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Review

Prunus Movement Across the Silk Road: An Integrated Evolutionary and Breeding Analysis

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Abstract: In the past, the Silk Road was a vital trade route that spanned Eurasia, connecting East Asia to the Mediterranean Sea. The genus *Prunus*, belonging to the Rosaceae family and encompassing plums, peaches, apricots, cherries, and almonds, thrived as human travel along the Silk Road increased. The majority of fruits within this genus, whether wild or cultivated, are naturally sweet and easily preserved by drying for storage and transport. The interaction along the Silk Road between wild populations and diverse varieties of *Prunus* fruits led to the development of various hybrids. This article provides a summary of archaeological findings related to prominent *Prunus* fruits such as peaches, apricots, plums, cherries, and almonds, shedding light on their evolutionary history, genetic diversity, population structure, and historical dynamics crucial for species conservation. The origins of biodiversity may involve factors like migration of pre-adapted lineages, in situ variation, or the persistence of ancestral lineages. Furthermore, climate change is affecting spatial genetic patterns and potentially further threatening rare *Prunus* species. Evaluating the scope and composition of genetic diversity within germplasm collections is essential for enhancing plant breeding initiatives and preserving genetic resources in this changing context. From a molecular point of view, techniques such as genome-wide association studies (GWASs) and the identification of quantitative trait loci (QTLs) and genes responsible for phenotypic changes in cultivars and germplasm collections should be of great interest in these breeding programs, while genomic estimated breeding values (GEBVs) derived from genome-wide DNA polymorphism information can facilitate the selection of superior genotypes.

Keywords: Silk Road; *Prunus*; diversity; domestication; breeding; interspecific hybridization; genetic structure; genomic; transcriptomic

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1. Introduction

In ancient times, the Silk Road was the name given to the road that traversed through the heart of Eurasia, linking East Asia and the Mediterranean (Figure 1). This area is now referred to as Central Eurasia or Central Asia and includes the modern countries of China, Afghanistan, Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan, and Turkmenistan. Along this path, we envision caravans of heavily laden camels trekking across grasslands, deserts, and mountain passes, making stops at oasis towns where bustling markets offered an array of silks and spices [1].

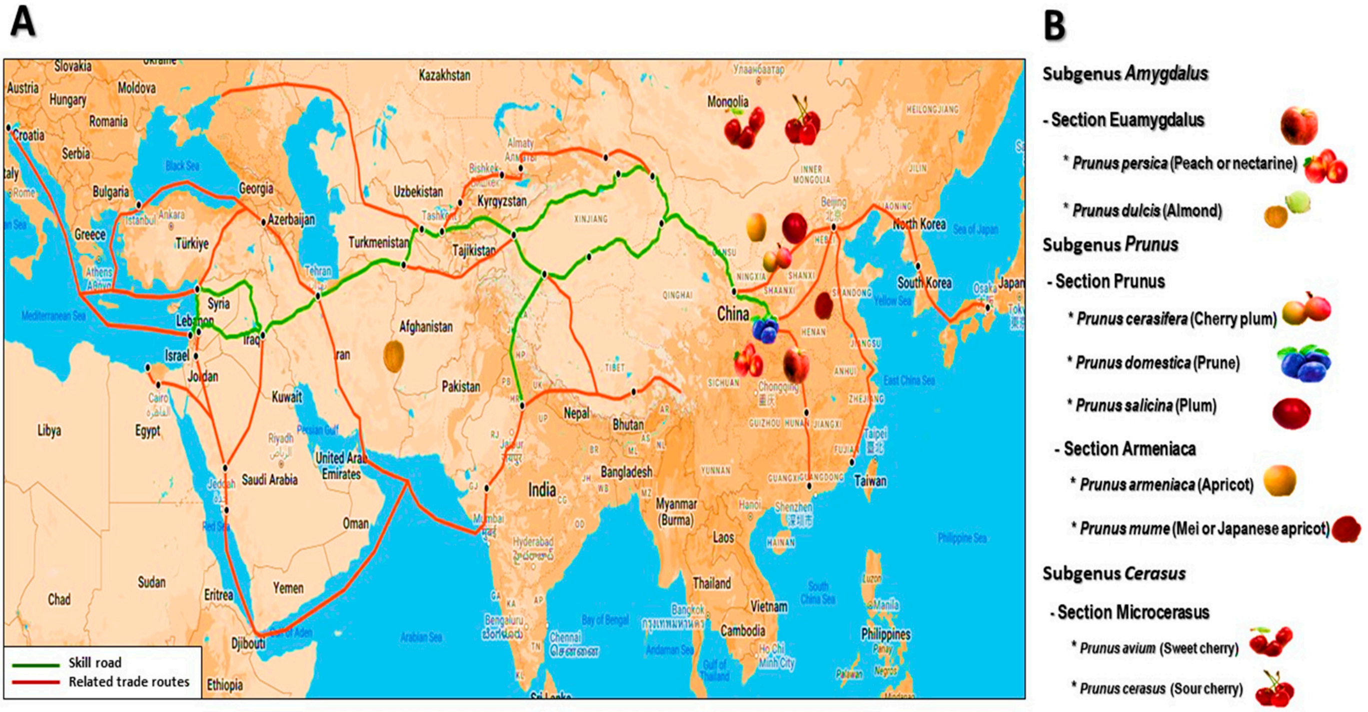

Figure 1. Map of Silk Road and other related trade routes in the Middle Ages indicating the geographic origin of the most cultivated *Prunus* species, including peaches and nectarines, plums and prunes, apricots, almonds and cherries (**A**), and the taxonomy of theses cultivated species inside the genus *Prunus* (**B**).

The term "Silk Road" is closely associated with the expanding economic interactions that connected societies in Central Asia to a geographically wider sphere [2]. The trade routes of the Silk Road traversed Asian mountain ranges, facilitating the movement of not only people and metal goods but also a diverse array of plants and commodities [3–5]. Much of this contact relied on high-elevation mountain valleys, often linking towns and caravanserais through alpine territories. This cultural exchange is thought to have reached a peak in the late first millennium A.D., and these exchange networks fostered the spread of domesticated plants and animals across Eurasia. Ancient accounts from Central Asia provide evidence of flourishing medieval urban markets and the extensive trade routes that facilitated their growth [2]. For instance, during his travels in Khorezm from 1130 to 1155, Abu Hamid al-Andalusi Gharanti marveled at the superior quality of the fruits there, stating that he had never seen anything like them in all his previous journeys [6]. Similarly, Nuruddin Mohammad Jahangir (1627–1569) described the cultivation of peaches, melons, apples, rice, millet, and exceptionally sweet apricots near Samarkand. Al-Jahiz, in a manuscript from the late first millennium, detailed the trade in luxury goods imported into the Abbasid capital of Baghdad, highlighting fresh and dried fruits as prominent and luxurious commercial commodities [7]. Existing documents also mention the importance of dry fruit exchange and explain that some people paid their taxes with dried fruits and nuts. Archaeological evidence also supports these written accounts by revealing the widespread transportation of fruits and nuts, as well as the utilization of various cultivated crops in medieval Central Asian cuisines [2].

Species of the genus *Prunus* are typically 5-merous flowering trees and shrubs with a single carpel, a fleshy mesocarp, and a hard endocarp containing a single seed [8]. While major stone fruit species originated from Asia or Europe, they have now spread worldwide and can be found on every continent except Antarctica, among both individuals and commercial producers [9]. *Prunus* is a commercially important fruit tree genus that includes popular diploid stone fruit trees like peach (*Prunus persica* Batsch) (2n = 2x = 16), apricot (*Prunus armeniaca* L.) (2n = 2x = 16), sweet cherry (*Prunus avium* L.) (2n = 2x = 16), Japanese plum (*Prunus salicina* Lindl.) (2n = 2x = 16), Japanese apricot (*Prunus mume*) (2n = 2x = 16), and almond [*Prunus dulcis* (Mill.) D. A. Webb.] (2n = 2x = 16), as well as tetraploid *Prunus cerasus* L. (2n = 4x = 32) and hexaploid European plum (*Prunus domestica* L.) (2n = 6x = 48) [10]. The main species of *Prunus* were introduced to the West in ancient times but were domesticated in Central and Eastern Asia [8]. Subsequently, species originated in Iran, Greece, Turkey, India, and China. Fruit cultures in Greece and Rome had reached a highly developed level by the Classical period [9].

This is the current taxonomic classification of *Prunus:*
Kingdom: *Plantae*
Division: *Spermatophyta*
Subdivision: *Angiospermae*
Class: *Magnoliopsida*
Order: *Rosales*
Family: *Rosaceae*
Subfamily: *Prunoidea*
Genus: *Prunus*

Prunus species are commonly found throughout Central Asia. *Prunus* species have a remarkable adaptability to various environmental conditions. They can thrive in humid, cool, desert, and subtropical climates. For instance, they grow well in the humid regions of southern China, northern Egypt, and the eastern United States, as well as in the desert climates of California, Spain, and Iran [11]. Additionally, peaches flourish in the cool climates of northern China and Canada and in the subtropical climate of Florida and Mexico [12]. At the global level, stone fruit production exceeds 48 million tons (Mt). Peaches and nectarines, with a current global production of more than 25 Mt, are the most produced stone fruit, followed by plums and prunes (12 Mt), almonds (4 Mt), apricots (3.5 Mt), and sour and sweet cherries (3 Mt). *Prunus* production has stabilized in recent years. In terms of cultivated area, plum is the most cultivated *Prunus* species, with 2.6 million hectares (Mha), followed by almond (2.1 Mha), peach (1.5 Mha), and cherry (0.8 Mha) [13].

The main objective of this review is the integration of archaeological findings related to prominent *Prunus* fruits such as peaches, apricots, and almonds with emerging genomic data. We shed light on the evolutionary history, genetic diversity, population structure, and historical dynamics crucial for species conservation, with more recent breeding and molecular analysis of the *Prunus* species in the context of ongoing climate change.

2. Evolutionary History, Domestication, and Diversity

2.1. Tracing Early Centers of Prunus

Prunus L. encompasses 250–400 species of trees and shrubs found across the north temperate zone and subtropical and tropical regions [14], with East Asia serving as the center of its diversity [15]. Many *Prunus* species hold economic significance as food crops, such as peaches, plums, almonds, and sweet cherries [16] (Figure 1). Additionally, numerous other species are valued for their ornamental, timber, and medicinal properties [17]. The diverse inflorescence types within *Prunus* species, including racemes, corymbs, and solitary flowers, make them an ideal subject for studying evolutionary transitions in inflorescence tissues. The genus *Prunus* has been categorized into five subgenera: Amygdalus L., Cerasus Mill., Lauro-cerasus Tourn. ex Duhamel, Padus Mill., and *Prunus* [18,19]. Researchers have utilized various genomic regions, such as plastid markers, nuclear ribosomal internal transcribed spacer (ITS), and other nuclear loci, to reconstruct phylogenetic relationships within the genus *Prunus* [19,20]. Different groups within *Prunus* have been identified based on synapomorphic inflorescence structures: the single flower group comprising *Prunus* subg. *Amygdalus* (L.) Foche and *P.* subg. *Prunus* (including section *Armeniaca* (Scop.) Nakai), the corymbose group encompassing *P.* subg. *Cerasus* (Mill.) Pers, and the racemose group including *P.* subg. *Lauro-cerasus* and *P.* subg. *Padus* [15,21].

Most species within the solitary and corymbose groups of *Prunus* are typically diploid, contrasting with the racemose group, where higher ploidy levels are more common [15,20]. The intricate evolutionary history of *Prunus* has been marked by extensive and ancient hybridization events, complicating the elucidation of phylogenetic relationships among these distinct groups. While plastid sequences have confirmed the monophyly of the racemose group [15], earlier studies identified it as paraphyletic [22], suggesting a complex multiple-hybrid origin, particularly characterized by polyploidy [19]. Recent research utilizing hundreds of single-copy nuclear genes and transcriptomic data points has provided strong support for the racemose group, further underscoring its genetic distinctiveness within the broader context of *Prunus* evolution [20].

2.1.1. Plums and Prunes

For thousands of years, people have been cultivating various fruit species, with plums and other *Prunus* species being particularly prominent [23]. Among the *Prunus* species, the plum is the most widely cultivated, together with peach. The earliest reference to plums can be found in classical texts, specifically in the writings of Archilochus Pollux in the 7th century BC, where the term “prumnon” (plum) was mentioned [24]. This species complex is believed to have originated from five distinct centers: Western Asia, Europe, Western and Central Asia, North America, and China. Various types of plums have been documented, such as *Prunus insititia* L. (Damson plum) from Western Asia, *P. domestica* L. (European plum or prune) from Europe, and *P. cerasifera* Ehrh. (Cherry plum) from Western and Central Asia, and *P. americana* Marsh. (American plum) from North America, while *P. salicina* Lindl. (Japanese plum) have distinct origins in different regions [25]. An image of different plum species and their ancestors is presented in Figure 1. The Caucasus Mountains near the Caspian Sea have been hypothesized as the center and place of origin of *P. domestica* and its ancestors by Luther Burbank [26] and Faust and Surányi [27]. Around 6000 BC, plums migrated from this area to regions such as ancient Syria, Mesopotamia, Egypt, and Crete [27]. It has been documented that natural hybrids between *P. ceracifera* Ehrh and *P. spinosa* L. originated from Asia Minor and spread as the seeds of these hybrids from Iran and Asia Minor, likely serving as the parent of *P. domestica* L. in Europe [28,29].

In Central Asia, the oldest attested term for plum is the Middle Persian word “ālūg” [30], which was later expanded and associated with the oasis city of Bukhara, giving rise to the Pashto term “ālū bukhārā”, meaning “plum” [31]. Plums have a long history of domestication, with evidence of their cultivation in Asia, Europe, and North America [32]. In Switzerland, excavations of ancient lake dwellers’ sites have uncovered stones from *P. spinosa* and *P. insititia*, suggesting their presence in the region [33]. Early archaeological findings also suggested the existence of *P. insititia* and cherry plums (*P. cerasifera*) in Germany and Bulgaria [25,34]. While these plums are believed to have originated in Western or Central Asia [27], the exact center of origin for each species remains unresolved [31]. This ambiguity is further compounded by the limited archaeological research conducted in Central Asia [31] (Figure 1).

2.1.2. Peaches

The “Iranian fruit” or “Persian fruit” was first mentioned in *the History of Plants*, the earliest surviving botanical treatise, around 322 BC by the Greek writer Theophrastus (372–287 BC) [35]. It has been suggested that this fruit referred to the peach, with Dioscorides and Pliny using the term in the first century [35]. The scientific name of the peach is derived from the Greek word *persikon malon* and the Latin name *malum persicum*, both meaning Iranian or Persian apple [31]. The name *Prunus persica* reflects this transmission route, not the origin of the species. Initially proposed by ancient Greek and Roman authors, this belief was later embraced by European botanists in the 19th century [27]. Presently, Iran is widely regarded as a key point for the dispersion of the peach [36]. The earliest written records of peaches can be traced back to the Greco-Roman period in the first century CE, as noted by Greek writers Dioscorides and Columella [37,38]. The term “šiftālūg”, which means peach in Middle Persian, is believed to have been derived from the word “plum” with the addition of šift, meaning “sweet” or “milky” [30].

Persia then played an important role as a transmission center of the peach. However, the cultivated peach originated in China. Current scientific consensus and modern archaeological and genetic studies establish that peaches originated in China (Figure 1), particularly in the southwest mountainous regions near the Yangtze River basin. Zheng et al. [39] proposed the lower Yangzi River valley as a region of early peach selection and domestication, suggesting that the process began at least 7500 years ago. The oldest archaeological peach stones are from the Kuahuqiao (8000–7000 BP) and Tianluoshan (7000–6500 BP) sites, and both stone samples segregate into two size groups, suggesting early selection of preferred types. The first peach stones in China most similar to modern cultivated forms are from the Liangzhu culture (ca. 5300 to 4300 BP), with peach stones significantly larger and more compressed than earlier stones. Similar peach stones have been reported from Japan much earlier (6700–6400 BP). Peach stones dating back 7000 years have also been discovered at the Hemudu site, with similar findings at the Erlitou Neolithic site, indicating early consumption and later cultivation. This large, compressed-stone peach was introduced to Japan, indicating a yet unidentified source population in China that was similar to the Liangzhu culture peach. All six species in the peach subgenus (Amygdalus) are native to China. Extensive forests of wild peach relatives are found in the Hengduan and Himalayan mountain ranges, identifying this area as the peach’s center of origin [39].

2.1.3. Apricots

The apricot, a fruit native to temperate and subtropical regions, has a global distribution [40]. Dioscorides references *mailon/armeniacon* in his “De Materia Medica” [38], while Columella mentions *pomum armeniacum/armeniaca arbor* in “De Re Rustica” [41], with Pliny further discussing it in his “Natural History”. The widespread presence of this fruit in ancient Greece and Rome at least since the beginning of the first millennium CE, as well as *malum armenicum* (Armenian apple), from which the later scientific name was derived, testifies to the ancient belief that this fruit had a Caucasian origin [31]. The English term “apricot” traversed various linguistic communities around the Mediterranean basin and Byzantine Greek [42], with zardālūg, meaning “apricot” in Middle Persian, combining the word ālūg for “plum” with the adjective zard (yellow) [30], spreading within the Persian cultural sphere [31] (Figure 1). Four major ecological groups have been identified within the *P. armeniaca* species [35].

The first group comprises the Central Asian regions, such as Fergana, the Zerevshan mountain range, Samarkand, and the Kopet-dag in northern Iran [35]. This group is considered the oldest and most diverse in terms of forms [35,43], spanning across Central Asia, China, Afghanistan, Baluchistan, Pakistan, and North India [35]. Apricot trees within this group are characterized by their longevity and late blooming [35]. Apricot trees are susceptible to diseases that limit their planting in wet areas [35]. The second group includes the Iranian–Caucasian group consisting of the Iran-Caucasus region and Dagestan (the western shores of the Caspian Sea), as well as Armenia, Georgia, Azerbaijan, Dagestan, Iran, Syria, Turkey, and North Africa [35]. Trees within this group have a shorter lifespan compared to those in the Central Asian group and exhibit lower winter resistance while initiating growth earlier in spring [35]. Additionally, the fruit produced by trees in this group is larger compared to the Central Asian variety [35]. The third group, known as the European group, is considered the youngest and least diverse in terms of origin. According to Kostina, they were brought to Europe from Armenia, Iran, and Arab countries during the last 2000 years [35]. Moving on to the fourth group, the Dzhungar-Zailij group is situated north of Almaty and the Tien Shan mountains [35]. Originating from the Panfilov, Taldy-kurgan, and Almaty regions of Kazakhstan, as well as from Ining in Xinjiang, these trees exhibit exceptional winter hardiness, withstanding temperatures as low as −30 degrees Celsius [35]. The genotypes of cultivated apricots in Xinjiang, North

China, and foreign apricot populations were mixed with large numbers of genotypes of wild apricot populations from the Ili River Valley. The wild apricot populations in the Ili River Valley contain the ancestral genotypes with the highest genetic diversity and are located in an area considered a potential glacial refugium for *P. armeniaca* [44].

2.1.4. Almonds

Almonds stand out botanically and horticulturally from other *Prunus* crops, with these distinctions having significant implications for the human history and dissemination of this crop [35]. Unlike other fruits, almonds are consumed as nuts, serving not only as a means of reproduction for cultivation expansion but also as a sought-after and relatively non-perishable food item that was tradable even in ancient times [35]. Early human societies traded wild almonds encompassing over 30 varieties distinguished by varying quality, morphology, and geographic origins [35]. The initial diffusion of this genetically diverse crop followed the emerging trade routes from Central Asia to the West and the Mediterranean region [35] (Figure 1). Almonds, owing to their convenient transportability, became a significant commodity in prehistoric trade across Asia, North Africa, and Europe [35]. The origins of almonds (*Prunus dulcis* (Miller) D. A. Webb) in Iran and the Middle East trace back to the Mediterranean basin, renowned for its rich species diversity [45]. Historical evidence suggests that almond species were first brought from Iran to Greece before 300 BCE and eventually spread to compatible regions within the Iranian basin, southern Europe, and northern Africa [46]. Tunisia, with its ancient center of Carthage and later as a pivotal granary during the Roman Empire, served as a crucial trade route facilitating the dissemination of almonds along the Persian coast and into Spain [46]. Subsequently, Spain emerged as a crucial hub for the dissemination of almonds to various corners of the globe, including North America, South America, South Africa, and Australia [47].

Wild almond species have garnered attention in breeding programs, primarily for their potential use as rootstocks or scion cultivars [48]. These bitter almonds, known for their toxic properties that can be lethal if consumed in even small quantities [49], also yield gum extracted from the bark and branches, as exemplified by *P. scoparia*. In traditional Iranian medicine, this gum, referred to as Persian gum, has been utilized to address a wide array of ailments ranging from cancer to toothache (Zargari). Widely distributed from Central Asia to the Caucasus and southwest to North Central Asia, wild almonds thrive in foothills and forested regions. Despite their significance, the precise ancestry of wild almond species remains elusive, with breeding experiments proving challenging due to extensive hybridization with other wild varieties [48]. The consensus among researchers points to Central and Western Asia as the likely origins of these valuable trees [50].

2.1.5. Cherries

Cherry (*Prunus avium*) was originally observed in the Ghilan forests, located in northern Iran, as well as Armenia. It spread from the north of China (Figure 1) to Iran and Europe, ranging from southern Russia to mountainous regions in Greece, Italy, and Spain (Figure 2) [51]. Due to its appeal to birds, it quickly proliferated, earning the moniker *Prunus avium* L., or bird cherry [51]. The species *P. avium* encompasses both cultivated sweet cherry with large fruits and wild forest cherry with small fruit known as mazzard, primarily utilized for timber production [52]. In addition, mazzard has been used as a rootstock in cherry cultivation for 2400 years due to its excellent graft compatibility. The Greeks and Romans used mazzard rootstock and spread it to other countries [53]. Cherry is a stone fruit that appears on the market during a period in the northern hemisphere when fruits and vegetables are scarce on the shelves, specifically from May to July. It is predominantly consumed fresh and enjoyed for its attractive appearance, color, and flavor [54]. In cherry cultivation, rainfall can negatively affect bee activity during the flowering period and cause fruit cracking during the maturation process after fruit set, making rainy conditions undesirable. However, cherries can achieve the highest quality maturation in cooler summer regions [55].

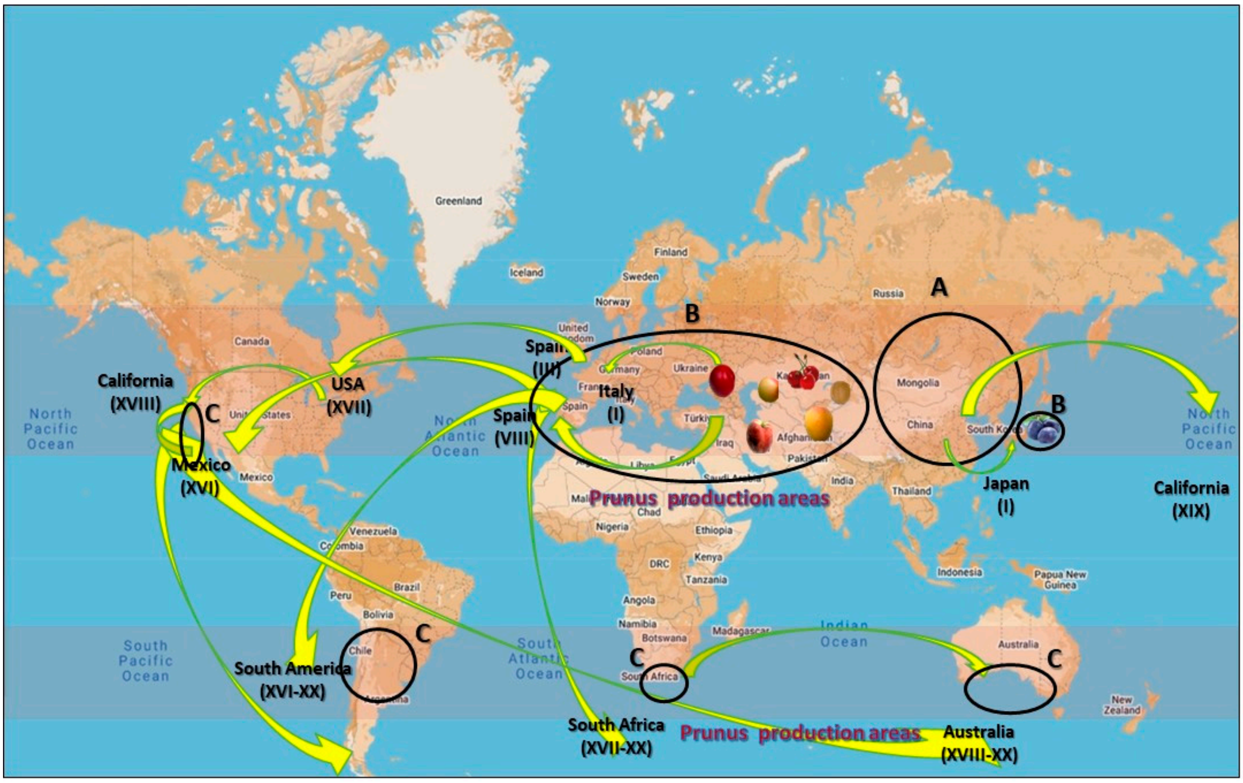

Figure 2. *Prunus* origin (A), diversification (B), and cultivation (C) areas across the world. *Prunus* fruits are located in the first diversification areas. The year of the dissemination to main countries is also indicated.

Finally, the sour cherry, *Prunus cerasus* L., originates from the heart of the Near East in Asia Minor, including regions of Iran, Iraq, and Syria [56]. Its distribution spans from the southern border of the Black Sea through Anatolia and the South Caucasus to Iran [57]. Cherry, known by the Latin name *P. cerasus* L., is named after Kerasus, the ancient name of the province of Giresun in the Eastern Black Sea region of Turkey. The flowers of this fruit species have a hermaphrodite structure and show heterostyly. Since there is no fertilization problem in the self-fertile sour cherry species, additional pollinator varieties do not need to be planted in orchard plantings [58]. *Prunus cerasus* L. is an allotetraploid species that emerged from the natural crossbreeding of unreduced pollen from the diploid sweet cherry (*Prunus avium* L. ($2x = 16$)) and the tetraploid ground cherry (*Prunus fruticosa* L. ($4x = 32$) [56,59]. Since sour cherries blossom late, they are less affected by late spring frosts [58,60].

2.2. Domestication of *Prunus*

Domestication is an evolutionary process where human selection drives phenotypic divergence of cultivated plants and domestic animals from their wild ancestors based on human-preferred traits [61]. Perennial species such as fruit trees evolve at a notably slower pace of domestication compared to annual plants due to their clonal propagation, leading to fewer sexual cycles experienced by these species [61]. The extended juvenile phases of fruit trees further contribute to this reduced evolutionary rate [62]. The domestication of plants typically involves multiple rounds of selection, starting with an initial domestication event that gives rise to native breeds, which are then further refined through selection to create enhanced modern varieties [61].

Crop domestication affects the genetic diversity and population structure of domesticated plants, which changes the economic and agronomic traits of the crop [63]. Understanding the mechanisms of plant domestication and diversification is crucial for genetic crop improvement in breeding programs, with insights gained by identifying genetic variation in wild and cultivated populations, as well as within populations. Research has shown that domestication tends to reduce the genetic variation of crops [64], prompting breeders to increasingly turn to wild relatives of domesticated crops as a source of new plant genetic material for the breeding of new adapted cultivars [65]. However, in fruit crops, the extent of domestication bottlenecks is weaker than in annual crops, if not absent entirely [66]. In addition, the breeder must consider the genetic background of the available material, new methods, and consumer preferences, as well as biotic and abiotic factors, to ensure the success of the new variety. The success of the design of new varieties hinges on a thorough understanding of these aspects, while the phenotyping and the selection of seedlings pose practical limitations in the breeding process.

The initial domestication of *Prunus* species likely involved wild species that held significant importance for early human societies [9]. While most stone fruits, except peaches, are cross-pollinated and, therefore, heterozygous, the propagation of these species through seeds is often inefficient due to extended juvenile periods and lower seedling quality compared to selected clones [9]. As a result, the foundation of stone fruit improvements predominantly relies on clonal propagation of wild seedlings, which has evolved through a combination of crossing superior clones and wild species, leading to substantial seedling variation.

In the simplest scenario of domestication, seeds or cuttings from wild populations are transferred to cultivated settings for sustained growth through clonal propagation [66]. This process involves selection during each sexual cycle, leading to the isolation of favorable variants that proliferate through clonal reproduction [66]. Perennial species often exhibit strong heterozygosity [67]. Clonal reproduction acts to maintain heterozygosity at the individual level [62] but promotes genetic homogeneity at the population level. A more realistic perspective suggests that the domestication of perennial plants unfolded as a dynamic spatio-temporal process spanning thousands of years. Seeds and cuttings were sourced from diverse wild populations, contributing to the domesticated gene pool through inadvertent gene flow or deliberate breeding efforts once introduced to cultivated environments [66].

2.3. Dispersion and Cultivation of Prunus

From their origin, *Prunus* species have been distributed across the world. The Asiatic stage included the initial domestication and expansion along major prehistoric trade routes. In the case of peach, almond, prune, and cherry, the range centers on present-day Iran, extending east to western China, northwest India, and northern Pakistan; northwest through Turkey; and southwest into the uplands and deserts of central Israel and Syria. *Prunus* culture continues to the present time in these areas, mainly under dryland and subsistence agricultural practices similar to those used in 2000 BCE. Cultivated *Prunus* appear to have been brought into Greece prior to 300 BCE and were subsequently introduced in other regions bordering the climate-moderating Mediterranean Sea. Subsequent introductions occurred in 500–600 CE with the conquest of North Africa by Arabs who also brought almonds into southern Spain and Portugal. In these regions, orchards were established in specific locations where well-defined ecotypes have evolved. Throughout the 18th and 19th centuries, almonds were distributed to North America, South America, and Australia [35,43,54,61,68] (Figure 2). The vegetative multiplication of local cultivars in the 20th century allowed for the stabilization of plant material constituting the starting material of breeding.

On the other hand, the Japanese plum has its origins in China, specifically in the Yangtze River basin, and is an ancient crop dating back to 300 BC. It was cultivated in China for several thousand years before being introduced to Japan more than two thousand years ago [27]. Its introduction worldwide did not occur until well into the 19th century (Figure 2). At that time, the breeder Luther Burbank introduced some Japanese plum genotypes such as 'Kelsey' and 'Abundance' to California (USA) from Japan [32], where Burbank began a genetic improvement program of plums by crossing them with other diploid species such as *P. americana*, *P. hortulana*, *P. munsoniana*, and *P. simonii* to improve their adaptation to local environments. Burbank's efforts resulted in the creation of several cultivars, including 'Santa Rosa', 'Beauty', 'Eldorado', and 'Burbank', among others, which spread from California to temperate areas around the world during the 20th century [69]. Some of these cultivars were subsequently crossed with other local plum species, such as *P. americana*, *P. angustifolia*, *P. nigra*, and *P. besseyi* in the United States, and *P. cerasifera* in South Africa and Australia. Therefore, the term "Japanese plum" refers to a heterogeneous group of interspecific hybrids derived from crosses involving up to 15 different *Prunus* species rather than representing a pure species [27].

In 1972, historian Alfred Crosby introduced the term "Columbian Exchange" to delineate the biological diffusion resulting from European colonization of the Americas. The widespread acceptance of New World products across the globe underscores the significant adaptability of plants to diverse agroecological conditions, serving as the foundation of this transformative process [70]. Studying the introduction and proliferation of crops in Europe, a well-documented historical event marked by swift adaptation, offers insights into crop resilience in novel environments, crucial for addressing future environmental and socio-economic shifts like temperature fluctuations, rainfall variations, and evolving consumer preferences. Numerous crops, including tomatoes, corn, beans, squash, potatoes, and tobacco, were transplanted from the Americas to Europe, marking a significant dissemination process characterized by diverse traits such as mating systems and ploidy levels. This historical diffusion serves as a lens to explore the genetic mechanisms underlying adaptation and genomic diversity [71].

2.4. Cultivation of Prunus Around the World

With a notable rise in the presence of *Prunus* fruit remnants dating back to the late fourth or early third millennium BCE, concrete proof of *prunus* fruit consumption has been established during the Neolithic period in both ends of the Eurasian continent [72]. Despite the considerable economic importance of *Prunus* from antiquity to the present, as well as the long and well-documented archaeological history of human consumption, many questions remain unanswered about its evolution. Particularly, how domesticated forms spread throughout Eurasia and North Africa is a topic that requires further exploration [31].

There is a series of questions that deserve answers about how *Prunus* cultivation spread around the world after its dispersal along the Silk Road. Over the past 30 years, production of peaches and plums has risen steadily (Figure 3) [13]. Understanding shifts along climatic gradients and through different cultures can help guide efforts to make breeding more effective and production more sustainable.

As global production rises, the range of traditional varieties used is declining. Many of the new varieties come from foreign improvement programs, which usually implies high royalties, lack of information, and late availability of the best varieties, as well as presenting problems of adaptation to local conditions, generally due to their high winter cold requirements. One aspect that deserves to be highlighted is floral self-incompatibility, which leads to the need to take it into account in the design of plantations by having intercompatible pollinating varieties that coincide in flowering time. Another serious problem is the incidence of pests and diseases, which causes significant damage, affecting both quality and production [68,73].

In addition, many diseases and pests are shared among *Prunus* crops. As an example of the difficulties this poses, there is no plant material of peach and Japanese plum resistant to the *Plum pox virus*, and all cultivated varieties are susceptible. Another problem that is present is the mediocre commercial quality of some of the cultivated *Prunus* varieties. The growing competitiveness of the markets, together with the new demands of consumers, leads to the need to produce a high-quality fruits characterized by an attractive appearance, adequate texture and firmness, and high taste quality. The need to address emerging challenges, mainly in the context of the present global warming, arises from various crop problems, the evolution of consumer demands and expectations, and increasing market competition, as well as new technological, agronomic, and environmental challenges, including the impact of climate change and ecological sustainability, requiring genetic improvement programs that respond to these needs by obtaining new varieties of high value and excellence that increase the genetic and phenotypic diversity of the species [73].

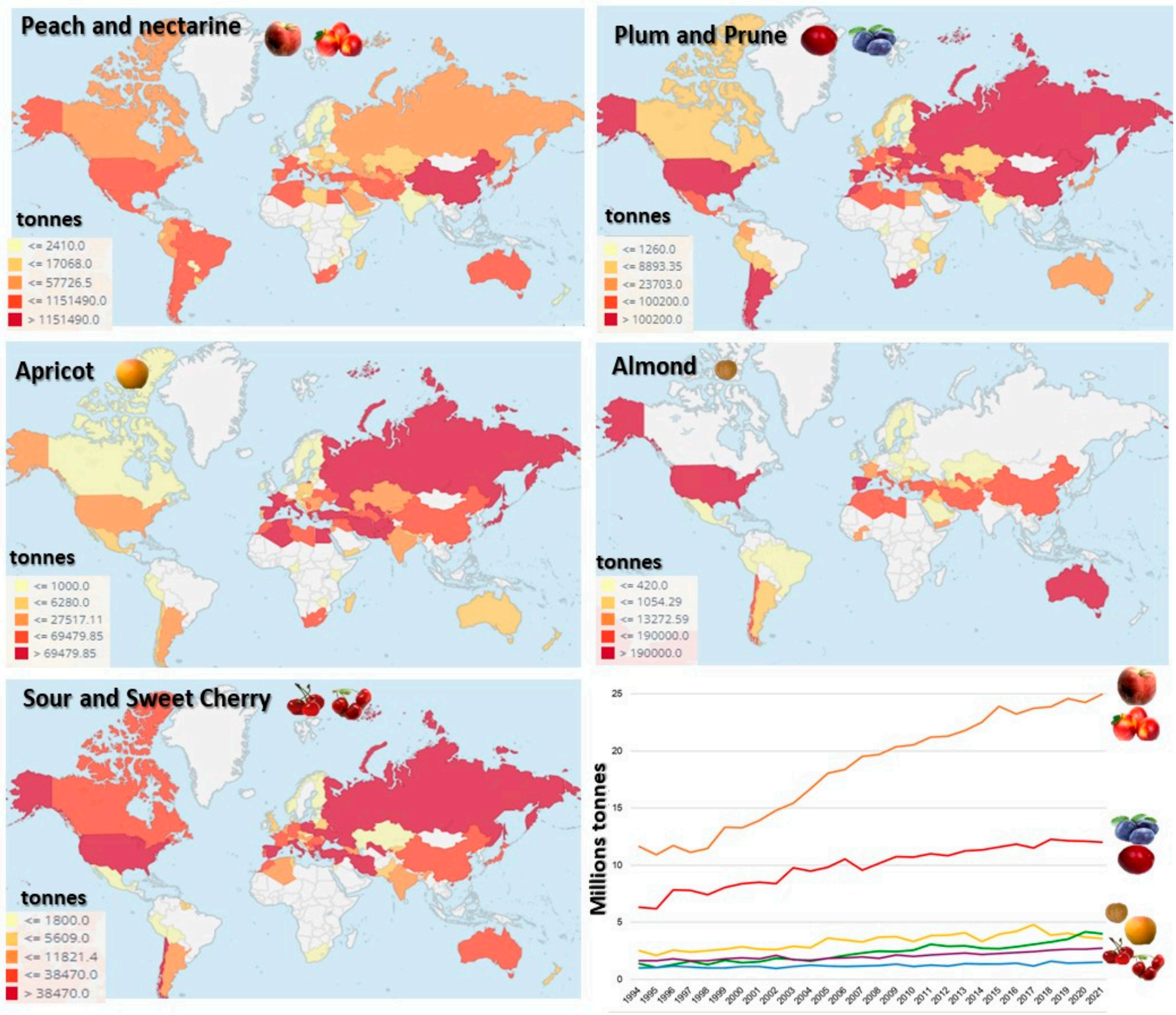

Figure 3. *Prunus* production around the world, including peach and nectarine, plum and prune, apricot, almond, and sour and sweet cherry, and evolution during the last thirty years [13].

3. Breeding and Impact of Climate Change on Genetic Patterns of *Prunus*

The objectives pursued in *Prunus* breeding programs may vary from one country to another, but in general, the focus has been on extending the production calendar and availability of fruit on the market; obtaining optimal firmness to facilitate handling, storage, and transport; guaranteeing high organoleptic quality and a good appearance of the fruit; and increasing the size of the fruit and improving its post-harvest suitability. Regarding the flowering date, the objectives may vary depending on the place of improvement, looking for extra-early varieties adapted to very warm areas or late varieties to reduce the risk of spring frosts. In addition, characteristics such as self-compatibility, climatic adaptability; productivity; and resistance, especially to PPV, are widely valued and desired in the genetic improvement of this species [73].

In this context, a very interesting question in relation to the dispersal of *Prunus* along the Silk Road is how it impacts further breeding. Impacts of this dispersal include the available genetic diversity across these wide territories, the use of interspecific hybridization, and the development of rootstock using these materials. Classical *Prunus* breeding is a long and tedious process similar to that of other fruit species, affected by its woody nature and the long juvenile period. For this reason, breeders must have rigorous and extensive knowledge of the species, the culture, and the genetic control of the most important traits to design new cultivars. Newly released cultivars have an impact in the sector (nurseries and growers) many years after they were created by a breeder. The minimum time to release a new almond cultivar hovers around 10 years, meaning that new cultivars only appear on the market slowly [73].

3.1. Genetic Diversity and Structure of *Prunus* Germplasm

In plant breeding programs and the conservation of genetic resources, it is crucial to evaluate the extent and composition of genetic diversity within germplasm collections [74]. The process of crop domestication, driven by human selection pressure compared to ancestral material, has led to the development of cultivated populations with altered traits [75]. In many crops [76], the gradual reduction in genetic diversity in domesticated forms is determined through population bottlenecks and the selection of important agronomic traits, caused by genetic drift and artificial selection, respectively. Researchers suggest that the domestication of fruit trees occurred several thousand years after the domestication of grains and legumes due to the perennial perspective and planning required to manage fruit trees [31]. This delay is attributed to the fact that most fruit species are more effectively propagated through grafting or budding, i.e., clonally, rather than from seed [31,77]. Vegetative propagation accelerates the pre-maturity stage compared to seed propagation, which can take three to five years, and offers better control over the selection of desired qualities [78]. Human intervention has led to changes such as increased fruit size and sugar content, reduced fruit acidity, and the loss of branch spines [9].

Due to habitat reduction and crop-to-wild gene flow, many wild crop relatives are facing threats [79]. Understanding the population subdivision and distribution of genetic diversity is crucial for conserving the biodiversity of wild crop relatives [80]. To ensure the preservation of valuable genetic resources and promote sustainable use, it is essential to study genetic diversity and establish ex situ germplasm collections [81]. Developing germplasm collections involves capturing a representative sample of individuals to encompass species diversity [82]. Perennial species collections offer advantages such as vegetative propagation and long-term maintenance as clones in field collections [83].

Throughout their origin in central and southwest Asia, wild populations of *Prunus* species have evolved a diverse range of morphological forms [84]. Botanists have documented species that have successfully adapted to diverse ecological niches in the deserts and mountains of Central Asia [84]. The *Prunus* genome exhibits a high level of homology at both the genomic [85] and transcriptomic levels, facilitating easy hybridization between *Prunus* species [86,87].

The *Prunus* genus encompasses a vast diversity of species and varieties globally, including wild, semi-wild, and cultivated forms. Considering its contribution to plant biodiversity, the preservation of wild plant resources, and its role in cultivation, it is crucial to establish databases, develop collaborative conservation strategies, and create various data repositories to prevent the extinction of the *Prunus* genus [26].

Habitat fragmentation and loss, as well as gene flow from crops to wild species, have placed many wild crop relatives at risk of extinction in many geographical areas along the Silk Road [79]. Understanding population subdivision and the distribution of genetic diversity is crucial for the conservation of biodiversity among wild plant relatives [80]. Research on the genetic variation of crops and their wild relatives is essential to conserve biodiversity and sustainably use valuable genetic resources through the establishment and development of ex situ germplasm collections [81]. The development and creation of germplasm collections requires the attainment of a suitable and sufficient number of individuals to represent species variation [88]. Woody species have the additional advantage of being able to be vegetatively propagated in field collections and maintained as colonies in perpetuity.

3.2. Interspecific Prunus Hybridization to Develop New Cultivars

Over the past century, numerous new varieties of major stone fruits have been introduced and commercialized worldwide, with a particular focus on Europe and the United States. These new varieties are primarily created through crosses, either through open pollination or controlled crosses, with only a small percentage resulting from bud sports [88]. Advanced breeding techniques for stone fruits include mutation breeding and somaclonal variation [89]. Intraspecific hybridization within *Prunus* spp. is a prevalent method for creating new fruit cultivars, contributing to the continuous development of the latest stone fruit varieties globally.

Hybridization is acknowledged as a critical element in the process of some domestication events, as emphasized by Darwin [90]. Extensive human-mediated gene flow resulting from breeding efforts has significantly influenced the re-evaluation and alteration of species boundaries within cropping systems [91]. In the past, the prevailing notion was that geographic isolation was the primary driver of reproductive isolation, ultimately leading to speciation [92]. However, with cultivated populations demonstrating the ability to interbreed with related species and produce viable offspring, a new gene pool system was proposed [91]. This paradigm shift gave rise to the gene pool system, which serves as a reservoir of genetic diversity comprising domesticated populations, their wild progenitors, and related species capable of genetic interchange with cultivated varieties.

The utilization of "interspecific hybridization" to generate novel *Prunus* cultivars is detailed in Table 1. The most important used commercial interspecific hybrids, such as cultivars, include plumcots, pluots, and Aprium apricot.

Table 1. Most relevant interspecific hybridizations in *Prunus*.

Hybrid	Origin	Characters	Pollination	References
Plumcots	It was named by Luther Burbank. This hybrid occurred naturally.	Combining *plum* and *apricot* [hybrids of *P. salicina* or *P. cerasifera* with apricots (*P. armeniaca* or *P. mume*)].	Partially self-fertile	[93,94]
Pluots	It was named by Floyd Zaiger and is the second hybrid generation of Plum-apricot.	If Plumcot is crossed again with the plum parent, the latter will have a 75% share in the new hybrid, and the apricot parent will have 25%. Hybrids of [(*Prunus domestica* × *P. armeniaca*) × *P. domestica* or (*P. salicina* × *P. armeniaca*) × *P. salicina*].	Self-incompatibility	[94,95]
Aprium	It was named by Floyd Zaiger and is the second hybrid generation of Plumcot with apricot.	The share of genetic contribution of apricot and plum parent is 75 and 25%, respectively [(*Prunus aremeniaca* × *P. domestica*) × *P. aremeniaca* or *P. armeniaca* × (*P. salicina* × *P. armeniaca*)].	It is usually self-fertilizing, but planting another compatible plum or apricot tree can promote fruit set.	[96]

3.3. Interspecific Prunus Hybridization to Develop New Roostock

This interspecific hybridization of *Prunus* species has also been used in the development of rootstock. The utilization of "interspecific hybridization" to generate novel *Prunus* rootstock is detailed in Table 2. Most relevant rootstock breeding strategies using interspecific hybridization of different *Prunus* species include interspecific crossing of commercial peach and almond.

Rootstocks are crucial in shaping the productivity and longevity of orchards in fruit cultivation [97]. The practice of grafting, which merges advantageous characteristics from multiple sources, can significantly impact the development of crops [98] and impact population genetic processes in grafted crops. The impact of rootstocks extends to various aspects of fruit quality, early fruiting, yield, tree size regulation, resistance to biotic and abiotic stressors, fruit respiration patterns, crop load management, and canopy maintenance strategies, as evidenced across multiple fruit crop varieties [99].

Table 2. The most relevant rootstock breeding strategies using interspecific hybridization of different *Prunus* species.

***Prunus* Rootstock**	**Origin**	**Characters**	**Used Scions**	**References**
Prunus rootstock, 'Cornerstone'	It was named by John K. Slaughter and Timothy J. Gerdts.	The present invention relates to a novel and distinct variety of *Prunus* rootstock (*P. dulcis* × *P. persica*), with a lower incidence and expression of crown gall (*agrobacterium tuberfaciens*).	'Cornerstone' is a new and distinct variety of rootstock that appears to be quite useful for almond, peach, nectarine, plum, and some apricot varieties.	[100]
Prunus rootstock, 'Warootone'	It was named by John Keith Slaughter and Kaylan M. Roberts.	A new and distinct variety of *Prunus* rootstock tree ([*Prunus dulcis* × *Prunus persica*] × [*Prunus davidiana* × *Prunus persica*]), which is denominated varietally as 'Warootone'. When utilized as a rootstock, it reduces the growth and height of fruiting cultivars	Peach, nectarine, plum, almond, and apricot	[101]
Prunus rootstock, 'Purplepac'	It was named by Jorge Pinochet.	The present invention comprises a new and distinct cultivar of peach–almond hybrid [(*Prunus dulcis* × *P. persica*) × (*P. persica* × *P. davidiana*)] used as a rootstock and known by the varietal name 'Purplepac'. It exhibits root-knot nematode resistance (*Meloidogyne* spp.)	Peach, nectarine, almond, and plum	[102]
Prunus rootstock, 'Tempropac'	It was named by Jorge Pinochet.	(*Prunus dulcis* × *P. persica)* × *P. persica.* It exhibits root-knot nematode resistance (*Meloidogyne* spp.).	Peach, nectarine, and almond varieties	[103]
Prunus rootstock, 'Myrocot'	It was named by Gennadiy Eremin.	*Prunus cerasifera* × *armeniaca.* It is resistant to root and leaf diseases, with high temperature and frost tolerance.	Plum and apricot	[104]
Peach rootstock, MP-29	It was named by Thomas G. Beckman, Jose X. Chaparro, and Wayne B. Sherman.	*Prunus* species hybrid × *Prunus persica* [inter-specific hybrid, 'Edible Sloe' plum (*Prunus* species hybrid) × 'SL0014' (*Prunus persica*)]. It is distinguished by its resistance to peach tree short life/bacterial canker complex, Armillaria root rot, and several species of root-knot nematodes.	Peach	[105]

Additionally, an evolutionary feature of significance in *Prunus* is self-incompatibility (SI), which aims to preserve heterozygosity within a species, thereby maintaining higher diversity and promoting better adaptation [106]. However, SI poses challenges for non-parthenocarpic crop species like stone fruit trees, where self-compatibility (SC) is more desirable for efficient pollination and fertilization, particularly in the *Prunus* genus, where the gametophyte SI (GSI) system operates [106]. Consequently, breeding efforts have focused on transitioning self-incompatible (SI) species such as sweet cherry (*Prunus avium* L.) and almond (*Prunus amygdalus* Batsch) to self-compatible varieties. These breeding programs were initiated without a clear understanding of the genetic mechanisms underlying SI/SC, but later research confirmed the successful transmission of SC traits to offspring [107].

Recent advancements in molecular methods have shed light on the intricate process of pollen–pistil interaction and the identification of genes crucial to this mechanism [108]. The genetic control of self-compatibility (SC) and self-incompatibility (SI) has been linked to a single polymorphic locus housing multiple genes, with one gene expressed in the pistil and another in the pollen [109]. In the Rosaceae family, S-RNase has been identified as a key player in pistil SI [110], while SFB, which is closely associated with S-RNase genes, has emerged as a promising candidate gene for pollen-S [111]. While the S-genotypes of many North American and European apricot cultivars are known, a study by Halász et al. [112] investigated the S-genotype diversity of apricots native to Turkey. Producers can use these findings directly to choose appropriate pollination partners for new orchard plantings, and researchers can utilize them to better understand the evolutionary history of this crop.

The first key decision of breeders is the selection of the genotypes that will be used as parents. This election determines the success or failure of the breeding program. A breeder usually crosses two cultivars with complementary characteristics to obtain a new cultivar that assembles the most interesting traits of both genitors. Transgressive seedlings (with lower or higher breeding values than genitors) for the main traits are usually selected to advance the improvement of these traits. The development of improved selection strategies for complex target traits in tree crops, which often have long juvenile periods and high heterozygosity, can be achieved through the use of genetic methods such as genomic (DNA), transcriptomic (RNA), and epigenetic studies. Furthermore, epigenetic markers associated with dormancy have been established in flower buds [113].

3.4. Genomic Markers and Evaluation of Genetic Diversity

Although only a few genes have been identified as candidate genes for traits, quantitative trait loci (QTL) have been found to influence numerous important traits [114]. The genetic enhancement of stone fruits (*Prunus* spp.) aims to produce affordable, high-quality fruits with extended shelf life, reduced damage from pests and diseases, and decreased production costs through enhanced productivity. To achieve these goals, it will be important to integrate genomics and new molecular tools into breeding programs [113]. These modern methods enhance the identification of essential genes at the molecular level, thereby improving the efficiency of breeding systems.

Genomic (DNA) approaches have been used in the development of markers for assisted selection and evaluated genetic diversity. Such genomic studies can be completed with analysis at RNA level (transcriptomic and gene expression) and epigenetic level (DNA methylation). Genome-wide association studies (GWASs) can identify the association of genotypes with phenotypes, allowing for inference about the genomic regions and genes that underly traits [115]. On the other hand, the genomic estimated breeding value (GEBV) is used to describe the potential genetic contributions that a particular male or female parent possesses, derived from genome-wide DNA polymorphism information. The GEBV facilitates the selection of superior genotypes [116].

Significant advances in genomic analysis technologies have enabled cost-effective and high-density genotyping of DNA polymorphisms at the genome level [117], opening new avenues for the promotion of plant breeding through technological advancements [118].

The rapid advancement of sequencing technology has enabled the provision of whole-genome information for non-sequenced species. Sequencing technology has generated large datasets of short sequences from millions of genomes, facilitating population genomics studies using techniques such as Genotyping by Sequence (GBS) and Restricted Site-Associated DNA Sequencing (RAD-seq) [117]. Additionally, recent advancements in genetic engineering, including cisgenesis, marker-free transformation, and targeted genome manipulation using CRISPR/Cas systems, have emerged as powerful tools in accelerating fruit breeding [119]. While these tools present wide potential compared to conventional fruit modification methods, they also pose challenges. Nevertheless, their significant impact on fruit cultivation has garnered attention from governments and entrepreneurs [120].

On the other hand, the process of gene discovery is expedited by whole-genome sequences and expressed sequence tag (EST) libraries, as exemplified by the development of a peach genomic resource serving as a model for gene identification in *Prunus* species [8]. The availability of the integrated peach genome sequence enhances access to genomic data for all *Prunus* species, also facilitating comparative genome studies and identification of crucial genes [121]. The released whole peach genome, considered the reference genome for *Prunus* species (versions 1.0 and 2.0), with existing databases like ESTree has provided comprehensive access to genomic data for *Prunus* species [121,122].

Preserving montane plants before climate change impacts their survival and uniqueness could unlock valuable scientific and economic opportunities for the breeding of new cultivars [123]. *Prunus* plants exposed to water deficit exhibit elevated levels of phytoprostanes (PhytoPs) and phytofurans (PhytoFs), which serve as plant markers of oxidative stress with potential health benefits for humans [124]. In addition, the anthocyanin content and antioxidant activity in the 'June Gold' peach cultivar were found to increase with higher altitudes, as reported in [125]. In early maturing peaches, the application of regulated deficit irrigation has been shown to increase the concentration of bioactive compounds [126]. Understanding the genomic dynamics of new *Prunus* diversity and discovering climate-hardy accessions with unique metabolic profiles are essential for fruit genetic improvement [123]. Further genomic analysis may unveil genetic changes induced by environmental challenges, including the enrichment and mobilization of SINE TEs due to climate change. Fruits from high-altitude trees host over 300 compounds, many of which are polyphenolics, showcasing the potential for specialized metabolites in these environments [123].

Various families of transcription factors (TFs), including NAC (NAM, ATAF, and CUC), MYB (myeloblastosis-associated proteins), WRKY (WRKYGQK), bZIP (basic leucine zipper domain), bHLH (basic helix–loop–helix), CAMTA (CaM-binding transcription activator), and ERF/AP2 (ethylene-responsive factor/apetala2), play crucial roles in both abiotic and biotic stress responses [127]. NAC TFs have been identified as key players in growth, development, abiotic stress responses, and disease resistance [128].

Overexpression of NAC family transcriptional regulators such as NAM/ATAF/CUC, has been shown to enhance plant drought tolerance [127]. Notably, an increase in conjugated phenolic acid, 3-O-feruloyl quinic acid, is linked to the insertion of a SINE upstream of a transcription factor containing the NAC domain (NAM/ATAF/CUC) [123]. Tibetan *Prunus* species have adapted to the harsh Himalayan plateau environment by accumulating beneficial metabolites, facilitated by the expansion of SINE retrotransposons [129,130].

3.5. Genomic Markers and Assisted Selection

The use of molecular markers as a valuable tool in locating important *Prunus* genes through linkage maps has been highlighted. These markers are utilized to describe genetic resources, identify cultivars, investigate traits, and create linkage maps in fruit trees. Various molecular markers such as random amplified polymorphic DNA (RAPD); fragment length polymorphisms (AFLPs); simple sequence repeats (SSRs); specific-locus amplified fragment sequencing (SLAF-seq) [131]; Start Codon Targeted (SCoT) [132]; and, more recently, single-nucleotide polymorphisms (SNPs) have been widely employed in this context [133].

Given the high genetic similarity among breeds, prioritizing the discovery of effective methods for breed identification is crucial. Therefore, the development of efficient DNA fingerprinting tools is crucial to prevent misidentification [134]. Genetic maps can be used not only to establish the location of QTLs but also to confirm the final location of specific genes associated with or involved in the expression of a trait [135]. Molecular markers closely associated with QTLs hold potential utility in Marker-Assisted Selection (MAS), where selection primarily relies on DNA polymorphisms [136]. The generated maps, QTLs, and identified genes, along with extensive information on DNA markers used in *Prunus*, are accessible in the Genome Database for Rosaceae (GDR) [135].

Marker-assisted selection (MAS) plays a crucial role in enhancing the efficiency of conventional fruit breeding methods by enabling the selection of economically significant traits that are challenging to identify early in the plant life cycle based on phenotype. Molecular markers linked to these traits offer significant advantages in MAS, especially when evaluating characteristics is resource-intensive or time-consuming and when gene expression is recessively controlled [137]. In the context of *Prunus* research, a substantial focus has been placed on MAS for graft cultivar growth in peach, given its economic significance and compact genome size, making it a prime candidate for genetic manipulation within the Rosaceae family [135,138]. Some markers related to dwarf/semi-dwarf tree structure, flesh color, flower type or size, fruit maturity date, etc., in peach have been widely applied in breeding [139,140].

The Genome Database for Rosaceae (GDR) website [135] was established in 2010, providing a valuable resource for accessing genetic and genomic information across various Rosaceae genera [141]. The peach genome sequence was released in 2013 by the International Peach Genome Initiative [142], with the current version, Peach v2.0, available in Phytozome and other databases such as Istituto di Genomica Applicata and GDR [135]. The emergence of genomics and advancements in DNA sequencing technologies have opened up exciting opportunities for developing new markers and unraveling the functional genes that govern crucial traits in fruit breeding [143].

At this moment, more than 20 *Prunus* genotypes have been sequenced, and their reference genomes are available, including almond, peach, apricot, mei, plum, prune, and sweet cherry [144]. This sequencing work started in 2013 with the development of the reference genome of the peach considered as the model *Prunus* species. The development of complete genomes is making any organism accessible and amenable for many kinds of studies, which will allow for a precise reference of the obtained molecular results and the development of high-throughput methods for genomic analysis involving the most abundant genetic variation and transcriptomic analysis at the differential gene expression (DEG) level in a new postgenomic perspective. This new postgenomic perspective integrating available reference genomes and new sequencing and bioinformatic methodologies will allow for the implementation of new Marker-Assisted Selection (MAS) to accelerate the breeding process. The application of these molecular tools will increase the viability and efficiency in the development of the new planned design. In this context, high-throughput sequencing technologies have resulted in great advances in the development and application of MAS strategies [145,146].

3.6. Gene Expression Analysis

Genomic studies at the DNA level are especially useful for the development of MAS strategies. In addition, proteomic (proteins and enzymes), transcriptomic (RNA), and epigenetic (DNA methylation and histone modifications) studies are being applied to breeding programs. These strategies at genomic, epigenetic, transcriptomic, and proteomic levels should be all integrated for a better understanding of the molecular mechanisms involved in the most important plant breeding aspects, which will facilitate the development and optimization of molecular markers to apply in the field exploitation of new varieties, offering and integrating complete technological strategies [146].

Regarding the adaptation of *Prunus* species to different environments, transcriptomic studies have shown increased expression of specific genes such as Arabidopsis *AtNAC* transcription factors *ANAC071* and *ANAC096*, *AP2/ERF* transcription factors *RAP2.6L* and *WIND1*, and *xylan endoglucosyltransferase/hydrolase genes XTH19* and *XTH20* in rootstock healing tissues [147]. This gene plays a crucial role in the successful integration of the graft and the establishment of a functional connection between the rootstock and scion [148].

Regarding biotic stress, through a candidate gene approach (including a prior hypothesis that particular genes of interest contain variants that may be associated with a trait or disease) utilizing over 40 RGA-like resistance gene analogs and RAG-like genes linked to resistance against Plum pox virus, powdery mildew, and parasitic nematodes, the resistance map for *Prunus* was successfully mapped [149]. Recently, companies based in the United States of America, Hungary, and Scotland have introduced commercially available products containing bacteriophages to combat bacterial plant diseases [150]. In a groundbreaking discovery, bacteriophages with activity against Phenol-soluble modulin *Psm NA3,* the pathogen responsible for bacterial canker, were isolated for the first time from cherry, plum, and apricot orchards across England [151].

Gene mapping has been utilized to identify resistance genes against pests and diseases in stone fruit, employing cross populations from known resistant sources and high-throughput analysis techniques such as microarray profiling and RNA-seq [152]. These advancements have facilitated the pinpointing of regions linked to desirable traits. Nevertheless, this process necessitates the phenotyping of extensive families and the development of markers covering the entire genome, which is a costly and time-consuming endeavor that previously focused on limited traits. Despite the quantitative inheritance of all crucial agronomic traits and the detection of numerous QTLs in *Prunus*, further work is essential before QTL-associated markers can be integrated into breeding selection programs.

The transport of mRNA between the rootstock and scion plays a crucial role in information transduction, facilitating rootstock–scion connections and contributing to plant phenotypic diversity [153]. These mRNAs have been demonstrated to be essential in enhancing traits in grafted plants, highlighting their significance in plant improvement [154]. Acting as signal molecules with regulatory functions, mRNA molecules can modulate plant phenotypic changes in target cells during transplantation [155]. Notably, m5C methylation has been identified as a key factor that triggers the long-distance transfer of mRNA between basal shoots in Arabidopsis grafting assays, shedding light on the mechanisms underlying this process [155].

Through the modulation of transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTGS), small RNAs (sRNAs) drive epigenetic modifications in plants, leading to the observed phenotypic variation during grafting and subsequent rootstock–scion recovery [148]. sRNAs, such as microRNAs (miRNAs) and small interfering RNAs (siRNAs), are pivotal in the growth and development of grafted plants [156]. In a grafting experiment involving a 'Gisela 6' sweet cherry rootstock grafted with an 'Emperor Francis' scion, it was demonstrated that the partial transfer of siRNAs from the rootstock to the scion conferred resistance to a virus in the non-transgenic sweet cherry scion [157].

On the other hand, grafting has critical implications for the success of the graft and the development and function of the scion, as it facilitates the transfer of DNA across short distances in cells near the junction with the rootstock [158]. Studies on grafted apple trees, through epigenomic and transcriptomic analyses, have revealed that grafted plants can inherit epigenomic elements from their donor plants [159]. Furthermore, Uthup et al. [160] reported significant alterations in DNA methylation patterns in grafted rubber trees. These studies suggest that the survival rate of grafts is positively associated with the level of DNA methylation changes that occur as a result of the grafting process [161].

The second wave of perennial woody domestication, catalyzed by the advent of grafting around 1800 BCE, paved the way for the widespread cultivation of new woody crops, particularly within the Rosaceae family [162]. In contemporary agriculture, grafting has significantly boosted the breeding efficiency of perennial crops [81]. By utilizing genetically diverse individuals as rootstocks, the enhancement of perennial crops is achieved, with each rootstock contributing distinct traits to the plant. Key mechanisms that facilitate rootstock–scion interactions during grafting include differential gene expression, the transfer of mRNA and sRNA, and DNA methylation [163].

3.7. Global Changes in the Genomes of the Prunus Genus and Future Prespectives

The scientific community has coined the term "winter weather whiplash" to describe abrupt and extreme shifts in weather patterns, ranging from drought to storms and heat to cold, that pose risks to both humans and natural systems [164]. Plants respond to stress primarily through transcriptional changes in inherited gene sets due to their rooted nature. This genetic adaptability allows new plant species to thrive in harsh environmental conditions, such as at high altitudes, contributing to the adaptive diversity of plants resulting from the natural colonization of new ecosystems.

Preserving genetic diversity in plant species through germplasm collections is crucial for breeders to adapt to future climate change scenarios [165]. Genetic modification through domestication involves selective pressure applied by plant breeders to specific populations, leading to the emergence of new gene variants through processes like polyploidy, structural changes in DNA, movement of transposable elements (TEs), copy number variants (CNVs), and combinations of these mechanisms [123].

Prunus mutants, selected or developed through controlled mechanisms, could prove beneficial in addressing these climate challenges, in addition to increasing the existent genetic variability. In addition, genome editing-mediated mutagenesis offers a swift approach to creating defined mutations in target genes, also using the observed *Prunus* variability, with the advantage of being regulatorily friendly, as new varieties do not require costly GMO approval or labeling. This method presents a promising perspective for addressing climate change concerns [165].

An array of sequenced genomes of Tibetan *Prunus*, including peach and related species, was also studied along an altitudinal gradient [130]. Intriguingly, the analysis revealed increased movement and replication of the short interspersed nuclear element (SINE) class of transposable elements (TEs) as a response to adaptation to high altitude. Certain SINE insertions have been identified to modulate the expression of genes linked to altitude adaptation. This adaptation strategy potentially facilitated the concentration of specialized metabolites by positioning these SINEs near crucial genes, such as those regulating phenolics that play a protective role in plants [130].

4. Conclusions

The *Prunus* genus contains many economically important tree products and exhibits domestication traits indicative of early grafting and cloning practices in long-generation perennials, particularly within the Rosaceae family. Archaeological evidence suggests a gradual process of maintaining and eventually cultivating wild species, or the hybridization of different populations of the same species, as evidenced by population genetic studies across the Silk Road. The distribution of *Prunus* crops along the Silk Road significantly influenced their domestication and adoption by farmers. As we strive to improve the genetic makeup of these fruits, understanding the genetics of new *Prunus* cultivars and discovering climate-tolerant accessions with distinct metabolic profiles are crucial. In this context, future research must include genetic studies on under-represented *Prunus* species or exploration of the impact of climate change on their genetic diversity. Adapting plant species to future climate change scenarios is of great importance for breeders, who can maintain genetic diversity through germplasm collections. From a molecular point of view, climate change poses significant challenges, and genetic changes, such as the enrichment and mobilization of the short interspersed nuclear element (SINE) class of transposable elements (TEs), may be uncovered through further genomic analysis. In addition, new gene variants can emerge through various processes, including polyploidy, structural changes in DNA, movement of transposable elements, copy number variants, and genetic modification facilitated by domestication and selective pressure from plant breeders.

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