EVOLUTION
Die Buche als
Art-Mosaik

MIKROBIOLOGIE
Mikrobiom trifft
Nervensystem

BOTANIK
Neophyten in
Deutschland

BIOLOGIE
IN UNSERER ZEIT

Artenschutz in Sambia

The beech, a Eurasian species mosaic
Bastards everywhere*

E. D. Schulze | G. W. Grimm

Beech forest in Iran, photographed in 2018 near the town of Amol, Mazandaran Province. The trunk height is up to 50 m, the diameter at breast height up to two meters. Noteworthy is the epiphytic growth of mosses and lichens on the smooth bark.
Photo: Mohammad Vatanparast (University of Copenhagen).

Ever since the European Beech has been declared a UNESCO Natural Heritage Site, it has a special status as a deciduous tree in Germany. A genetic analysis of beech evolution shows that the eight current-day beech species were closely interconnected via wind pollination until the Pleistocene, with pollen flow enabling gene exchange over long distances.

Thus, modern beeches are closely intertwined hybrids. The most ancestral population of Fagus sylvatica *sensu lato, is the Iranian beech, which today belongs to the eastern European* Fagus orientalis*. The Iranian beech and not the central European beech is the real genetic resource in terms of biodiversity conservation.*

Terms marked with a green arrow are explained in the glossary on page.

The diversity of ➤·species (Box SPECIES CONCEPTS) is generally seen as the result of ➤·dichotomous evolution: A predecessor species splits into two new species. The underlying model is the phylogenetic tree ('species tree') that keeps branching out, the 'Tree of Life'. Especially in the case of wind-pollinated genera, this model reaches its limits: Species arise and perish in the interplay of gene exchange (➤ gene flow) and isolation (➤ gene drift). Pollen, and thus the paternal gene variants, are transported in the atmosphere and enabling long-range genetic exchange, especially between species. In course of ➤ hybridization, the ovule, the carrier of the maternal gene variants, is pollinated in the flower by the pollen of another species. So-called ➤ "F1 hybrids" (bastards) are formed. These hybrids are either infertile, hybrid larches for example, or fertile as in oaks, corn, and sycamores (plane trees). New 'hybrid species' can arise [1] propagating both parental genomes to future generations. Plants can overcome genomic incompatibility by the so-called "allopolyploidisation". The parental genomes are fused

and stabilized in the hybrid, allowing for normal cell division and sexual reproduction [2]. Plant hybrids are often characterized by increased vigour (➤ heterosis) and the ability to interbreed with one or both parent species (e.g., cultivated, hybrid 'London Plane', and the naturally occurring 'Oriental Plane'). The hybrid competitively replaces the parent species, but carries on their ➤ genotypes.

In principle, interspecific gene exchange is also possible in insect-pollinated plants, provided that the parent species grow geographically close enough to each other, i.e. can be reached by the same pollinator. Species formation in the genus *Sorbus* (whitebeams, rowans, etc.) would be an example of this [3]. If managed appropriately, several species of *Sorbus* occur in the same stand (e.g., coppice forest) and this promotes hybridization between species that are ➤ phylogenetically very close. In the case of wind pollination, geographically extensive gene exchange can occur, so-called ➤ "introgression": genes from one species are passed to another.

* English translation by DeepL, edited by the authors

SPECIES CONCEPTS

Species diversity is typically determined by the number of species that occur in an area. It is assumed that species represent "natural", stable, and biologically generally definable units. However, it is often overlooked that not all species are the same.

a) In current botanical practice, Carl von Linné's phenotypical species concept is still largely applied: Species are determined on the basis of anatomical and morphological differences (in the picture: circles, stars with different numbers of points, pentagons).
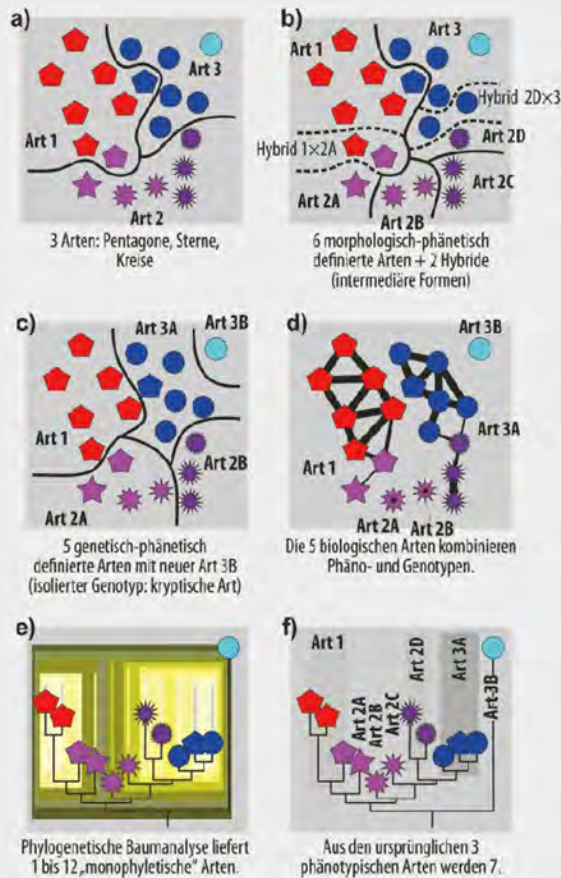
b) The subsequent phenetic species concept defines species based on general similarity without consideration of evolutionary relationships (phylogenetic relationships), e.g. by recording morphometric data (in the example: number and size of tips).

c) Today, the phenetic species concept (see above) is mainly applied to microorganisms in the form of the x % rule: if gene variants (represented by colour shades in the picture) differ by more than e.g. 3 %, they are counted as species [17].

d) In addition, there is Ernst Mayr's biological species concept, which is popular in zoology but hardly applicable to plants: A species is defined by interfertile populations.

e) The cladistic (or phylogenetic) species concept, which is based on the ideas of Willi Hennig, is hardly used, but frequently promoted: Species are defined by inferring a rooted phylogenetic tree under the assumption that each subtree (clade) [18] represents a so-called "monophyletic" group: a group of populations comprising all descendants of the same, exclusive to them, ancestor.

f) Since the cladistic species concept only recognizes nested hierarchies, but does not provide criteria for when a subtree is to be described as a species, it is not applicable in practise. Phylogenetic trees are therefore mainly used to verify and refine already existing phenotypic-phenetic or biological/ genotypic-phenetic species concepts.

a) 3 Arten: Pentagone, Sterne, Kreise

b) 6 morphologisch-phänetisch definierte Arten + 2 Hybride (intermediäre Formen)

c) 5 genetisch-phänetisch definierte Arten mit neuer Art 3B (isolierter Genotyp; kryptische Art)

d) Die 5 biologischen Arten kombinieren Phäno- und Genotypen.

e) Phylogenetische Baumanalyse liefert 1 bis 12 „monophyletische" Arten.

f) Aus den ursprünglichen 3 phänotypischen Arten werden 7.

In addition to introgression and hybridization, genetic mixing can also occur via back-crosses with the parent species. The extant species are products of a ➤ phylogenetic network, the so-called ➤ "reticulate" evolution. They do not represent a species tree, but a 'species coral'. A model for this form of evolution are the beech trees (genus *Fagus*).

The recent beech species are genetic ➤ mosaics [4], end products of different, intertwining lineages whose origins date back to the early Tertiary, the Paleogene. The 'European Beech' in a broader sense, *Fagus sylvatica* sensu lato, with its subspecies *orientalis*, the 'Oriental Beech', is an aggregate of two to four beech species living geographically separated today, in which at least three genetic lineages converge. One of the lineages is dominant in the > 6500 km away Japanese sister species, the 'Japanese Beech' or 'Buna' (from Japanese; also known as 'Siebold's Beech'), *Fagus crenata*. The European Beech sensu stricto has, in addition, gene variants of North American origin: evidence for introgression in the Miocene. The phylogenetic diversity in the genome of the European Beech is probably the basis for its success and its dominance over other forest trees across Europe.

Wind pollination and species

The development of an insect-pollinated flower is the key innovation in the evolution of the flowering plants, the angiosperms. Nevertheless, wind pollination is found, which dominates in the gymnosperms until today, also in some groups of the angiosperms. Especially the grasses,

IN BRIEF

– As a wind-pollinating plant genus, beech is a **prime example of so-called "reticulate" evolution**. Species arise and perish in an interplay of gene exchange (gene flow via pollen flow) and isolation (gene drift via the geographically stationary ovule).

– Gene transfer (introgression) between populations and species plays just as important a role as species fusion (hybridisation, allopolyploidisation). **Genetically** heterogeneous **species**, so-called "genetic mosaics", form.

– In contrast to the polymorphic nuclear genome, the **maternally inherited chloroplasts** are mainly subject to gene drift. They are only passed on locally via seeds and primarily show the geographical history of the mother populations and species complexes.

– Today's beech species carry in certain chromosomal segments the genetic heritage of about 50 million years (since the early Tertiary) of reticulate evolution. **They form a species network**, a "species coral", and not a species tree.
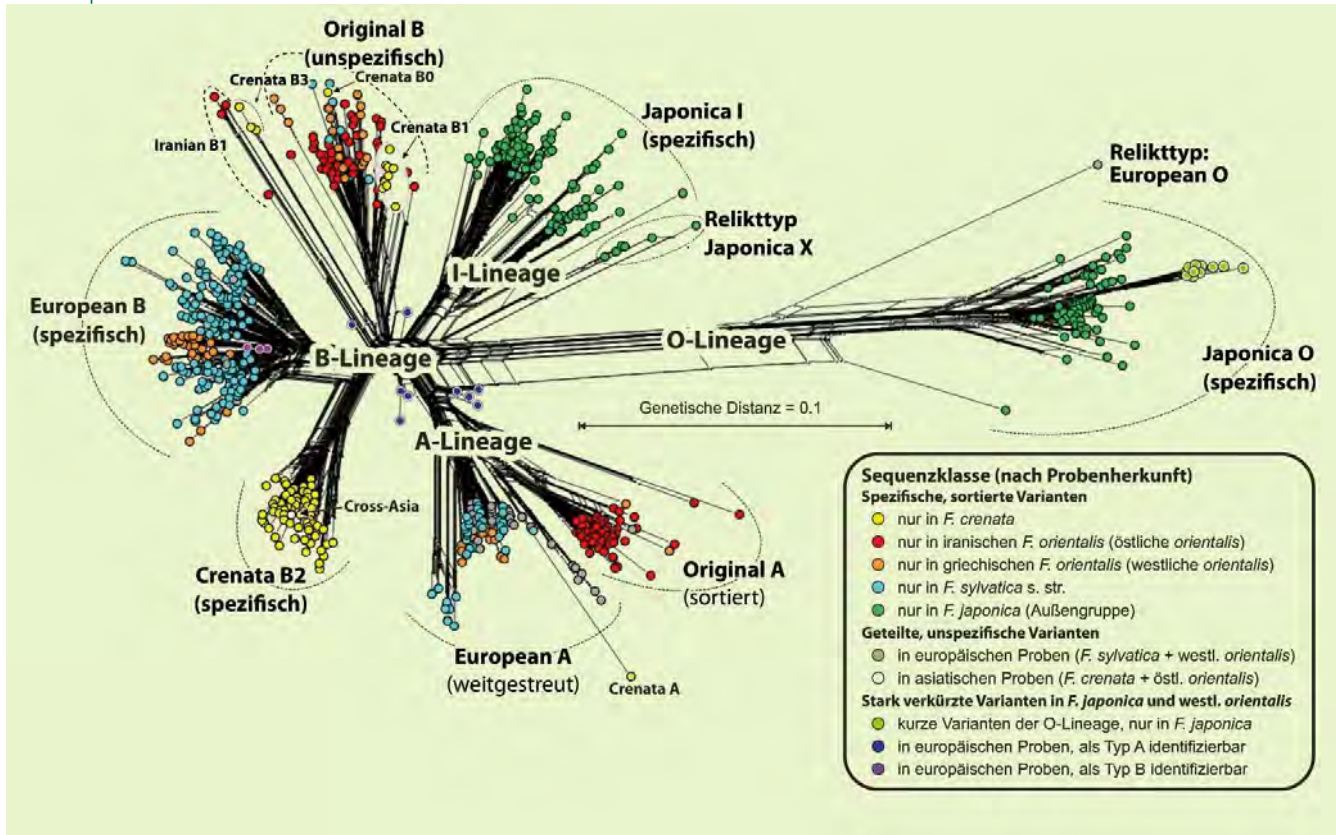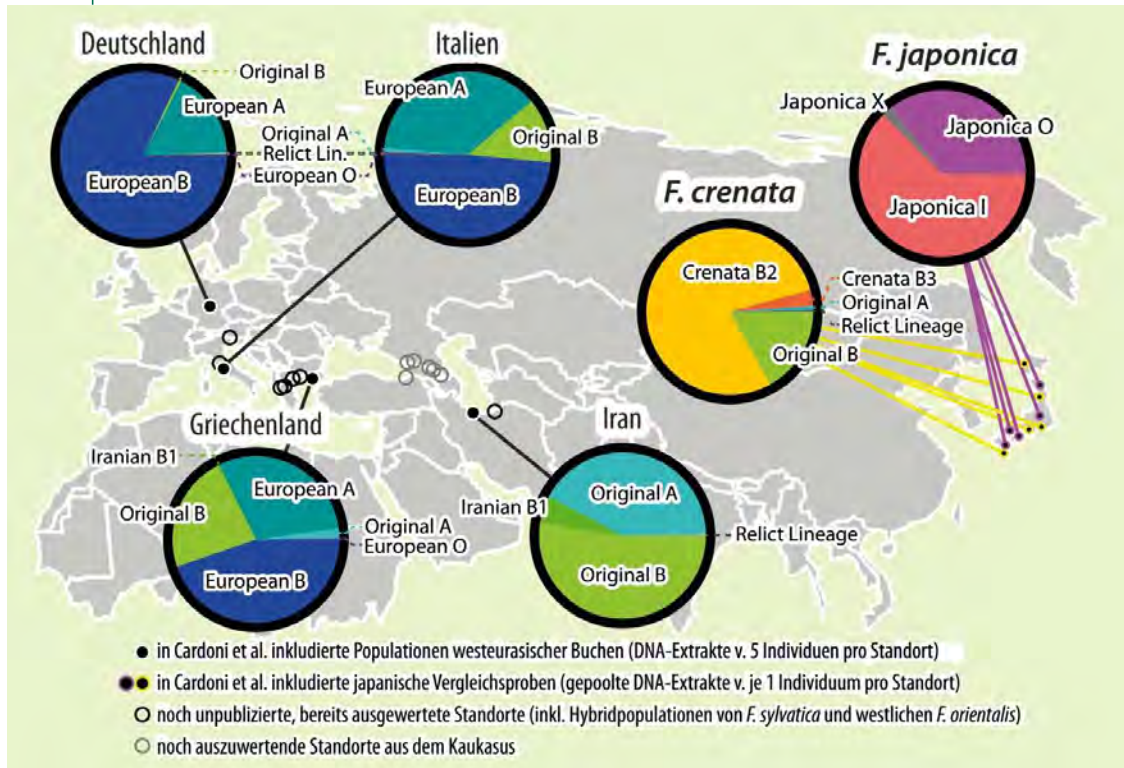
The figure shows a so-called "neighbor-net splits graph" of 686 5S-IGS sequence variants with a minimum detection frequency of 25, colour-coded according to origin (sampled species and locations) and specificity. Graphic from [4], translated into German.

part of the monocotyledons, are known as a lineage that changed back to wind pollination very early in the Tertiary. Within the "Rosidae", the large group of rose-like plants including many native European tree genera the Fagales (beech relatives) are known for many wind-pollinated genera. The beech relatives include the widespread genera *Juglans* (walnut), *Alnus* (alder), *Betula* (birch), *Carpinus* (hornbeam), *Corylus* (hazelnut), *Quercus* (oak) and *Fagus* (beech). With the exception of birch and alder, the beech relatives usually have fairly large fruits that are dispersed regionally over relatively short distances, primarily by winter-stockpiling jays (sedentary birds) and small mammals. In contrast, wind pollination allows gene exchange via pollen, dispersed over a wide area. The pollen interconnects species, while the ovule preserves the local genome of the parent species. Gene flow by wind pollination, introgression, is therefore mostly asymmetric, i.e. genes introgress from species A to species B, but not from species B to species A. Pollen flow, thus the direction of gene flow, is determined by the prevailing wind direction during the flowering season in spring. The female flowers

are located at the ends of the branches and effectively trap pollen from the main air flow. The size of the mother plants is hence an important factor in linking pollen flow to atmospheric flow. European Beech (*Fagus sylvatica*), Oriental Beech (*F. orientalis* s. l.), and their Japanese sister species (*Fagus crenata*), grow over 40 m tall. Their pollen is carried over more than 1000 km [5], and even at great distances some pollen retain their fertility. Under such conditions, the isolation of a population, i.e. speciation, depends on a low connection to atmospheric circulation (wind-protected locations). Another factor contributing to ➤ species stabilisation is population size and distance between populations. The closer the beech sites are to each other, the higher the homogenisation between populations and species (introgression, hybridisation). Thus, single individuals of the co-occurring (➤ sympatric) Chinese species *F. longipetiolata* and *F. lucida* show gene variants that are typical for the other species [4, 6].

Shown is the composition of the 5S-IGS gene pool in Japanese and West Eurasian beech samples. The pie charts indicate the overall proportional composition by phylogenetic groups (lineages). In contrast to Figure 1, the colours here indicate the major variants, the 5S-IGS lineages, and their subtypes. Included are all variants found by Cardoni et al [4] with a minimum frequency of 4; in total 145,643 sequence 'reads' split into 4,693 different variants. Figure language: German.

Analogies can be found especially in widespread gymnosperms. 'Scots Pine' (*Pinus sylvestris*) is a species for which pollen dispersal has been recorded across the Atlantic Ocean and whose range in Eurasia extends from the Atlantic to the Pacific Ocean. Its distribution area lies in the main flow of the Westerlies, a global wind system. This has certainly contributed to the homogenisation of the species. A similar pattern is found in the Arctic 'Dwarf Birch' (*Betula nana*). Although this species is more of a shrub species, it grows in the open landscape of bogs and is therefore connected to atmospheric flow, albeit differently than forest trees. In addition, birches are not only wind-pollinated, but also wind-dispersed. In contrast to pines and birches, oaks have been divided into hundreds of species [7], especially in North America. This high species number is possibly related to their generally lower tree height than in beeches, pollen morphology, ecological adaptability, and more regional circulation in Mediterranean climates and low latitudes. Between these extremes are the beech trees, which have a very low number of species (8 species in classical floras; considering genetic differentiation, there are 13–14 species). On a global scale, there are large gaps between the species (Atlantic Ocean, Central Asia, western North America). Even disjunct species can show high morphological similarities over large distances, as in the case of the European Beech and Siebold's Beech (6,500 km air-distance). They differ mainly in leaf shape and margin, as well as their overall morphological variability [8]. In the following, we will sketch the evolution of these species and the genus *Fagus* across Eurasia, based mostly on the work of Cardoni et al [4] and the literature cited there.

The studies of Cardoni et al [4] and Jiang et al [6] were made possible by modern sequencing methods the so-called "next generation sequencing" or "NGS". Cardoni et al. focused on a specific nuclear ➤ gene locus known for its ability to conserve intragenomic variability: the spacers of ➤ 5S rDNA (5S-IGS), non-coding nucleotide sequences between 5S rRNA genes [9]. Jiang et al. "fished" 28 nuclear gene regions from the nuclear genome. In this case, the selection of genes is random: computer algorithms filter potential ➤ homologs from thousands of gene snippets, which are then collected and compared. Both data sets show a high degree of admixture and genetic patterns that can only be explained by secondary contact and gene flow between species, i.e. introgression and hybridisation.
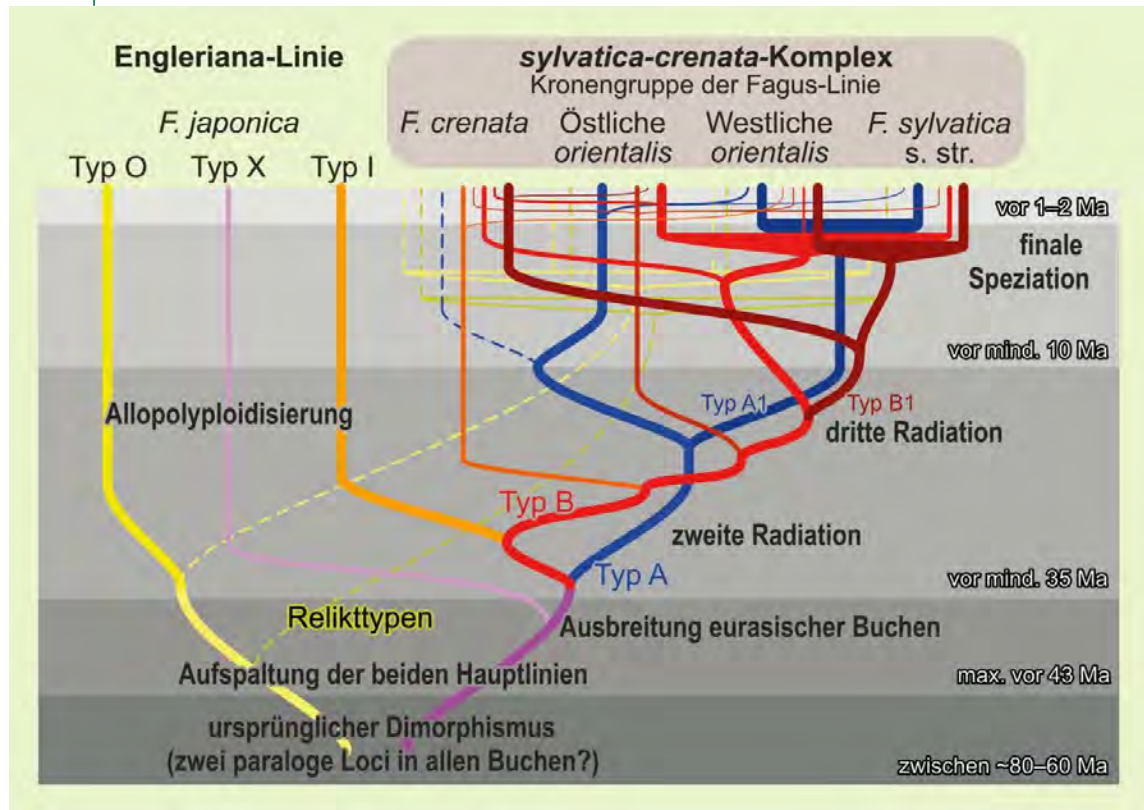
The coloured lines indicate the respective evolutionary lineages within the 5S-IGS sequence variants found. The coexistence of three distinct ancient lineages with different origins in *Fagus japonica* indicates an early allopolyploidisation event. The complex pattern in the subgenus Fagus crown group (*sylvatica-crenata* complex) is the result of sorting, homogenisation, and primary and secondary ➤ gene exchange. Graphic after [4], translated into German.

A genetic potpourri

the complex relationships and connectivity of the *sylvatica-crenata*-complex can be visualized by a network-based similarity analysis of the 5S-IGS variants found (Fig. 1). In the genome arrays of 5S rRNA, one can identify different genetic lineages (➤ phylogenetic lineage). The A and B lineages represent the major types in the *sylvatica-crenata* complex; I (➤ 'ingroup'), O (➤ 'outgroup'), and X (unknown origin) show the corresponding variants in the second Japanese species, *F. japonica* ('Dog' or 'Black Buna'), a distant relative. These lineages represent groups of spacer variants that can be traced back to a specific basic sequence type, the same primordial sequence, i.e. represent a so-called "common origin". All species studied show an admixture of different lineages (Figure 2).

The two Japanese species, *F. crenata* and *F. japonica*, belong to two different evolutionary lineages (informal subgenera) that were already separated in the late Eocene, at least 43 million years ago (➤ Ma: Mega-annum). In the network, this is reflected by a high genetic distance.

However, *F. japonica*, a member of 'subgenus Engleriana' (China, Korea, Japan), is by no means homogeneous. One lineage, the "I lineage" is clearly more similar to the *sylvatica-crenata* complex than the other main lineage, the "O lineage". The third lineage, the "X lineage", lives a shadow existence next to the two main variants (Figure 2). This indicates that the last common ancestor of both subgenera, the ➤ 'last common ancestor' or 'LCA' of all present-day beeches, was already the product of a reticulate speciation process (hybridisation with allopolyploidisation). *Fagus crenata* also shows remnants of interspecific mixing, especially with the European beeches in a broader sense (*F. sylvatica* s. l.). Among the European beeches, the Iranian beech, the 'Eastern *F. orientalis*', is distinguished from the European Beech, *F. sylvatica* s. str. and the Greek, 'Western' *F. orientalis*. In all western Eurasian beeches variants of two main lineages – the "A lineage" and "B lineage" – are found but to varying degrees: B-variants dominate over A-variants in the European Beech, whereas A- and B-variants are equally represented in Iranian beeches, the Eastern *F. orientalis*.

FIG. 4 | "SPECIES CORAL" OF THE GENUS *FAGUS*
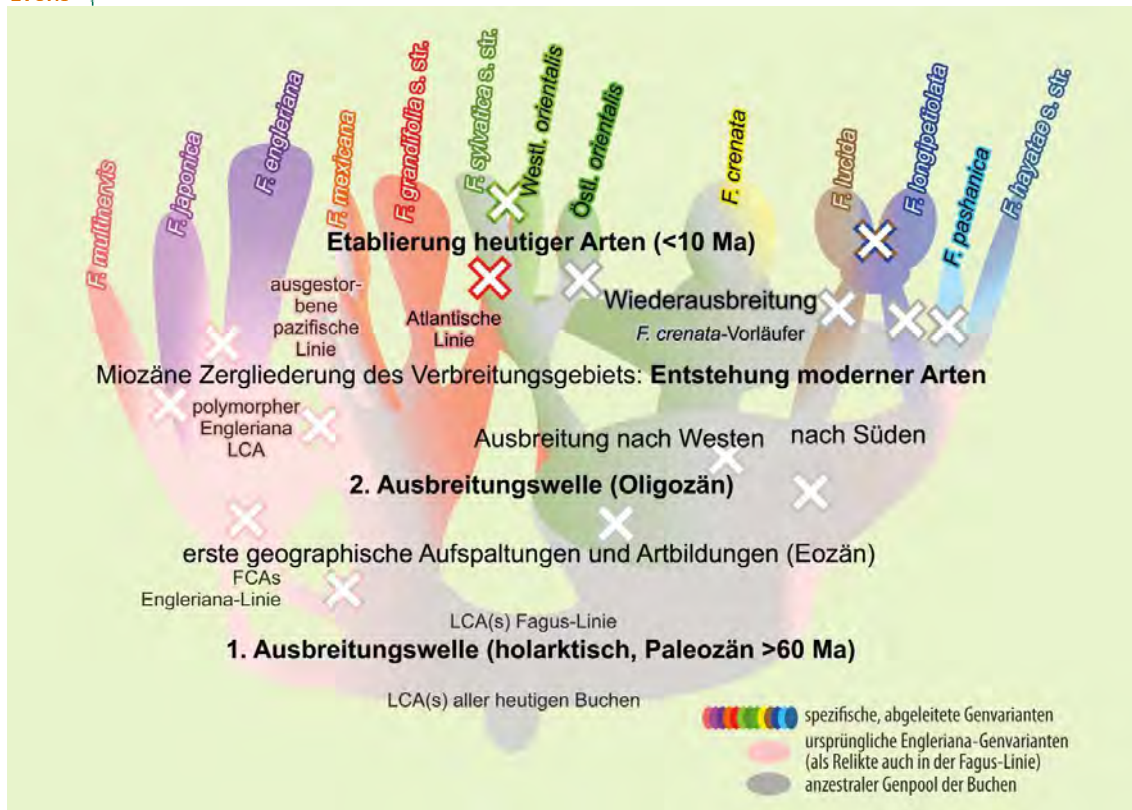
Not a species tree, but a "species coral" describes the evolution of beech trees culminating in today's species. Abbreviation: FCA = first common ancestor; LCA = last common ancestor; × = interspecific gene flow/ anastomoses (introgression or hybridisation). Graphic after Data S1, Fig. S21, in the supplement to [4], translated into German.

Furthermore, the proportion of specific B-variants within the European beeches increases from east (Greek *F. orientalis*) to west (Greek and Italian *F. sylvatica*) and north (German *F. sylvatica*) (Fig. 2).

Polymorphic beginnings

Taking into account other evidence, such as the historical (fossil) distribution of the ancestors of today's beeches, the distribution of the distinct genetic lineages among the different beech species can be traced back in space and time (Figure 3). The separation of the A, B, I, O and X lineages corresponds to phases in which genetic drift due to isolation and local adaptation must have been much stronger than gene exchange between populations and sister species. The accumulation of different 5S-IGS lineages in one species or population can only be explained by a reticulate evolution, a species network, in which hybridisation is the rule rather than the exception. The ancestors of *F. japonica* – and thus probably of the entire subgenus Engleriana – were also ➤ polymorphic, i.e. the product of hybridisation, probably allopolyploid

speciation. The gene data suggest that one of the subgenus Engleriana ancestors was derived from the subgenus Fagus lineage (I-lineage variants). The O-lineage-like relict variants in all samples of the *sylvatica-crenata* complex show that there was also gene flow between the early representatives of these two subgenera. Although nowadays geographically and morphologically separated, these species have exchanged genetic material until the recent past. Accordingly, it is difficult to separate these species by any molecular marker (genomic sequences) so far studied (Fig. 4).

Populations of the last common ancestor (LCA) of the *sylvatica-crenata* complex were presumably part of *F. castaneifolia*—a fossil species that was widespread across Eurasia during the Oligocene (Fig. 5). With a west-east distribution of 6000 km, genetic differentiation must have already been present at the time of its disintegration. In western Eurasia, *F. castaneifolia was* successively replaced by a new ➤ phenotype, *F. haidingeri* (Fig. 6), a transition coinciding with the formation of *F. palaeocrenata* and others in northeast Asia [10].
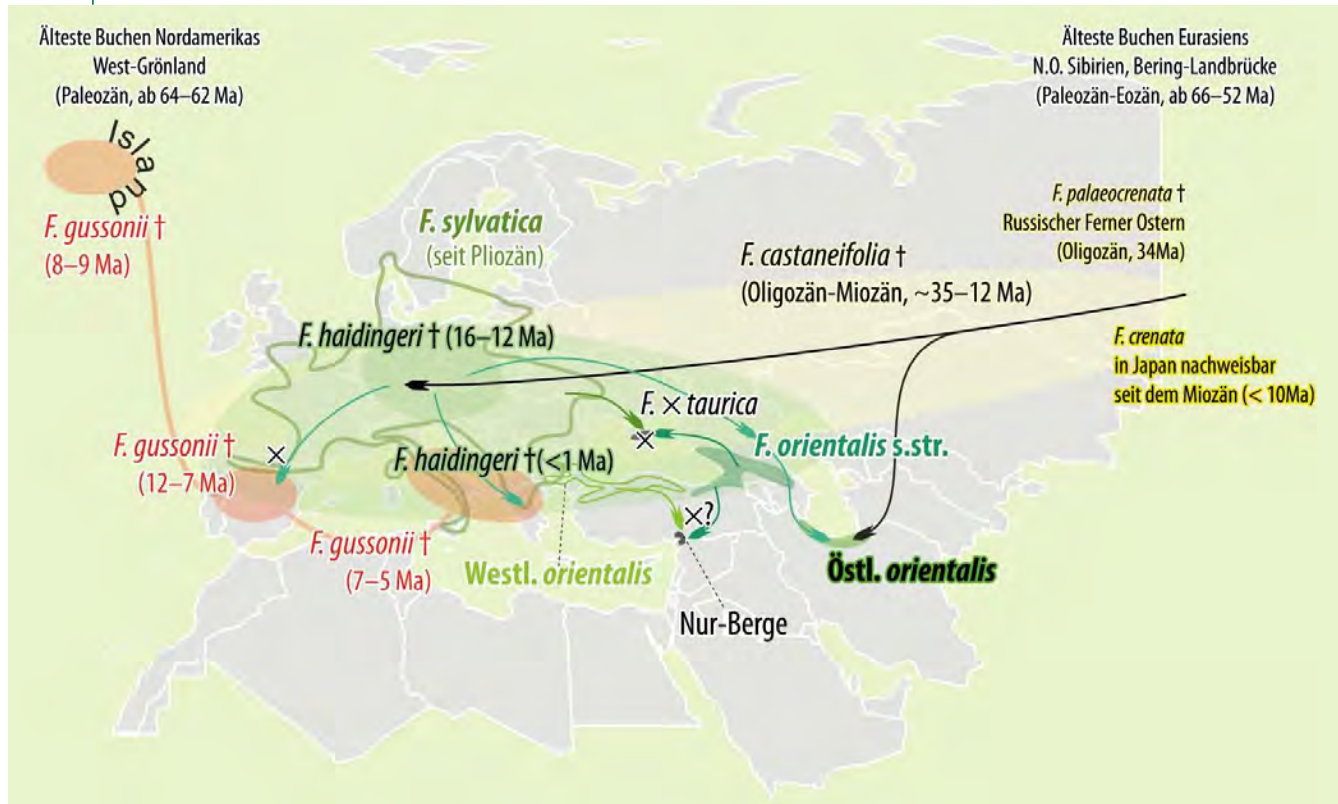
Recent distribution (following [11]) **of the genus** *Fagus* **in western Eurasia in direct comparison with the precursors of today's beeches** [10, 12]. **Yellow to green hues represent the evolutionary lineage of the European Beech in the broader sense (***F. sylvatica*** s.l.).** *Fagus gussonii* **is a fossil form representing the easternmost offshoot of the New World beeches (red colour, see Fig. 4). The Crimean beech,** *F. x taurica*, **may be of hybrid origin, formed by glacial contact between European** *F. sylvatica* **s.str. and the Caucasian** *F. orientalis* **s.str.** [15]. Figure language: German.

Together, these fossil species are the direct ancestors of the modern species *F. sylvatica*, Western *F. orientalis*, Eastern *F. orientalis,* and *F. crenata.* New World genetic material entered the *F. haidingeri* populations via the North Atlantic Land Bridge (Icelandic-Mediterranean *F. gussonii* fossils) [4]: In the course of its dispersal to the southwest, *F. haidingeri* took over parts of the Iberian-Mediterranean *F. gussonii.* Their remnants, re-presented by the Icelandic populations, became extinct during the global cooling at the end of the Miocene (~8 Ma). Their genetic heritage survived in the direct ancestors of European beeches. Meanwhile, in East Asia, admixture occurred between the ancestors of *F. crenata* and the continental Asian species. The pronounced plastome polymorphism in the genomes of the two present-day Japanese species [11] suggests numerous secondary species contacts in north-eastern Asia.

50 million years of networked evolution

Molecular dating, taking into account known fossils [12], has shown that beech trees had already divided into three main lineages by the Eocene, i.e. 50–45 million years ago: the two (informal) subgenera Engleriana and Fagus, and the separation of the latter into New World and Old World beeches. Morphologically, the subgenus Engleriana becomes recognizable about 35 million years ago at the end of the Eocene. Since the Oligocene, gene flow between both subgenera is improbable. They exist sympatrically in north-eastern Asia and can be clearly separated morphologically. To date, there is no evidence of ongoing or recent gene exchange (using specific nuclear markers) between Engleriana and Fagus species in China (*F. engleriana* ↔ *F. longipetiolata, F. lucida, F. pashanica*) or Japan (*F. japonica* ↔ *F. crenata*). Gene flow between the north-east Asian and west-Eurasian populations of the *sylvatica-crenata* complex ceased about 15–10 million years ago when Siberia became too cold and too dry

as the central Asian mountain ranges, especially the Qinghai-Tibet Plateau, continued to rise [13]. In this regard, the present Iranian population is closest to the genetic core area of the *sylvatica-crenata* LCA. *Fagus crenata* contains hardly any remnants of the A lineage, which still characterizes the Iranian beeches, the Eastern *F. orientalis* (Fig. 2). Regarding the Convention on Biological Diversity (CBD) effort to conserve biodiversity, it is important to realize that Iranian, Eastern *F. orientalis*, turns out to be the actual European natural heritage in the *sylvatica-crenata* complex.

The dynamics of speciation that occurred in the western range is expressed by different A and B sublineages in the data of Cardoni et al [4], or genetic polymorphism in the data of Jiang et al [6] (Fig. 4). In course of ongoing speciation processes, the gene pool has been increasingly fragmented: New B-types emerge (in the European species) that are no longer propagated into the Iranian populations, the easternmost species. It is notable in this context that still in the Pliocene to the beginning of the Pleistocene of Europe, one can find the morphologically more primitive parent(s) of *F. sylvatica*, *F. haidingeri* phenotypes. The progenitor species (one or more) occur contemporaneously with modern forms (*F. sylvatica* s. str.), which successively replace their ancestors (Fig. 5).

FIG. 6 | EVOLUTION OF THE LEAF MORPHOLOGIES OF THE WEST EURASIAN BEECHES SINCE THE OLIGOCENE
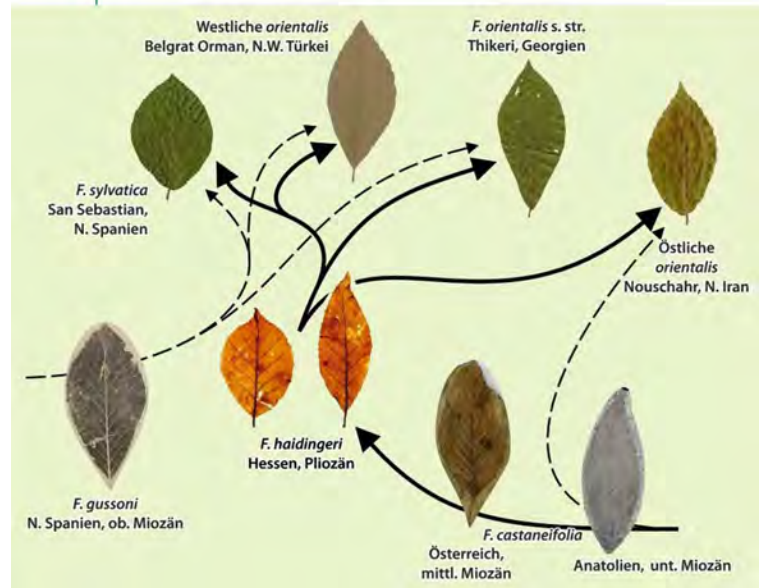
The arrows indicate the evolutionary pathways and inter-species relationships, taking into account today's genetic differentiation patterns (cf. Fig. 5). Leaf photos provided by Thomas Denk (Naturhistoriska riksmuseet, Stockholm). Figure language: German.

FIG. 7 | DICHOTOMOUS VERSUS RETICULATE EVOLUTION
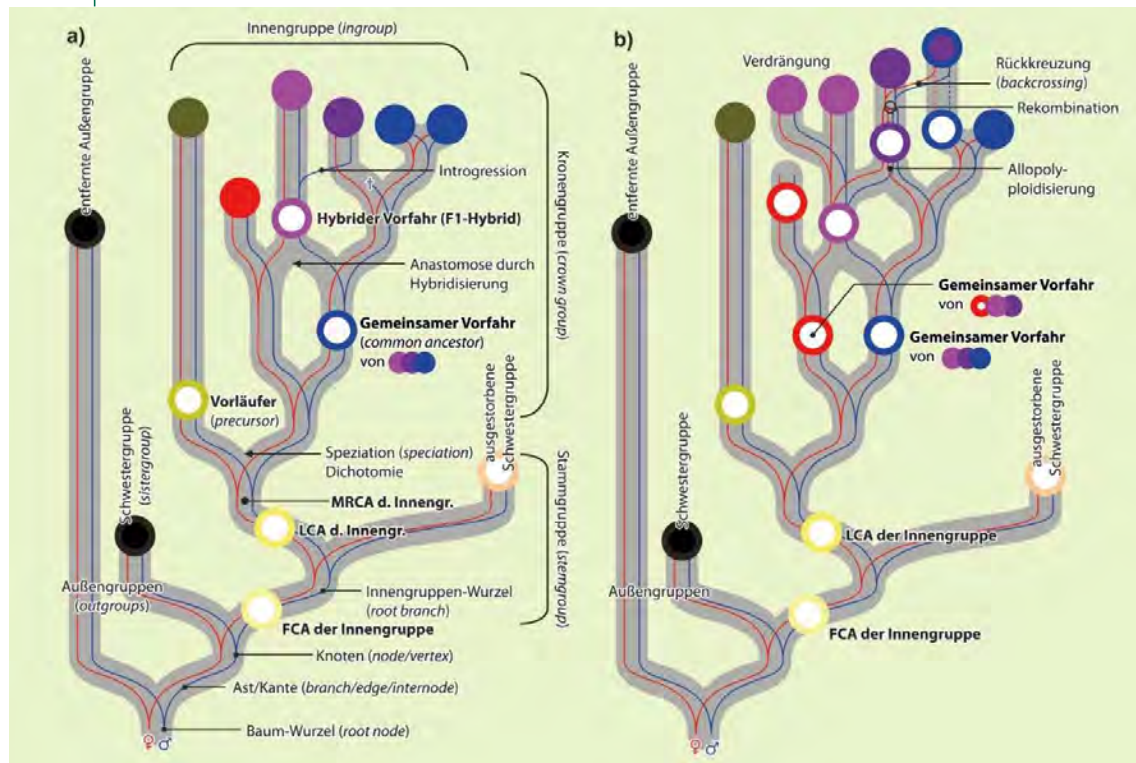
a) Hybridisation without heterosis effect. b) Hybridisation with heterosis effects ("*hybrid vigor*"): The hybrids (purple) displace or take over the donor species (red, blue). Open circles: extinct species/ organisms (including ancestors), closed circles: species/ organisms still occurring today. Figure language: German.

5S rDNA: *The genes of the 5S rRNA, the 5S rDNA, are – like the genes of the other ribosomal subunits (18S, 5.8S, and 25S or 28S rRNA) – encoded in the nuclear genome as tandems; in the case of angiosperms and vertebrates, the (usually identical) gene copies are each separated by noncoding spacers (***5S-IGS*** or ***5S-NTS***). For the genetics, phylogeny-information content, sequence variability and function of nuclear rDNA and its spacers, see [9]. In the only beech studied so far, two* paralogous *(→ homologous) 5S loci (→* locus*) could be detected per chromosome set [24].*

Allopolyploidisation: *In plants, a widespread form of hybrid speciation in which the nuclear genomes of the parent species ("donors") are fused. Allopolyploid species (e.g. tobacco) carry different gene copies (→ polymorphism) of the original donors; however, these can be at least partially lost again (or 'silenced') through genome reorganization (Figure 7b).*

Species: *defined here as a group of related individuals/ populations characterized by morphological and/or genetic traits [21, 22] (→ Box Species Concepts).*

Species stabilisation: *A process, often complex and incomplete in plants, in which intra-species gene flow ensures the homogenisation of the gene pool of a species, while gene drift in combination with reticulate evolution (inter-species gene flow) leads to its heterogenisation (mosaicism, polymorphism).*

Outgroup *and* **Ingroup**: *Phylogenetics mostly rely on rooted phylogenetic trees. The root of the ingroup subtree is defined by adding one (better: many) outgroup(s) – more or less distantly related species of sister genera etc. – into the phylogenetic analysis (see also Fig. 7).*

Clade: *In phylogenetic tree analysis, the general term for a sub-tree in a rooted tree [18], defined by an* **edge** *(term from graph theory) or* **branch** *(→ phylogenetics; Fig. 7). Clades often, but not always, represent monophyletic (holophyletic) systematic groups (also called "clades", in biological systematics, → Cladistics).*

Dichotomous evolution: *the splitting of a parent species/ lineage into two daughter species/ lineages (Fig. 7); basis of most phylogenetic analysis. See also reticulate evolution.*

F1 hybrid: *First generation of bastardisation (hybridisation) of two species (Fig. 7a). Well-known examples are the 'Grolar Bear', fertile F1 hybrids of polar bears and grizzlies, two bear species (genus* Ursus*), and the mule, a F1 hybrid of horse and donkey (genus* Equus*) which cannot reproduce (is infertile).*

Gene exchange, primary ↔ secondary: *New sequence variants of highly variable gene segments are primarily exchanged between neighbouring populations of a species, or during the splitting process, speciation or species divergence. If related, already isolated species come into contact through (re-)dispersal, secondary gene exchange may occur (hybridisation, introgression).*

Gene drift: *In a specific, population-genetic sense: the (random) change in the frequencies of paternal and maternal gene variants (alleles) in populations. In a general, phylogenetic context: the (random) accumulation of unique genetic traits within populations, species, species complexes, and evolutionary lineages. Often a consequence of geographic isolation and small population size.*

Gene flow: *Gene exchange between populations ("inbreeding"), species and evolutionary lineages ("outbreeding"; introgression, hybridization), e.g. through immigration or emigration of individuals.*

Gene locus *(pl.:* **loci***): The position of a gene segment on a chromosome. If a gene is present in different loci, it is called a* **paralog***. Apart from a few exceptions, paralogs differ in their function.* **Orthologs** *are genes of the same locus and the same function (***homologs***; → homologous).*

Genotype: *In the general sense: the totality of the genes (genome) of an individual, or the genomes of a species or evolutionary lineage; in genetics: a particular genome variant, gene combination.*

Heterosis (hybrid vigour): *refers to the higher vigour and productivity of heterozygous and hybrid organisms; generalizes to the higher evolutionary fitness of hybrid species (Fig. 7b), ecotypes, and populations, respectively (e.g., [25]).*

Homologous *(opposite:* **paralogous***): In phylogenetics, genes that are descended from a common ancestor (ancestral gene). In genetics, term for genes with the same function (cf.* locus*).*

Hybridization: *In evolution, mixing of phylogenetic lineages by crossing different parent species; hybrids (F1 hybrid) or hybrid species are often characterized by intermediate phenotypes and mixed (paternal plus maternal alleles) genotypes (allopolyploids) (Fig. 7).*

Introgression: *Mostly asymmetric gene flow from one species into another (Figure 7); process in reticulate evolution. As in hybridization, intermediate phenotypes and mixed genotypes or new combinations of geno- and phenotypes may occur.*

Cladistics: *A currently dominant philosophical school within phylogenetic systematics, going back to Willi Hennig, according to which only those taxa are valid and may be named that can be traced back to a single, exclusive common ancestor (i.e. an inclusive [!] common origin): the so-called "monophyla" or "holophyla" (→ Box Species Concepts).*

Cryptic speciation: *Species that are reproductively largely isolated and therefore genetically clearly separable, but share the same phenotypes. Examples are* Fagus hayatae ↔ F. pashanica*;* F. engleriana ↔ F. multinervis*;* Acer campestre *(Field Maple)* ↔ A. orthocampestre *(Caucasian Field Maple). Not to be confused with* **pseudocryptic species:** *species with similar or overlapping phenotypes recognized on the basis of genetic data (Ex.: currently four species of giraffes; or* F. sylvatica *[s.str.]* ↔ Western F. orientalis ↔ Eastern F. orientalis *(→ Box How many species of beech are there worldwide?).*

LCA—last common ancestor *(see also Fig. 7): The last progenitor, from which all present species of a phylogenetic lineage have evolved or can be derived. Time-wise close to but not identical with the* **MRCA** *(***most recent common ancestor***), a hypothetical construct of phylogenetic tree analysis. The counterpart of the LCA is the* **FCA** *(***first common ancestor***), the ancestor of all present and extinct species of an evolutionary lineage (kin group).*

Ma (rarely: **MA**): Abbreviation for one million (mega-) years (lat.: annum) used especially in palaeontology and stratigraphy. Other common abbreviations are **MYA** (also: **MA**) for "million years ago", in contrast to **myr/myrs** for "million years", as an indication of a time span. 1000 years are abbreviated accordingly as **ka** (kilo-annum).

Monophylum: Term introduced by Ernst Haeckel [26] for a group of organisms with a common ancestry, i.e. members of the same phylogenetic lineage. In contrast to **polyphylum**: group of similar organisms belonging to different evolutionary lineages. In a narrower sense (→ cladistics) synonym to **holophylum** [27], a group of organisms comprising all descendants of a common ancestor; in contrast to **paraphylum**: group of organisms comprising only some of the descendants of a common ancestor. A clade in a computed rooted phylogenetic tree is often a necessary (cladistics) but rarely a sufficient criterion for holophyly.

Mosaic: describes in genetics and phylogenetics a special state of genetic polymorphism, in which several gene or phylogenetic lineages converge in one organism. Genetic mosaics are the natural consequence of reticular evolution.

Phenotype: the physical (anatomical-morphological) appearance of an organism, to this day the basis of most accepted species (Box SPECIES CONCEPTS). A "good" species is characterized by a high correlation (coherence) between phenotype(s) and genotype(s) [21]. In plants, the phenotype is partly determined by the genotype, partly by site/environmental parameters (keywords: gene expression, epigenetics). If genetically clearly isolated species cannot be separated phenotypically, they are referred to as cryptic species.

Phylogenetics: A subdiscipline of biology developed in the 19th century (e.g. Charles Darwin, Albert Gaudry, Franz Hilgendorf), which deals with the evolutionary history (phylogeny) of organisms and the relationships between species or other biological units (so-called "taxa"). The terms "phylogeny", "monophyletic" and "polyphyletic" are attributed to Ernst Haeckel [26]. Often erroneously [18] treated in synonymy with cladistics, the dominant school within phylogenetic-biological systematics in the 2nd half of the 20th century (Willi Hennig, Norman Platnick, Steve Farris).

Phylogenetic tree: The standard model of phylogenetics is the **species tree**, in which there are no anastomoses (mergers of species/lineages) or reticulations (gene flow between species; see also dichotomous evolution). The possibly first known phylogenetic (species) tree is found in Hilgendorf's 1863 dissertation. In the same paper, Hilgendorf also conceptualized a first phylogenetic network [28]. The first numerical (calculated, inferred) phylogenetic tree was published 94 years later by Charles Michener and Robert Sokal [29].

Phylogenetic lineage: In phylogenetics, a commonly used term for a kin group (species, genera, etc.; genes and their sequence variants) in an evolutionary context that can be traced back to a common ancestor (monophylum). In cladistics synonymous with clade/holophylum or a subunit thereof.

Phylogenetic network: Any phylogenetic graph (reconstruction) showing anastomoses and linkages; a generalisation of the phylogenetic tree. The simplest phylogenetic networks consist of dichotomous splits and anastomoses, e.g., as a result of introgression and hybridisation (Fig. 7). The metaphor for the resulting **species network** is the **coral** (keyword: Coral of Life, https://en.wikipedia.org/wiki/Coral_of_life).

Polymorphism: In genetics, the umbrella term for any form of genetic variation within a genome, population or species (→ mosaic). Genetic polymorphism is the basis for heterosis effects.

Sympatric: Species occurring in the same area are sympatric. In plants, allopolyploidization as a result of hybridization can lead to sympatric speciation, as can the temporal dissociation of flowering time or pollen flight between populations. In contrast, **allopatric speciation** is caused by gene drift due to geographic and reproductive isolation.

Subtree: Part of a tree graph (keyword: graph theory); in phylogeny defined by an **edge** (also: **internode**) in the phylogenetic tree. In rooted phylogenetic trees synonymous with clade; the ingroup corresponds to the subtree defined by the ingroup root (Figure 7a).

Reticulate evolution: includes all mechanisms of non-dichotomous speciation and evolutionary processes: Allopolyploidization, hybridization, introgression (Fig. 7); reticulate evolution can only be visualised and summarised by a species network.

HOW MANY SPECIES OF BEECHES ARE THERE WORLDWIDE?

If we regard species as a group of populations that can be recognized and diagnosed as belonging together [21], there are not only 8 but up to 14 beech species worldwide.

*In the case of the West-Eurasian beeches (*F. sylvatica s.l.*), the eastern representatives, the Iranian* F. orientalis, *represents a distinct species (= Eastern* F. orientalis*) that can be characterized morphologically and genetically, i.e. represents a so-called* ➢ *"pseudo-cryptic" species. Another species are probably the Caucasian beeches (*F. orientalis *s.str.), possibly also the beeches of the Nur Mountains in south-eastern Turkey [15, 23]. The Western* F. orientalis *(NE Greece, SE Bulgaria, NW. Turkey) may either be treated as a subspecies of* F. sylvatica *s.str. or as a sister species.*

The Mexican relict beeches, F. grandifolia *subsp.* mexicana, *represent a similar borderline case: Their unique leaf morphology is probably triggered by environmental factors. However, their polymorphic nuclear genomes typically comprise ancestral gene variants lost in the genomes of their widespread sister,* F. grandifolia *s.str., which is not threatened with extinction [4,6]. If the populations were to come back into contact, they would most likely fused and eventually become a homogeneous species again.*

In contrast, F. hayatae *s.l. (including subsp.* pashanica*) and* F. engleriana-F. multinervis *are examples of* ➢ *cryptic speciation: The two respective (sub)species, previously defined purely based on their geography, are clearly separated genetically, but morphologically indistinguishable.*

If one assesses the current species concept of beech, its species diversity is probably underestimated in North America and ignored in western Eurasia (split-up of F. sylvatica *and the different lineages of* F. orientalis*), while in East Asia, the species represent biological units of different quality. Notably, all beech species studied so far show a generally higher intraspecific diversity than most other tree species of the temperate zone.*

The separation of *F. sylvatica* (s. str.) from the Western *F. orientalis* (SE Europe, NW Turkey) began about 1–2 million years ago [14]. Looking into the future, in view of global warming, the Oriental beeches, the 3–4 species collected in *F. orientalis*, seem to have greater chances also in Central Europe [16]. They could replace *F. sylvatica in the* short term. There are forestry trials that have already been carried out to test the success of the more heat-loving and, in some cases, more drought-resistant oriental Oriental beeches. However, if a new ice age were to come, *F. sylvatica* would disappear, except for remnants on the (southeastern) Balkans, or (re)merge with its sister species, the Western F. orientalis. As the most pristine relict of the species (or species) that once covered the entire Parathethys and Europe, the Iranian Eastern *F. orientalis* and presumably also the Caucasian *F. orientalis* s.str. populations represent the actual genetic resource.

Summary

Beech trees - a Eurasian mosaic of species

Beech (genus Fagus*) is one of the best-known deciduous trees in the northern hemisphere. On the basis of numerous fossils, its history can be traced back to the Late Cretaceous period (c. 80 million years ago). Possibly because of its complex genetics and only a few accepted species, it has remained largely unnoticed by systematists and phylogeneticists. At the same time however, it is the key model for reticulate evolution, a common phenomenon in plant speciation. Species emerge and disappear (become extinct) due to the interaction of gene flow and gene drift. In the course of this process, genetic material is exchanged between species. Current species are the product of a dynamic past which was influenced by global processes such as tectonics and climate change. As a result, the nuclear and plastid genomes of current beech species carry diverse traces of earlier interspecific contacts (hybridisation). They are genetic mosaics reflecting the dynamic history of their genus. This article summarizes the newest insights into the complex, highly reticulate evolution of beech species in Europe and Asia.*

Literature

[1] J. Mallet (2008). Hybridization, ecological races, and the nature of species: empirical evidence for the ease of speciation. Phil. Trans. Roy. Soc. London B 363, 2971-2986.

[2] R. A. Volkov et al. (2017). Evolutional dynamics of 45S and 5S ribosomal DNA in ancient allohexaploid Atropa belladonna. BMC Plant Biol. 17, Doc. No. 21 [EPubl.]

[3] Federal Agency for Nature Conservation (2018). Red list of endangered animals, plants and fungi of Germany. Naturschutz Biol. Vielfalt Heft 10, Band 7: 1-778.

[4] S. Cardoni et al. (2022). 5SIGS rDNA in windpollinated trees (*Fagus* L.) encapsulates 55 million years of reticulate evolution and hybrid origins of modern species, The Plant J. 109: 909-926.

[5] H. Zwander (1997). Studies on pollen dispersal in the open landscape. Carinthia II 187, 423-445.

[6] L. Jiang et al. (2021). Phylogeny and biogeography of *Fagus* (Fagaceae) based on 28 nuclear single/lowcopy loci. J. Syst. Evol. DOI:10.1111/jse.12695.

[7] A. L. Hipp et al. (2020). Genomic landscape of the global oak phylogeny. New Phyt. 226, 1198-1212.

[8] T. Denk, B. Meller (2001) Systematic significance of the cupule/nut complex in living and fossil *Fagus*. Int. J. Plant Sci. 162, 869-897.

[9] V. Hemleben et al. (2022). Personal perspectives on plant ribosomal RNA genes research: from precursorrRNA to molecular evolution. Front. Plant Sci. 12, Doc. No. 3027 [EPubl.]

[10] T. Denk and G. W. Grimm (2009). The biogeographic history of beech trees. Rev. Palaeobot. Palynol. 158, 83-100.

[11] J. R. P. Worth et al. (2021). Chloroplast genome sequencing reveals complex patterns of ancient and recent chloroplast sharing in Japanese *Fagus*. Presentation. *ResearchGate* DOI:10.13140/ RG.2.2.10679.24485.

[12] S. S. Renner et al. (2016). Species relationships and divergence times in beeches: new insights from the inclusion of 53 young and old fossils in a birthdeath clock model, Phil. Trans. Roy. Soc. B 371, Doc. No. 20150135 [EPubl.].

[13] C. R. Scotese, A. J. Boucot, C. Xu (2014). Atlas of Phanerozoic climatic zones (Mollweide Projection), Volumes 16. PALEOMAP Project PaleoAtlas for ArcGIS. PALEOMAP Project, Evanston, IL

[14] D. Gömöry et al. (2018). Phylogeny of beech in western Eurasia as inferred by approximate Bayesian computation. Acta Soc. Bot. Poloniae 87, doc. No. 3582 [EPubl.]

[15] D. Gömöry, L. Paule (2010). Reticulate evolution patterns in western Eurasian beeches, Bot. Helv. 120, 63-74.

[16] D. Dagtekin et al. (2020). Past, present and future distributions of Oriental beech (*Fagus orientalis*) under climate change projections. PLoS ONE 15, Doc. No. e0242280 [EPubl.].

[17] E. Stackebrandt, B. M. Goebel (1994). Taxonomic note: a place for DNADNA reassociation and 16S rRNA sequence analysis in the present species definition in bacteriology. Int. J. Syst. Bacteriol. 44, 846-849.

[18] J. Felsenstein (2004). Inferring phylogenies. Sinauer Associates Inc, Sunderland, MA.

[19] T. A. C. Reydon, W. Kunz (2019). Species as natural entities, instrumental units and ranked taxa: new perspectives on the grouping and ranking problems. Biol. J. Linn. Soc 126, 623-636.

[20] J. Mallet (2010). Why was Darwin's view of species rejected by twentieth century biologists? Biol. Philos. 25, 497-527.

[21] J. Mallet (1995). A species definition for the Modern Synthesis, Trends Ecol. Evol. 10, 294-299.

[22] J. Mallet (2001). The speciation revolution. J. Evol. Biol. 14, 887-888.

[23] T. Denk (1999). The taxonomy of *Fagus* in western Eurasia, 1: *Fagus sylvatica* subsp. *orientalis* (*F. orientalis*). Feddes Repert. 110, 177-200.

[24] T. Ribeiro et al. (2011). Evolution of rDNA FISH patterns in the Fagaceae. Tree Genet. Genomes 7, 1113-1122.

[25] B. M. Fitzpatrick, H. B. Shaffer (2007). Hybrid vigor between native and introduced salamanders raises new challenges for conservation. Proc. Natl. Acad. Sci. 104, 15793-15798.

[26] E. Haeckel (1866). General Morphology of Organisms. Georg Reiner, Berlin.

[27] P. D. Ashlock (1971). Monophyly and associated terms. Syst. Zool. 20, 63-69.

[28] D. A. Morrison (2016). Genealogies: pedigrees and phylogenies are reticulating networks not just divergent trees. Evol. Biol. 43, 456-473.

[29] C. D. Michener, R. R. Sokal (1957). A quantitative approach to a problem in classification. Evolution 11, 130-162.

Internet addresses

– Peter Stevens' *Angiosperm Phylogeny Website*, a comprehensive collection of all research on the evolution and phylogeny of flowering plants (angiosperms): https://www.mobot.org/mobot/research/

– Tree as a graph-theoretic concept: https://de.wikipedia.org/wiki/Tree_(graph-theory)

– Christopher Earle's *The Gymnosperm Database*, the data and knowledge bank for conifers and other gymnosperms: https://www.conifers.org/

– *Global Biodiversity Information Facility* collects location data on all plants and animals: https://www.gbif.org/

– *Genealogical World of Phylogenetic Networks*, scientific blog (currently inactive) initiated by David Morrison around phylogenetic networks and methods including their history up to Charles Darwin: https://phylonetworks.blogspot.com/

– *Tree of Life* webpage, summarizing the Tree of Life based on numerous phylogenetic (mostly cladistic) tree analyses: http://tolweb.org/tree/phylogeny.html

– Who is Who in Phylogenetic Networks by Phillipe Gambette and collaborators collects literature, research activities, and computer programs related to the topic of phylogenetic networks: https://phylnet.univmlv.fr/

– All technical terms used in this article (see glossary) and species mentioned can also be looked up on the German and English Wikipedia.

– Data and image access via *figshare* (reusable via Creative Commons license CCBY):
   https://doi.org/10.6084/m9.figshare.16803481
   https://doi.org/10.6084/m9.figshare.11603547

More blogposts

Further blogposts with diagrams by G. Grimm (freely reusable under CCBY license) and D. Morrison on the topic

– The first Darwinian evolutionary tree https://phylonetworks.blogspot.com/2013/06/the-first-darwinian-evolutionary-tree.html

– The challenging and puzzling ordinary beech - a (hi)story https://researchinpeace.blogspot.com/2018/04/the-challenging-and-puzzling-ordinary.html

– Cladistics vs Phylogenetics: What's the difference? https://researchinpeace.blogspot.com/2018/11/cladistics-vs-phylogenetics-whats.html

– Can we depict the evolution of highly conserved genes, such as the ribosomal RNA genes: https://phylonetworks.blogspot.com/2019/02/can-we-depict-evolution-of-highly.html

– A fully resolved, and perfectly misleading, species tree: https://researchinpeace.blogspot.com/2021/09/a-fully-resolved-and-perfectly.html

– Monophyletic species: https://researchinpeace.blogspot.com/2021/12/monophyletic-species.html

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