Hawaiian Islands | nrITS/           | Divergence on different islands and habitat divergence                        | All species originated (based on biogeographic modelling) | Landsis et al. (2018) |
| *Artemisia* (Asteraceae) | Hawaiian Islands | pDNA/           | Habitat divergence                                                            | Speciation began ~1.45 Mya (BEAST analysis of nrDNA)  | Hobbs and Baldwin (2013) |
| *Bident* (Asteraceae) | Polynesia (Hawaiian, Marquesan, Society, Austral Islands) | pDNA/           | Divergence on different islands and habitat divergence                        | All 41 species originated (BEAST analysis)             | Knope et al. (2020) |
| Azorina, *Campanula*, *Musschia* (Campanulaceae) | Macaronesia (Azores, Cape Verde, Madeira) | pDNA/           | Divergence on different islands and habitat divergence                        | Some speciation (BEAST analysis)                      | Menezes et al. (2017) |
| *Cheirolophus* (Asteraceae) | Macaronesia (Canary Islands)                 | pDNA/           | Divergence on different islands and habitat divergence                        | All species originated (Based on BEAST analysis)      | Vitales et al. (2014) |
| *Crambe* (Brassicaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | nrITS/           | Divergence on different islands and habitat divergence                        | Some speciation (MultiDivTime analysis)                | Kim et al. (2008)  |
| *Echium* (Boraginaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | pDNA/           | Divergence on different islands and habitat divergence                        | Some speciation (MultiDivTime analysis)                | Kim et al. (2008)  |
| *Festuca* (Poaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | pDNA/           | Climatic oscillation, polyploidy                                               | Some speciation                                       | Inda et al. (2008) |
| *Gesnouinia* (Urticaceae) | Macaronesia (Canary Islands)                 | pDNA/           | Climatic oscillations                                                          | Two endemic species diverged in Pleistocene (BEAST analysis) | Schüller et al. (2019) |
| *Limonium* (Plumbaginaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | pDNA/           | Divergence on different islands and habitat divergence                        | Considerable speciation (ML in RAxML, Bayesian Inference in MrBayes) | Koutroumpa et al. (2021) |
| *Lotus* (Fabaceae) | Macaronesia (Canary Islands, Azores, Madeira, Cape Verde) | pDNA/           | Divergence on different islands and habitat divergence                        | Considerable speciation (BEAST analysis)              | Jaén-Molina et al. (2021) |
| *Melicope* (Rutaceae) | Indian/Pacific Ocean: Mascarene Islands, Polynesia (especially Hawaiian Islands) | pDNA/           | Wider ecological niches, bird-dispersal, geographic isolation                 | Considerable speciation (BEAST analysis)              | Appelhans et al. (2018) |
| *Metrosideros* (Myrtaceae) | Hawaiian Islands                            | nrITS/           | Not specified                                                                   | All species originated since ~1 Mya (based on age of sub-fossils and islands) | Wright et al. (2001) |
| *Oxera* (Lamiaceae) | New Caledonia                                | pDNA/           | Habitat isolation and divergence                                              | Considerable speciation (BEAST analyses)             | Barrabé et al. (2019) |
| *Pericallis* (Asteraceae) | Macaronesia (Canary Islands, Azores, Madeira) | pDNA/           | Divergence on different islands and habitat divergence                        | Considerable speciation (BEAST analyses)             | Jones et al. (2014) |
| *Psidium* (Asteraceae) | Mascarene Islands (Mauritius, Reunion, Rodrigues) | pDNA/           | Geographical isolation and habitat divergence                                 | Considerable speciation (PL in r8s and BEAST analyses) | Strijk et al. (2012) |
| *Psychotria* (Rubiaceae) | New Caledonia                                | pDNA/           | Spatial isolation                                                              | Considerable speciation (BEAST analysis)              | Barrabé et al. (2014) |
| *Scalesia* (Asteraceae) | Galapagos Islands                            | pDNA/           | Habitat divergence within islands and some divergence between islands          | All 15 species originated since ~0.74–0.63 Mya (BEAST analysis) | Fernández-Mazeucos et al. (2020) |
| Sideritis (Lamiaceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | nrITS/           | Divergence on different islands and habitat divergence                        | Some speciation (MultiDivTime analysis)                | Kim et al. (2008)  |
| *Sancohus* (Asteraceae) | Macaronesia (Canary Islands, Madeira, Cape Verde) | nrITS/           | Divergence on different islands and habitat divergence                        | Some speciation (MultiDivTime analysis)                | Kim et al. (2008)  |
| *Haplostachys*, *Phyllostegia*, *Stenogyn* (Lamiaceae: Stachhydeae) | Hawaiian Islands                            | pDNA/           | 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 (Pelser 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 divaricate 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 it 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: *Argyroxyphium 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 – *Argyroxyphium/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, *Psidia* (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 *Convulvulus* 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 *Psidia* 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 Nevada 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 interspecific 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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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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