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Review

Autochthonous Conifers of Family Pinaceae in Europe: Broad Review of Morpho-Anatomical and Phytochemical Properties of Needles and Genetic Investigations

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Abstract: Gymnosperms are a very old and small group of plants compared to angiosperms. Contemporary science recognizes about 650 extant conifers worldwide. This review focuses on species of the Pinaceae family found in Europe. There are 23 species from the genera *Abies*, *Larix*, *Picea*, and *Pinus*. Some of them are widespread in Europe, but others have fragmented and limited distribution and are classified as relic, endemic, or endangered. The aim of this review is providing cumulative information about the variability of needle morpho-anatomy, terpenes, and *n*-alkanes, as well as the genetics of the Pinaceae species, native to Europe. The first morpho-anatomical examinations of needles were conducted in the 19th century. A lot of species have been investigated up to now, but the population variability of many conifer species is still not known. The composition and abundance of terpenes differ between genera and families but also within the same genus, pointing to their taxonomic importance. *n*-Alkanes on the needle wax surfaces of conifers are sometimes very useful markers of species and population variability. The most abundant *n*-alkanes in *Abies* species are nonacosane (C29), hentriacontane (C31), or heptacosane (C27), whereas in *Larix decidua* and the majority of *Picea* species, C31 is predominant. C31 and C29 are the dominant *n*-alkanes in the genus *Pinus*. The most extensive population-genetic studies of European representatives of the Pinaceae family have focused on *Abies alba*, *Picea abies*, *Pinus nigra*, and *Pinus sylvestris*, but also examined endemic species such as *Abies borisii-regis*, *A. cephalonica*, *A. nebrodensis*, and *Picea omorika.* These studies hold significant practical value in assessing species' evolutionary potential, devising strategies for long-term species conservation, identifying centers of diversity, detecting relict and ancestral populations, unveiling cryptic species and hybrids, and elucidating the taxonomic significance of species. These investigations are of great value not only on the biodiversity level, but also on the levels of ecology, physiology, taxonomy, and evolution.

Keywords: Europe; Pinaceae; conifers; needle morphology; needle anatomy; terpenes; *n*-alkanes; genetic markers

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1. Introduction

Conifers, ancient plants with a history spanning at least 300 million years [1], thrived during the Jurassic period with over 100 species. Presently, there are approximately 650 extant conifer species worldwide, significantly fewer compared to angiosperm species.

The southernmost regions inhabited by conifers are the islands of New Caledonia (43 species) and Borneo (39 species), collectively hosting twice as many species as Europe. Europe only has 41 types of coniferous trees now, most of which are from the Pinaceae family [2]. In the phylogeny of extant conifer families (Pinophyta), the Pinaceae family is considered basal, although its fossil records appear later in geological time compared to those of other families [1]. According to [1] and references cited therein, the Pinaceae family first appeared approximately 155 million years ago (mya) during the Upper Jurassic (Kimmeridgian) period. Apart from Pinaceae, several other extant conifer families also emerged during the Middle Jurassic period: Taxaceae around 180 mya, Cupressaceae around 173 mya, and both Sciadopytiaceae and Cephalotaxaceae around 170 mya. A brief history of gymnosperms, their classification, biodiversity, phytogeography, and ecology was also published by Anderson et al. [3].

The aims of this study were to investigate how many Pinaceae species are native to Europe, to quote them, and to collect and list articles in terms of their morpho-anatomy, terpenes, and *n*-alkanes variability and their genetic properties. Based on this information, one could find unexplored species in terms of analyzed properties. According to our knowledge, this type of review has not been published so far.

The list of 23 extant species of Pinaceae in Europe is as follows:

- six *Abies* species:
  1. *Abies alba* Mill.—Silver fir,
  2. *Abies borisii-regis* Mattf.—Bulgarian fir,
  3. *Abies cephalonica* Loudon—Greek fir,
  4. *Abies nebrodensis* (Lojac.) Mattei—Sicilian fir,
  5. *Abies nordmanniana* (Steven) Spach—Caucasian fir, and
  6. *Abies pinsapo* Boiss—Spanish fir;
- two *Larix* species:
  7. *Larix decidua* Mill.—European larch, and
  8. *Larix sibirica* Ledeb.—Siberian larch;
- four *Picea* species:
  9. *Picea abies* (L.) H. Karst.—Norway spruce,
  10. *Picea obovata* Ledeb.—Siberian spruce,
  11. *Picea omorika* (Panč.) Pürkyne—Serbian spruce, and
  12. *Picea orientalis* (L.) Link—Caucasian spruce;
- eleven *Pinus* species with two or five needles in distributary:
  13. *Pinus brutia* Ten.—Turkish pine,
  14. *Pinus cembra* L.—Swiss pine,
  15. *Pinus halepensis* Mill.—Aleppo pine,
  16. *Pinus heldreichii* Christ.—Bosnian pine,
  17. *Pinus mugo* Turra—Dwarf mountain pine,
  18. *Pinus nigra* J.F. Arnold—Austrian pine,
  19. *Pinus peuce* Griseb.—Macedonian pine,
  20. *Pinus pinaster* Aiton—Maritime pine,
  21. *Pinus pinea* L.—Stone pine,
  22. *Pinus sylvestris* L.—Scots pine, and
  23. *Pinus uncinata* Ramond ex DC.—Mountain pine.

2. The Main Properties of European Conifers of the Pinaceae Family

European firs: *Abies alba*, *A. borisii-regis*, *A. cephalonica*, *A. nebrodensis*, *A. pinsapo*, and *A. nordmanniana* are conifers that, except for *A. nordmanniana*, are found in the Mediterranean environment [2,4–7]. Also, *A. alba* extends deep into the European continent to the Baltic Sea [8]. Other listed firs have fragmented and limited distributions. From a phylogenetic point of view, all the listed species belong to the section *Abies*; they have synonyms, as well as lower taxonomic categories. *A. alba* represents a species that is widespread and stands out among other firs for its economic value, followed by *A. nordmanniana* [2,4]. In optimal conditions, fir trees can reach up to 50 m in height and 1.5 m in diameter and live to be 200–500 years old. The wood has no resin or colored heartwood. Branches stand in vertebrae, mostly horizontally laid. The bark is greyish and smooth, later cracking in square scales. In some species, the needles are horizontally divided into two sides, green, flat, up to 2.5 mm wide, 17 to 30 mm long, rich in essential oils. Firs are monoecious species that bloom in spring and ripen the same year in October when the scales and seeds fall apart. Young cones are rich in turpentine and essential oils. The seed is yellowish, tightly fused with the wing, and carries a turpentine blister [7].

Larix decidua and *L. sibirica* are deciduous gymnosperms and fast-growing pioneer species, with a range in the Alps, Sudetes, Carpathians, and central Polish plains, and Siberian larch is also found in the north of Europe [2,4,6,9]. Both species have several synonyms and subspecies. Their trees can grow up to 40 m in height, and their trunks can grow up to 1.5 m and 1 m in diameter (Europaean and Siberian larch, respectively). When young, the bark is smooth, but in old age, it cracks and peels. Over time, the wood acquires a red heartwood, which has an intense resin smell. The branches are in the vertebrae, and the secondary branches are mostly hanging. The needles are in tufts, 30–40 together, about 3 cm long. Female and male flowers are located on the same branches; pollination takes place in the spring, and the seeds in small cones ripen in the same year.

The genus *Picea* includes about 40 species in the temperate northern hemisphere. In Europe, we find *P. abies*, which is one of the most important species of forest trees in Central Europe [10], then the endemic-relict species of intermittent range *P. omorika* [11], then *P. orientalis* and *P. obovata*. All species have synonyms, and *P. abies* stands out in particular because it has a high number of synonyms and lower taxonomic units [2,10]. Spruces grow up to 40 m in height and over 1 m in thickness, except for *P. obovata*, which is much lower [2,4]. Spruces develop a shallow root system and suffer from wind blasts. Their bark is thin, grayish, cracked, but smooth on young trees. The needles are rhombic in cross-section and pointed at the top, they are up to 15 to 25 mm long and 1 mm wide and remain on the branches for 7 years or more. Species of the genus *Picea* are monoecious plants. They bloom from April to June, depending on exposure and altitude. The cones ripen in the second half of September; they are brown, and the seeds fall out of them until January–March. The seeds are black to brown, up to 4 mm long, ovoid, and have transparent wings that are easily separated from the seed [2,4,12].

In the genus *Pinus* from the conifer subclass, we find about 100 species in the northern hemisphere, from the polar region to the tropics around the Equator [2,4]. They are systematically divided into several sections, and in Europe, we find the section *Pinus* (two-needle pines with two subsections: *Pinus* and *Pinaster*) and the section *Strobus* (five-needle pines) [6].

In the subsection *Pinus*, we found *P. mugo*, *P. uncinata* [11], *P. nigra*, and *P. sylvestris.* According to some research, *P. mugo* and *P. uncinata* belong to the same species, so they are subspecies, i.e., lower taxonomic categories [13]. All *Pinus* species have numerous synonyms. *P. nigra* and *P. sylvestris* grow up to 50 m in height [3]. The trees have cracked bark, the branches are in vertebrae, and the buds are up to 1–2 cm long; they flower and pollinate during May. The cones, 4 to 8 cm long and 2 to 4 cm wide, ripen in the second year after flowering. Seeds are grayish brown to dark brown, about 3–7 mm long and 2–4 mm wide. Their wood is valued for its durability, but they are used to a limited extent due to the large amount of resin in the wood [2,4]. *P. mugo* and *P. uncinata* grow on high mountains, from 1400 m to 2000 m [13]. *P. mugo* grows in the Alps, Dinarides, and Carpathians, while *P. uncinata* grows in the Western Alps and Pyrinees [13]. They usually grow as bushes lay down on the ground. Their bark is reddish-ashy, quite thin, and cracks in the form of small scales. Buds are elongated ovoid. They bloom in June and July and ripen in the third year after flowering. The cones are 2–7 cm long and 2.5 cm wide. The wood is not appreciated, but these two species are important in preventing soil erosion, torrents, and avalanches on high mountains.

The subsection *Pinaster* is represented by the following: *Pinus heldreichii* (relict and Balkan subendemic), *P. halepensis*, *P. brutia*, *P. pinaster*, and *P. pinea* [2,4]. All these species grow in a distinctly Mediterranean climate except for *P. heldreichii*, which grows on the high mountains of the sub-Mediterranean [14]. Morphologically, these species are distinctly differentiated from each other, for example, *P. pinea* with an umbrella canopy and *P. heldreichii* with its plate-like canopy and longevity [2,4,9]. *P. halepensis* and *P. brutia* are morphologically very similar, while *P. pinaster* in its characteristics is between them and the previously described species. They can grow up to 20–30 m in height, with a diameter of over 1 m. They bloom in May and June, and the cones ripen in the second year, except for *P. halepensis* and *P. brutia* where they can remain closed for several years and only be opened by fire. Their wood is valued for the durability that the resin gives it [2,4].

The five-needle pine section *Strobus* in Europe is represented by *Pinus cembra* and the relict-endemic species *P. peuce*. *P. cembra* grows in the Alps and the Carpathians at altitudes above 1400 m, while *P. peuce* is found in the mountains of the southwestern and southeastern Balkans [2,6,9]. They grow up to 20 and 40 m in height, respectively. The trees have dark gray fissured bark, and branches are located in vertebras. Buds are up to 1–2 cm long; they flower and pollinate during May–June [4,5]. The cones of these species are of different lengths and shapes and 3–5 cm wide; they ripen in the second year after flowering. The seeds are dark, about 3–7 mm long and 2–4 mm wide. The wood of *P. cembra* is hard and valued for its durability, while the wood of *P. peuce* is less used because of the resin in the wood [9].

3. Morpho-Anatomical Needle Characteristics of Listed European Conifers

The first compressive morpho-anatomical investigations of needles were published in the 19th century [15]. By incorporating anatomical tests, it becomes possible to identify hybrids or lower taxonomic units with a relatively high level of certainty. Needle morphology is instrumental in species identification and their classification within plant systematics [16]. For example, needle length can be critical in identifying hybrids (Florence, 1973; Snyder and Hamaker, 1978 as cited in [17]). Hybrids can also be verified by the number and position of the resin ducts. Lower systematic units, like in *Pinus nigra* Vidaković 1982, as cited in [2] along with ecotypes, provenances, geographical races, and the impact of external environmental factors, can be verified through morpho-anatomical examinations (as cited in [17] and references therein). The number of hypodermis layers can indicate population diversity [18]. Sometimes, the results of morpho-anatomical analyses of needles are validated through comparison with chemical [19] or genetic analyses [20,21].

The largest number of morpho-anatomical studies of European Pinaceae species have focused on *Abies alba*, *Picea abies*, *Pinus halepensis*, *Pinus nigra*, and *Pinus sylvestris*, which is understandable considering their widespread distribution, but attention has also been given to endemic and relict species such as *Picea omorika*, *Pinus heldreichii*, and *Pinus peuce*.

They remain intriguing both in terms of their variability and taxonomic as well as phylogenetic classification (Table 1). The observed variations within the species undoubtedly stem from factors such as the source of the examined trees (whether from natural populations or artificially cultivated plantations), ecological conditions, as well as the age of the needles under examination and the methodology employed for anatomical preparation.

Table 1. Morpho-anatomical characteristics of leaves (needles) of 23 European Pinaceae species.

Morphological Properties		Anatomical Properties						
Length (mm)	**Width (mm)**	**Thickness (mm)**	**Epidermis Thickness (µm)**	**Hypodermis Thickness (µm)**	**No of Resin Ducts**	**Resin Ducts Diameter (µm)**	**Country**	**Reference**
				1. *Abies alba*				
15–30	2–2.5							[2]
17.9–22.0	2.1–2.4 (2.3)	2.1–2.4	17–77 (36.7–51.3)	13.0–44.5 (25.9–32.1)	(2)	49.5–297.0 (133–164)	North Macedonia	[22] *
10–29 (18.9)	1.3–2.4 (1.9)	0.6–1.3 (1.0)		13–26 (17.0)	(2)	44.0–180.0 (110)	Poland	[23] *
12–23 (16.8)	1.7–2.5 (2.1)	0.8–1.3 (1.1)		13–31 (22)	(2)	70–200	Poland	[24] *
						(150)	Romania	[25]
9–31 (18.8)	1–2.5	(0.4–1)	7–21	9.9–26.6	(2)	67–172	Serbia	[26]
24.7	1.9	0.6	18.0	17.9	(2)	104.8	Greece	[27] *
23.2	1.9	0.66	20	19	(2)	101	NE Europe	[28] *
(13–25)	(1.9–2.1)	(0.2–0.4)	(18–24)		(2)		Germany	[29] *
				2. *Abies borisii-regis*				
≤30								[2]
(17.1–24.8)	(2.0–2.2)	(0.6–0.65)	(18–19)	(41)	(2)	(65–70)	Bulgaria, Greece	[30] *
				3. *Abies cephalonica*				
20–25								[2]
20–21	18.2–20.0						Greece	[31] *
20.4	2.2	1.0	25.8	21.5	(1.99)	91	Greece	[27] *
20.5	2.1	1.0	26	22	(2)	86	Turkey	[28] *
(17.1–26.8)	(1.8 –1.9)	(0.8)	(19–21)	(40.5–45.8)	(2)	(60–62)	Greece	[30] *
				4. *Abies nebrodensis*				
10–12								[2]
14.9	2.2	0.9	25.1	21.7	(2)	83	Italy (Sicily)	[27] *
				5. *Abies nordmanniana*				
15–30	2–2.5							[2]
						(100)	Romania	[25]
23	1.9	0.8	23	19	(2)	78	Turkey	[28] *
				6. *Abies pinsapo*				
8–15								[2]
(10.6–13.3)	(2.2–2.3)	(1.1–1.25)	(23.4–25.2)	(22–23)	(1.97)	(130)	Spain	[32] *
11.9	2.2	1.2	26	21	(2)	131.5	Spain	[28] *
				7. *Larix decidua*				
20–40						5–7.5		[33]
10–30	<1							[2]
				8. *Larix sibirica*				
30–40	≤1							[2]
				9. *Picea abies*				
10–20 (25)	1.0							[2]
15–25								[34]
12–24						30	Romania	[35]
(18.1–19.1) * (18.6)	(1.09–2.5)	(0.3–1.95)	(8.1–25.5)	(9.9–26.3)	(2)	(33.0—172.4)	Serbia	[26] *
9–13.3	0.55–0.98	0.9–1.2						[36]
12.06 ± 2.08	0.96 ± 0.11		3.1				Artificial origin	[37]
10–20 (25)	1.0							[2]
				10. *Picea obovata*				
10–18								[2]
				11. *Picea omorika*				
10–20	≤2							[2]
15.2–18.5	2.4–2.8		12.5–19.9	9.5–20.0				[38]
(9.0–13.3)	0.95–1.94							[39]

9.9								
≤22								[34]
(12.1–19.7) 15.5–19.0	(1–2.1) 1.3–1.7	0.7–0.9				70.7–87.3		[40]
-	(1.1–1.8) 1.4	(1.1–1.8) 1.4	(0.6–0.9) 0.8			28.0–165.0 (81.5)		[41]
(8–20.5) 13.6 ± 0.06	(0.9–2.2) 1.49 ± 6.32	(0.5–1.2) 0.8 ± 3.1	(16.6–29.1) 22.8 ± 0.10	(12.5–25.0) 17.5 ± 0.09	0–2 (0.74)	(16.6–145.6) 51.2 ± 0.62	Serbia	[17] *
13.74 ± 2.04	0.87 ± 0.15		1.1					[37]
12. *Picea orientalis*								
6–8 (10)								[2]
6–12								[34]
13. *Pinus brutia*								
120–180	1–1.5	0.6–0.8	14–18	62–77	3–10	62–77 (108)		[2]
171.0	1.05	0.57			(10.1)		Greece	[42] *
136.1	1.12	0.68			(9.84)		Greece	[43] *
107.2–125.0 (116.6)	1.09–1.26 (1.17)	0.70–0.84 (0.75)			(1.31–3.0) (2.15)		Italy, plantation	[18] *
122–137	1.07–1.24				(7.38–9.71)		Krit, Greece	[44] *
150								[34]
14. *Pinus cembra*								
50–80 (120)	1							[2]
71							Turkey	[45]
80								[34]
15. *Pinus halepensis*								
60–100	0.79–1.20	0.5– 0.7		77–85	2–10	77–85		[2]
(102.8–143.9)	(0.81–1.03)	(0.49–0.69)			(4.68–8.60)		Greece	[42] *
92	0.95	0.58			(6.83)		Greece	[43] *
60–110								[34]
66							Mediterran	[45]
107.4–119.2							Spain	[46] *
16. *Pinus heldreichii*								
60–100	1.5–2							[2]
60–80							Serbia	[47] *
60–90								[34]
51–102 (71)	1.2–1.8 (1.5)	0.6–1.1 (0.8)	12.5–23.6 (17.7)		3–11	24–123	Yugoslavia	[48] *
35–113 (71–77)							Greece	[49] *
50–98 (72)							Greece	[50] *
-		9–10	25.8–27.8	29–30.6	2–11 (5.5)	110	Serbia	[51] *
-		9	27.3	28.8	3–10 (6.1)	92.4	Bosnia & Herzegovina	[51] *
-	-	9	27.3	26.6–29.2	2–12 (5.7)	76.3	Bulgaria	[51] *
60–100	1.30–1.34	7.5–8.4	16–22		(4)		Serbia	[52] *
85–124 (97)	1.3–1.5 (1.4)	7–9 (8)			3–5 (4.5)	37.5–97.5 (67.5)	Serbia	[53] *
63–116 (72–100)	1.4–1.6	9–10			4–10	60–135	Serbia	[54] *
96–104	1.2–1.5	6–8			5–6.3		Bulgaria	[55] *
59.5–82.0	1.22–1.31	0.71–0.76			(2.42–3.86)		Bulgaria	[56] *
59–155 (83)	1.5	9	16.6–25.0 (22.4)	17.6	4–10	65	Serbia	[57] *
51–123 (73–82)	1.4–1.5		11.4–37.5	19–23.5	0–13	22–51	Montenegro	[57] *
17. *Pinus mugo*								
30–40	1.5–2							[2]

(8)								
40–60								[34]
46.2–132.6								[58] *
46.7	1.4	0.8	0.4					[59] *
				18. *Pinus nigra*				
80–160	1–2							[2]
ssp. *nigra*	1.58	0.97	22–40	14–29	(9.5)			[2]
ssp. *gočensis*	1.44	0.85	22–32	14–25	(8.3)			[2]
var. *illyrica*	1.50	0.91	18–32	14–29	(7.6)			[2]
ssp. *dalmatica*	1.76	1.08	25–40	18–34	(11.1)			[2]
ssp. *pallasiana*	1.68	0.99	18–32	22–36	(7.4)			[2]
120–160								[34]
129	1.7	1.0			2–16 (8.4)		Greece	[60] *
					7–12.6		Croatia (Dalmatia)	[61] *
124	1.4	1.0			(6)		Croatia	[62] *
				19. *Pinus peuce*				
70–100	<1							[2]
70–120	1.0	7.2–7.6	13–16	≤ 26–32	(2)		Serbia	[52] *
80–120								[34]
114							Mediterran	[45] *
48–102 (71.4)	0.58–1.79 (0.86)	0.44–0.93 (0.66)	6.7–21.2 (13.3)	9–30 (16.2)	0–2 (1.98)	18.4–111.9 (52.5)	Serbia and Montenegro	[63] *
				20. *Pinus pinaster*				
100–200								[2]
197							Mediterran	[45] *
				21. *Pinus pinea*				
100–150	1.5–2							[2]
<160								[34]
				22. *Pinus sylvestris*				
40–70	2							[2]
50–70								[34]
51	1.3	0.7		24.5	(9.7)			[64] *
45.5	1.4	0.7	0.3					[59] *
	1.1	0.5	25.6		(9.8)			[65]
65	1.2	0.7						[66]
				23. *Pinus uncinata*				
49–82 (66.4)	132–199 (160)	77–106 (91)	28–38 (32)		1–5.7 (3.6)			[67] *

Mean values are given in parentheses; * population studies.

The degree of variation in needle characteristics corresponds to their geographical distribution. For instance, when comparing results for *A. alba* across North Macedonia, Poland, Serbia, Greece, Germany, and NE Europe, it is evident that needle length in the Serbian population has the greatest variation (9–31 mm). This can be attributed to the collection site where the common fir coexists with its pyramidal variety (Table 1). The greatest variation in Serbia could be the consequence of its very variable environmental conditions, too. Furthermore, certain species, such as *Pinus halepensis* and *Pinus brutia* in Greece, are known to form spontaneous interspecies hybrids, the confirmation of which often relies on a combination of morphological and genetic markers [20]. Also noteworthy are the findings regarding the wide range of diameters of resin ducts in *A. alba* in North Macedonia (Table 1) [22]. Additionally, the information regarding *P. heldreichii* and *P. omorika*, known for their high interpopulation variability, exhibits notable diversity (Table 1), [17,57]), a trait attributed to their endemic-relict status. Influence of genetic and environmental factors to such variation surely exists, but their part in overall variation were not examined.

4. Terpene Composition of Needles of Listed European Conifers

Terpenes constitute the largest and most abundant group of secondary metabolites [68] present in nearly all plants, including both gymnosperms (where they often dominate) and angiosperms. Conifers, in particular, are known to contain many monoterpenes, diterpenes, and sesquiterpenes [69]. While not essential for growth and development, certain terpenes play a crucial role in plant defense against various stressors ([68,70], and references cited therein). Essential oils exhibit antioxidant properties [71] and possess bioactive characteristics such as antimicrobial, antifungal, and toxic effects [72–74], primarily due to their terpene composition. Consequently, they can serve as effective repellents [75], sources of fruity aromas [76], and geroprotectors [77].

Furthermore, terpenes can play a crucial role in detecting interspecific hybrids [78], as well as lower taxonomic categories [79,80] and chemotypes [81], and are frequently employed in chemosystematics to delineate differences between genera [82,83] and subsections [84] and in determining the systematic position of endemic-relict species [85] and other conifers [86].

The composition and abundance of terpenes differ not only between genera and families but also within the same genus [87,88]. They also exhibit seasonal variations [89] and can differ across various tissues within the same species [90] with certain terpenes being regulated by genetics [91].

In some conifers, a correlation has been identified between terpene composition in wood and needles [92]. Our knowledge of terpene biosynthesis and the origin of their skeletal structures [93,94] continues to evolve and expand.

The main terpene compounds of needles of 23 European Pinaceae species are given in Table 2.

Table 2. The main terpene compounds of leaves (needles) of 23 European Pinaceae species.

Main Terpene Compounds						Origin	Reference
1	**2**	**3**	**4**	**5**	**6**		
1. *Abies alba*							
Bornyl acetate > *	Camphene >	3–Carene =	Tricyclene >	Limonene		Artificial	[95]
β-Pinene >	Limonene/β-Phellandrene >	Camphene >	α-Pinene >>	Tricyclene >	Bornyl acetate	Bosnia and Herzegovina, Serbia, North Macedonia, Bulgaria	[96]
β-Pinene >>	α-Pinene >	Camphene >	Limonene >	Bornyl acetate >	β-Phellandrene	Bosnia and Herzegovina, Serbia, North Macedonia, Bulgaria	[72]
2. *Abies borisii-regis*							
β-Pinene >	α-Pinene >	Camphene >	Limonene/β-Phellandrene>	Tricyclene >	(*E*)-Caryophyl-	Bulgaria, Greece	[96]
β-Pinene >	α-Pinene >	(*E*)-Caryophyl- >	Limonene >	Camphene >	Bornyl acetate	Bulgaria, Greece	[72]
3. *Abies cephalonica*							
β-Pinene >	α-Pinene >>	Camphene >	Limonene/β-Phellandrene>>	Tricyclene >	Myrcene	Greece	[96]
β-Pinene >	α-Pinene >>	Camphene >	β-Phellandrene >	Limonene >	Bornyl acetate	Greece	[72]
4. *Abies nebrodensis*							
β-Pinene >>	α-Pinene >	Camphene >	β-Phellandrene >	Santene =	Bornyl acetate	Artificial	[97]
5. *Abies nordmanniana*							
α-Pinene >	β-Myrcene >	β-Pinene =	Camphene			Georgia	[98]
δ-3-Carene >	β-Caryophyl- >	Camphene =	α-Chumullene =	α-Pinene >	*p*-Cymene	Turkey	[99]

7. *Larix decidua*							
α-Pinene >>>	β-Pinene >	Myrcene >	δ-3-Carene >	β-Phellandrene =	Limonene	Germany	[100]
8. *Larix sibirica*							
δ-3-Carene >	α-Pinene >	β-Pinene >	β-Phellandrene >	Germecrene D >	Terpinolene	Russia	[101]
9. *Picea abies*							
Camphene >	Limonene >	α-Pinene >	Myrcene >	Limonene >	Tricyclene	Sweden	[102]
10. *Picea obovata*							
Bornyl acetate >>>	Camphene >	Limonene >	α-Pinene >	δ-3-Carene >	β-Myrcene	Southern Siberia	[101]
11. *Picea omorika*							
Bornyl acetate >>>	Limonene >	Camphene >	Isoborneol =	Exoborneol >	γ-Cadinene	Bosnia and Herzegovina	[103]
Bornyl acetate >>	Camphene >	α-Pinene >	Limonene >	α-Cadinol >	Santene	West Serbia	[104]
12. *Picea orientalis*							
Bornyl acetate >	Limonene/β-Phellandrene>	δ-3-Carene >	β-Pinene >	β-Myrcene >	α-Pinene	Turkey	[105]
13. *Pinus brutia*							
β-Pinene >>	α-Pinene >	Germacrene D >	3-Carene			Greece	[106]
Tricyclene >	β-Pinene >	α-Pinene >	Myrcene =	δ-3-Carene >	Thujene	Greece, artificial	[78]
β-Pinene >>	α-Pinene >	β-Caryophyllene >>	α-Humulene >	δ-3-Carene >	α-Terpineol	Morocco	[107]
α-Pinene >>	β-Pinene >	Myrcene				Italy, artificial	[90]
β-Pinene >	α-Pinene >>>	Limonene >	Myrcene			Portugal	[108]
β-Pinene >	α-Pinene >>>	δ-3-Carene >	β-Caryophyllene >	Limonene/β-Phellandrene		Turkey	[109]
β-Pinene >>	α-Pinene >	β-Caryophyllene >	α-Terpineol >	δ-3-Carene >	Myrcene	Turkey	[110]
β-Pinene >	α-Pinene >	Germacrene D >	β-Caryophyllene >	Myrcene =	α-Terpinyl acetate	Greece or artificial	[88]
14. *Pinus cembra*							
α-Pinene >>>	Limonene/β-Phellandrene =	α-Cadinene				Romania	[111]
Germacrene D =	α-Pinene >	β-Phellandrene >	Bicyclogermacrene >	β-Pinene >	δ-Cadinene	Greece or artificial	[88]
α-Pinene >	Limonene >	β-Phellandrene >	β-Pinene >	δ-Cadinene >	Germacrene D	Poland, Artificial origin	[112]
15. *Pinus halepensis*							
α-Pinene >	Limonene >	β-Pinene >	Germacrene D			Greece	[106]
α-Pinene	β-Myrcene	β-Caryophyllene	Terpinolene	Sabinene	β-Pinene	Morocco	[107]

>	>	>	>	>			
Myrcene >	α-Pinene >>	β- Caryophy-llene >	Terpinolene >	Sabinene >	α-Humulene	Italy	[113]
α-Pinene >>	Myrcene >	Sabinene >	δ-3-Carene >	β-Pinene		Italy Artificial origin	[90]
(*Z*)-β-Caryo-phyllene >>>	α-Humullene =	Aromadendrene >	Myrcene >	α-Pinene >	Sabinene	Algeria	[114]
α-Pinene >	β-Pinene >	Myrcene >	Limonene >	Camphene =	α-Phellandrene	Portugal	[108]
α-Pinene >>	β-Caryophyl- >	Caryophyllene >	β-Myrcene >	β-Pinene =	α-Humulene	Turkey	[109]
β-Pinene >	α-Pinene >	β-Caryophyllene >	Germacrene D >	Limonene >	α-Terpinyl ace-tate	Turkey	[110]
β-Caryophyllene >	β-Myrcene >	α-Pinene >	α-Humulene >	β-Pinene >	Sabinene	Greece or artificial	[88]
(*E*)-Caryo-phyllene >	Thunbergol >>	Phenylethyl 3-methylbutanoate >	α-Humulene >	Myrcene >	α-Pinene	Greece	[115]
Caryophyllene >	β-Pinene >	α-Pinene >	Cembrene >	α-Hu-mulene >	β-phenylethyl isovalerate	Morocco	[116]
16. *Pinus heldreichii*							
Germacrene D >	Limonene >	β-Caryophyllene >				Serbia	[117]
Limonene >>	α-Pinene >	Germacrene D >	(*E*)-Caryophyllene >	Aristolene >	β-Pinene >	Greece	[118]
Limonene >>	α-Pinene >	Germacrene D >	(E)-Caryophyllene >	β-Pinene >	δ-3-Carene >	Greece	[106]
Limonene >	Germacrene D >	β-Caryophyllene >	δ-3-Carene >	β-Pinene >	β-Myrcene	South West Serbia	[119]
Limonene >	Germacrene D >	δ-3-Carene >	α-Pinene >	β-Pinene >	Myrcene	Natural or artificial origin	[88]
Germacrene D >	Limonene >	α-Pinene >	β-Caryophyllene >	β-Pinene		North Macedonia	[15]
Limonene >>	Germacrene D >	α-Pinene >	(E)-Caryophyllene >			Serbia (Kosovo)	[120]
Limonene >	Germacrene D >	α-Pinene >	(E)-Caryophyllene >	β-Pinene		Serbia and Monte-negro	[121]
Limonene >	α-Pinene >	Germacrene D >	β-Pinene >	β-Caryo-phy-llene >	β-Myrcene	Serbia (Kosovo)	[122]
Limonene >	α-Pinene >	Germacrene D >	β-Pinene >	Myrcene >	α-Humulene	Bulgaria	[115]
17. *Pinus mugo*							
δ-3-Carene >	α-Pinene >	β-Pinene >	β-Phellandrene			Serbia	[123]
Bornyl acetate >	α-Terpineol >	(*E*)-Caryophyl- >	α-Cadinol >	Terpinen-4-ol		Italy	[124]
α-Pinene >	Germacrene D >	δ-3-Carene >	Myrcene >	Sabinene		Greece or artificial	[88]
δ-3-Carene >	α-Pinene >	β-Pinene >	Limonene/β-Phel-landrene >	Ger-macrene D		Serbia (Kosovo)	[125]
δ-3-Carene	β-Phellandrene	α-Pinene	β-Caryophyllene	β-Pinene	Germacrene D	Slovenia	[126]

>	>	>	>	>			
α-Pinene >	δ-3-Carene >	(E)-Caryophyllene >	Germacrene D >	Limonene >	β-Pinene	Serbia (Kosovo)	[120]
δ-3-Carene >	α-Pinene >	Limonene/β-Phel-landrene >	(*E*)-Caryophyllene >	β-Pinene		South Serbia and surroundings	[84]
δ-3-Carene >	α-Pinene >	Limonene/β-Phel-landrene >	Terpinolene >	Bornyl ace-tate >	(*E*)-Caryo-phyllene >	Southwest and South Serbia	[127]
δ-3-Carene >	β-Phellan-drene >	α-Pinene >	(*E*)-Caryophyllene >	Bornyl ace-tate >	Terpinolene	Bulgaria	[128]
δ-3-Carene >	α-Pinene =	α-Terpinolene >	β-Phellandrene >	β-Caryo-phy-llene >		Serbia (Kosovo)	[122]
α-Pinene >	δ-3-Carene >>	Limonene/β-Phel-lan-drene >	β-Pinene >	Camphene >	Terpinolene	J. Alps, Carpathi-ans and Balkan Peninsula	[129]
			18. *Pinus nigra*				
α-Pinene >	Germacrene D >	Limonene >	β-Pinene			Greece	[106]
α-Pinene >>	Myrcene >	Terpinolene >	Sabinene >	δ-3-Carene >	β-Pinene	Portugal	[108]
α-Pinene >>>	Caryophy-llene oxide >	18-norabieta-8,11,13-triene >	Dehydroabietal >	Palustral >	Abieta-8,11,13-triene	Turkey	[109]
α-Pinene >>	β-Pinene >	Germacrene D >	β-Caryophyllene			Turkey	[110]
Germacrene D >	α-Pinene >	β-Caryophy-llene >	β-Pinene >	α-Hu-mulene >	δ-Cadinene >	Greece or artificial	[88]
α-Pinene >	Germacrene D >>	(*E*)- Caryophyllene >	β-Pinene >	Limonene		Serbia	[79]
Germacrene D >>	(E)-Caryo-phyllene >	δ-Cadinene >	α-Humulene			Serbia	[84]
α-Pinene >	Germacrene D >>	(E)- Caryophyllene >	β-Pinene >	Limonene		Serbia	[121]
α-Pinene >	Germacrene D >	β-Pinene >	Limonene/β-Phel-landrene			South Serbia	[127]
α-Pinene >	β-Pinene >	Camphene >	Germacrene D >	Limonene >	β-Caryophyllene >	Serbia (Kosovo)	[122]
			19. *Pinus peuce*				
Isobornyl acetate >>	Caryophyllene oxide >	Isoborneol >	Terpinenyl acetate >	α-Pinene		Montenegro	[130]
α-Pinene =	γ- Muuro-lene >	δ-3-Carene =	Sabinene =	Bornyl ace-tate		Serbia	[117]
α-Pinene =	β-Pinene >	Citronellol >	Bornyl acetate			Greece	[131]
α-Pinene >	Germacrene D >	β-Pinene >	(*E*)-Caryophyllene >	Myrcene		Greece	[118]
α-Pinene >	Germacrene D >	β-Pinene >	(*E*)-Caryophyl- >	Myrcene		Greece	[106]
α-Pinene >	Bornyl acetate >	β-Pinene >	Camphene >	α- Terpinyl acetate		Republic North Macedonia	[132]

α-Pinene >	Germacrene D >	β-Pinene >	β-Caryophyllene >	Bornyl acetate >	Camphene	Natural or artificial origin	[88]
α-Pinene >	β-Pinene >	Germacrene D >	α-Terpineol >	Camphene >	β-Phellandrene	Serbia (Kosovo)	[120]
α-Pinene >>	Germacrene D >	Camphene >	β-Pinene =	Bornyl acetate >	(*E*)-Caryophyllene	South West Serbia, South Serbia and Montenegro	[121]
α-Pinene >>>	β-Pinene >	Camphene =	Bornyl acetate >	Germacrene D >	Limonene/βPhellandrene	South Serbia	[127]
α-Pinene >	β-Pinene >	Camphene >	Germacrene D >	Limonene	β-Myrcene	Serbia (Kosovo)	[122]
20. *Pinus pinaster*							
β-Pinene =	Germacrene D >	α-Pinene >	β-Caryophyllene >	Limonene >	δ-3-Carene	France Artificial	[133]
α-Pinene >	Germacrene D >	(*E*)-Caryophyl- >	Cembrene >	α-Humulene >	δ-Elemene	Greece	[118]
α-Pinene >	Germacrene D >	(E)-Caryophyllene >	Cembrene >	α-Humulene >		Greece	[106]
β- Caryophyllene =	α-Pinene >>	γ-Muurolene >	Guaiol =	α-Humulene >	D-Limonene	Morocco	[107]
β- Caryo-phyllene >	Germacrene D >	Phenylethyl-3-methyl 1 butanoate >	α-Humulene >	δ-Cadinene		Italy	[113]
β-Pinene >	α-Pinene >>	Myrcene >	Limonene			Portugal	[108]
β-Pinene >	α-Pinene >>	Myrcene >	Limonene/β-Phellandrene >	δ-3-Carene		Spain	[134]
Isoabienol >	Sclarene >	Germacrene D >	Abietadiene >	Abienol >	Abietatriene	Greece or artificial origin	[88]
α-Pinene >	β-Caryophyl- >	Abietadiene >	β-Pinene >	Rimuen >	Abietatriene	Turkey	[109]
α-Pinene >>	β-Pinene >>	β-Caryophyllene >	β-Myrcene >	Germacrene D >	Limonene	Portugal	[135]
21. *Pinus pinea*							
Limonene >>	Germacrene D >	α-Pinene >	β-Pinene			Greece	[106]
Limonene >>>	β-Phellandrene >	α-Pinene >	Myrcene >	β-Pinene		Italy	[113]
Limonene/β-Phellandrene >>>	α-Pinene >	β-Pinene				Turkey	[109]
α-Pinene >>>	Farnesyl acetate >	Phenylethyl isobuturate >	α-Eudesmol >	β-Pinene >	Farnesol	Morocco	[107]
Limonene >>>	α-Pinene >	Myrcene >	β-Pinene			Portugal	[108]
β-Pinene >>>	α-Pinene >	Germacrene D >	α-Terpineol >	β- Caryophyllene >	Myrcene	Turkey	[110]

Limonene >>>	Abienol >	Sylvestrene >	α-Pinene >	Germacrene D >	Methyl levopimarate	Greece or artificial origin	[88]
22. *Pinus sylvestris*							
α-Pinene >	β-Pinene >	Limonene >				Turkey	[136]
α-Pinene >	β-Pinene >	δ-3-Carene >	Myrcene >	Limonene >	Terpinolene	Portugal	[108]
18-norabieta-8,11,13-triene >	α-Pinene >	Caryophyllene oxide >	Dehydroabietal >	Abieta-8,11,13-triene >	19-norabieta-8,11,13-triene	Turkey	[109]
α-Pinene >>	Germacrene D =	β-Pinene >	β- Caryophy-llene >	δ-Cadinene		Turkey	[110]
α-Pinene >>>	n.i. >	δ-Cadinene >	Bicyclogermacrene >	Germacrene D >	β-Caryophyllene	Greece or artificial origin	[88]
α-Pinene >>>	δ-Cadinene >	δ-3-Carene =	β-Pinene =	Germacrene D		South Serbia	[127]
α-Pinene >>	β-Pinene >	δ-Cadinene >	Germacrene D >	β-Myrcene	β-Caryophyllene	Serbia (Kosovo)	[122]
23. *Pinus uncinata*							
Bornyl acetate >	α-Pinene >	(*E*)-β-Caryo-phyllene >	Limonene >	Camphene >	Myrcene	Poland	[137]

*—symbols refer to Petrakis et al. 2001 [118] are used to denote differences in compound amounts presented as percentages of total terpene amount: 0.1–1.0% (=); 1.1–5.0% (>); 5.1–15.0% (>>); more than 15.0% (>>>).

All species of the family Pinaceae and the genus *Abies* (species 1–4) have notable levels of α-pinene and β-pinene (Table 2). The primary terpene compound found in natural populations of *Abies* species is β-pinene, followed by α-pinene and camphene (refer to Table 2). Interestingly, in the population from Georgia, α-pinene is the most abundant, while in artificial plantations of *A. alba*, bornyl acetate dominates, and *A. nordmanniana* exhibits a prevalence of δ-3-carene.

The terpene profiles of *Larix decidua* and *L. sibirica* differ significantly, beginning with their main components (α-pinene and δ-3-carene, respectively) (Table 2).

α-Pinene is found in the profiles of the main terpene components in almost all analyzed species of the genus *Picea* with bornyl acetate emerging as the most prevalent component (species 9–12, Table 2).

Within the natural populations, β-pinene and α-pinene are predominant in *Pinus brutia*, while α-pinene dominates in *P. cembra*. In *P. halepensis*, alongside these, myrcene and caryophyllene occasionally appear (as shown in Table 2). In natural populations of *P. heldreichii*, limonene or germacrene D are the most abundant, accompanied by notable levels of α- and β-pinene. In all presented results for *P. mugo*, δ-3-carene or α-pinene dominate, except in samples from Italy, where bornyl acetate is the most abundant and α- and β-pinene are absent. In *P. nigra*, α-pinene and, occasionally, germacrene D dominate. The population from Turkey exhibits different abundant components compared to other populations (Table 2).

In all the data presented for *P. peuce*, α-pinene is the dominant component. However, in the population from Montenegro, isobornyl acetate takes precedence, and the other major components also show significant differences. In natural populations, *P. pinaster* is dominated by α-pinene and β-caryophyllene, while artificial populations exhibit some other components. Limonene is the prevailing compound in the leaves of *P. pinea*, with α- or β-pinene appearing less frequently. In most of the presented data for *P. sylvestris*, α-pinene is predominant, while in *P. uncinata*, bornyl acetate is the primary compound.

The variations in the obtained results may arise from differences in the origin of the needles, as well as potential sampling errors and discrepancies in the conditions of chromatographic analyses.

5. *n*-Alkane Composition of Needles of Listed European Pinaceae Species

The leaves of conifer species have various aliphatic compounds in their epicuticular waxes, including fatty acids, primary alcohols, alkyl esters, and aldehydes [138]. Very-long chain even- and odd-numbered *n*-alkanes, in addition to the previously mentioned compounds, particularly nonacosan-10-ol, have a significant role in shaping the crystal structure of epicuticular wax. In the Pinaceae family, this wax forms small branched tubules that can only be observed under a scanning electron microscope [139].

n-Alkanes are particularly important in chemotaxonomic research, e.g., in the genus *Picea* [140] or in Pinales [141], as well as other areas such as in detecting hybrids and lower taxonomic units, conducting phylogenetic research, chromatographic analyses, air pollution studies, ecological investigations, paleological research, and beyond. In many of the studies mentioned, alongside identifying the range and prevalence of alkanes, parameters like the carbon preference index (CPI) and average chain length (ACL) are also calculated and applied in various contexts, including chemotaxonomic investigations [142] (Herbin and Robins, 1968) and studies concerning environmental conditions ([143,144], among others).

The main *n*-alkanes in the leaves of 23 European Pinaceae species are presented in Table 3. In *Abies* species, the most prevalent *n*-alkanes were typically nonacosane (C29), hentriacontane (C31), or heptacosane (C27), whereas in *Larix decidua* and the majority of *Picea* species, C31 was the most abundant. Within the genus *Pinus*, C31 and C29 were dominant. The initial research results showed a prevalence of odd alkanes in the epicuticular wax of conifers, a trend also found in the European Pinaceae species analyzed (refer to Table 3). In artificial tree populations, the most abundant alkane in the leaves was C31, whereas in trees from natural populations, C29 and C27 predominated (Table 3).

The origin, whether natural or artificial, clearly influences the predominant alkanes more than the effects of age and timing of needle collection. This observation holds true not only for species like *P. heldreichii* and *Picea omorika* but also for numerous other references cited in Table 3.

Table 3. The main *n*-alkanes in leaves (needles) of 23 European Pinaceae species.

Species	Main *n*-Alkane C atoms	Origin	Reference
	Abies sp.		
1. *A. alba*	C31, C25, C28, C29	Artificial	[141]
	C27, C29, C31, C25, C23	Natural	[145]
2. *A. borisii-regis*	C29, C27, C25, C23	Natural	[145]
3. *A. cephalonica*	C29, C27, C25, C31	Natural	[145]
5. *A. nordmanniana*	C31, C25, C23	Artificial	[141]
6. *A. pinsapo*	C27, C18, C22	Artificial	[141]
	Larix sp.		
7. *L. decidua*	C31, C24, C30, C29	Artificial	[141]
	Picea sp.		
9. *P. abies*	C31, C24, C25, C23, C26	Artificial	[141]
	C33, C31, C29, C35	Artificial	[140]
10. *P. obovata*	C27, C33, C31, C29	Artificial	[140]
11. *P. omorika*	C27, C25, C23, C21	Artificial	[140]
	C31, C24, C25, C22	Artificial	[141]
	C29, C31, C27, C25	Natural	[146]
	C29, C23, C27, C25	Natural	[147]
12. *P. orientalis*	C33, C29, C27, C22, C23	Artificial	[140]
	C31, C26, C24, C25	Artificial	[141]

	Pinus sp.		
14. *Pinus cembra*	C31, C27, C26, C25, C24	Artificial	[141]
	C29, C27	Artificial	[73]
16. *P. heldreichii*	C31, C24, C25, C26	Artificial	[141]
	C23, C25, C27, C21, C29	Natural	[148]
	C27, C29	Artificial	[73]
	C29, C27, C25, C23, C20	Natural	[149]
	C29	Artificial	[73]
18. *P. nigra*	C31, C23, C25, C24, C22	Artificial	[141]
	C25, C27, C29, C23	Natural	[150]
	C29, C27	Artificial	[73]
	C27, C25, C23, C29	Natural	[151]
19. *P. peuce*	C29, C25, C27, C23, C31	Artificial	[73]
	C29, C25	Artificial	[73]
	C29, C25, C27, C23	Natural	[152]
20. *P. pinaster*	C27	Artificial	[153]
	C29, C27	Artificial	[73]
21. *P. pinea*	C31, C29, C33, C27	Artificial	[142]
	C24, C25, C23, C31	Artificial	[141]
	C29, C27	Artificial	[73]
22. *P. sylvestris*	C31, C24, C25, C23	Artificial	[141]
	C29, C25	Artificial	[73]

6. Molecular Markers of Listed European Pinaceae Species

The largest number of population-genetic studies of European representatives of the Pinaceae family was conducted with the species *Abies alba*, *Picea abies*, *Pinus nigra*, and *Pinus sylvestris*, which is expected considering their wide area, although a significant number of studies were also performed with the endemic species *Abies borisii-regis*, *A. cephalonica*, *A. nebrodensis*, and *Picea omorika* (Table 4). These studies were widely used in determining the evolutionary potential of species and assessing the possibility of survival of a given species in changing environmental conditions [154], in defining strategies for long-term conservation of the species [155], in determining the so-called centers of diversity that may indicate the existence of local refugiums of a given species [156], as well as in the detection of relict and ancestral populations and cryptic species [157]. In addition, population-genetic studies of European Pinaceae species were widely used in solving certain taxonomic issues [158], as well as for the detection of hybrids [155].

Table 4. Molecular markers of 23 European Pinaceae species.

Molecular Markers	Country	Reference
	1. *Abies alba*	
cpDNA	Bosnia and Herzegovina and Croatia	[159]
Isoenyzmes	Croatia	[160]
mtDNA: nad5-4	No data	[161]
mtDNA: nad5-4	Bulgaria, North Macedonia, Italy	[162]
SNPs	Spain, Austria, Italy, Romania	[163]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Slovenia, Romania	[154]
Allozymes	France	[164]
nDNA: nSSRs	Bulgaria	[165]
nDNA: nSSRs	Italy, Bulgaria, North Macedonia	[166]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Spain, France, Switzerland, Germany, Italy, Czech Republic, Croatia, Skovakia, Romania, Bulgaria, North Macedonia	[167]

nDNA: nSSRs	Andorra, Spain, Poland, Ukraine	[28]
AFLPs cpDNA: cpSSRs	Spain	[168]
Allozymes	Merkada's arboretum (origin Italy, Croatia)	[169]
cpDNA: PCR–RFLPs mtDNA: nad5-4	Austria, Montenegro	[155]
Allozymes cpDNA: RFLPs (trnT, trnL, trnF) RAPDs	Italy	[170]
RAPDs	Forstbotanischer Garten, Eberswalde, Germany	[171]
Allozymes cpDNA: PCR–RFLPs RAPDs	Italy	[172]
cpDNA: cpSSRs	Germany, Italy	[173]
RAPDs	No data	[174]
Allozymes RAPDs	Romania, France	[175]
	2. *Abies borisii-regis*	
mtDNA: nad5-4	Greece	[162]
SNPs	Greece, Bulgaria	[163]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Greece	[154]
Allozymes	Greece	[164]
nDNA: nSSRs	Greece	[166]
cpDNA: PCR–RFLPs, cpSSRs	North Macedonia	[167]
nDNA: nSSRs	Bulgaria	[28]
Allozymes	Merkada's arboretum (origin Greece)	[169]
cpDNA: PCR–RFLPs mtDNA: nad5-4	Greece	[155]
	3. *Abies cephalonica*	
mtDNA: nad5-4	No data	[161]
mtDNA: nad5-4	Greece	[163]
SNPs	Greece	[163]
cpDNA: PCR–RFLPs; cpSSRs mtDNA: nad5-4	Greece	[154]
Allozymes	Greece	[164]
nDNA: nSSRs	Greece	[165]
nDNA: nSSRs	Greece	[166]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Greece	[167]
nDNA: nSSRs	Greece	[28]
Allozymes	Merkada's arboretum (origin Greece)	[169]
cpDNA: PCR–RFLPs mtDNA: nad5-4	Greece	[155]
RAPDs	Forstbotanischer Garten, Eberswalde, Germany	[171]
cpDNA: cpSSRs	Greece	[173]
RAPDs	No data	[174]
ISSRs RAPDs	Greece	[31]
	4. *Abies nebrodensis*	

SNPs	Italy	[163]
nDNA: nSSRs Allozymes cpDNA: RFLPs (trnT, trnL, trnF)	Italy	[28]
RAPDs	Italy	[170]
RAPDs	Italy	[171]
RAPDs	Italy	[176]
	5. *Abies nordmanniana*	
mtDNA: nad**5**-4	No data	[161]
SNPs	Turkey	[163]
nDNA: nSSRs	Turkey, Georgia, Russia	[165]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Georgia	[167]
nDNA: nSSRs	Turkey	[28]
Allozymes	*Gazi* Institute for Education (origin Turkey)	[169]
RAPDs	Forstbotanischer Garten, Eberswalde, Germany	[171]
	6. *Abies pinsapo*	
mtDNA: nad**5**-4	No data	[161]
SNPs	Spain	[163]
cpDNA: PCR–RFLPs, cpSSRs mtDNA: nad5-4	Morocco	[167]
nDNA: nSSRs	Spain	[28]
AFLPs cpDNA: cpSSRs	Spain	[168]
Allozymes	National Forest Research Institute of Spain (origin Spain)	[169]
cpDNA: cpSSRs mtDNA: nad5-4	Spain, Morocco	[177]
RAPDs	Botanischer Garten, Frankfurt am Main, Germany	[171]
	7. *Larix decidua*	
SNPs cpDNA: matK, trnL-intron, trnT–trnL, trnL–trnF mtDNA: cox1-1, matR-1, nad1- b/c, nad3-1, nad5-1 RAPDs	Provenance- Québec, Canada (origin-Germany, Slovakia, Poland, Austria, Italy, France, Switzerland, Denmark, Hungary)	[178]
SSRs	Romania	[179]
satDNA	Forest Park Tharandt	[180]
RAPDs	Romania	[181]
ISSRs, AFLPs RAPDs	Czech Republic (provenance)	[182]
SSRs	Switzerland	[183]
	8. *Larix sibirica*	
ISSRs	Russia	[184]
SNPs cpDNA: matK, trnL-intron, trnT–trnL, trnL–trnF mtDNA: cox1-1, matR-1, nad1- b/c, nad3-1, nad5-1 RAPDs	Provenance- Québec, Canada (origin Russia)	[178]

RAPDs	Russia	[185]
satDNA	Staatsbetrieb Sachsenforst Graupa	[180]
SSRs	Russia	[186]
RAPDs	Russia	[187]
SNPs	Russia	[188]
SSRs	Russia	[189]
SNPs cpDNA: cpSSRs	Russia	[190]
	9. *Picea abies*	
cpDNA: *matK*, *rbcL*, *trnH-psbA*, *trnL-trnF*, *rpl20-rps18*, *trnV*, *ycf1*, *ycf2*	Dendrological Garden of the Poznan University of Life Sciences, Poland	[191]
Isoenzymes	Bosnia and Herzegovina	[159,192,193]
RAPDs	Italy	[194]
RAPDs	Italy	[195]
RAPDs	Italy	[196]
RAPDs	No data	[197]
RAPDs	Italy	[198]
RAPDs	France, Poland, Romania, Czech Republic, Germany, Switzerland	[199]
cpDNA: trnK, rbcL, trnTLF mtDNA: nad1-2	Canadian Forest Service, Laval Arboretum of Centre d'étude de la forêt, Québec, Canada	[200]
cpDNA: trnC-trnD, trnT-trnF mtDNA: nad5-1	Botanic Garden, Kunming Institute of Botany, Yunnan, China	[201]
RAPDs	British Columbia Tree Center (Survey), Canadian Forest Service (Fredericton), and Quebec Ministry of Forestry (Bertierville) (Provenance in Canada, Romania, Litvania and Czech Republic)	[202]
	10. *Picea obovata*	
cpDNA: trnK, rbcL, trnTLF mtDNA: nad1-2	Holden Arboretum, Ohio, U.S.A.	[200]
cpDNA: trnC-trnD, trnT-trnF mtDNA: nad5-1	China	[201]
ISSRs	Russia	[184]
nDNA: nSSRs	Russia	[203]
	11. *Picea omorika*	
Isoenzymes	Bosnia and Herzegovina	[203]
16 loci in 12 enz.systems	Bosnia and Herzegovina	[204]
mtDNA: nad1-2	Serbia, Bosnia and Herzegovina	[205]
nDNA: nEST-SSRs mtDNA: nad1-2	Serbia, Bosnia and Herzegovina	[156]
cpDNA: trnK, rbcL, trnTLF mtDNA: nad1-2	Arnold Arboretum, Massachusetts, U.S.A.	[200]
cpDNA: trnC-trnD, trnT-trnF mtDNA: nad5-1	Royal Botanic Garden, Kew, UK	[201]
RAPDs	British Columbia Tree Center (Survey), Canadian Forest Service (Fredericton), and Quebec Ministry of Forestry (Bertierville) (provenance in Germany)	[202]
cpDNA: cpSSRs	Serbia, Bosnia and Herzegovina	[206]
	12. *Picea orientalis*	

cpDNA: trnK, rbcL, trnTLF mtDNA: nad1-2	Arnold Arboretum, Massachusetts, U.S.A.	[200]
cpDNA: trnC-trnD, trnT-trnF mtDNA: nad5-1	Jordan Botanic Garden, Geneva, Switzerland	[201]
Isoenzymes	Turkey	[207]
nDNA: nEST-SSRs, nSSRs	Natural Growth, Seed Stand, Gene Conservation Forest, Turkey	[208]
cpDNA: Trn, matK	Turkey	[209]
ITS1	Arnold Arboretum, Jamaica Plain, Massachusetts, USA	[210]
	13. *Pinus brutia*	
cpDNA: cpSSRs	Turkey, Cyprus	[211]
RAPDs	Syria	[212]
SNPs	Greece, Turkey, Israel, Eshtaol nursery	[213]
ITS-ribosomal DNA	Turkey	[214]
ISSRs RAPDs	Turkey, Syria, Tunisia	[215]
RAPDs	Turkey	[216]
cpDNA: cpSSRs	Turkey	[217]
cpDNA: cpSSRs	Turkey	[218]
cpDNA: trnV-trnH	Greece	[219]
	14. *Pinus cembra*	
cpDNA: cpSSRs	Switzerland	[220]
nDNA: nSSRs cpDNA: cpSSRs	Poland, Slovakia, Ukraine, Romania	[221]
SNPs	Experimental garden, 131 of the Swiss Federal Research Institute WSL, Birmensdorf, Switzerland	[222]
cpDNA: cpSSRs	Poland, Slovakia, Ukraine, Romania	[223]
Isozymes	Poland, Slovakia	[224]
cpDNA: cpSSRs mtDNA: nad1-2	Switzerland	[225]
nDNA: nSSRs cpDNA: cpSSRs	Austria, Switzerland, France, Germany, Italy, Poland, Romania, Slovakia, Ukraine	[226]
cpDNA: cpSSRs	Switzerland, Poland, Slovakia, Ukraine, Romania	[227]
SNPs	Austria	[228]
RAPDs	Romania	[229]
	15. *Pinus halepensis*	
nDNA: nSSRs	Spain	[230]
cpDNA: cpSSRs mtDNA: nad1-2	Spain, Morocco	[177]
nDNA: nEST-SSRs	Croatia	[231]
cpDNA: cpSSRs	Turkey, Spain, Greece, Italy, Tunisia, Morocco	[211]
SNPs	France, Tunisia, Spain, Israel, Greece, Eshtaol nursery	[213]
ITS-ribosomal DNA	Turkey	[214]
ISSRs RAPDs	Turkey, Syria, Tunisia	[215]
nDNA: nEST-SSRs	Spain, Italy	[232]
cpDNA: trnV-trnH	Greece	[219]
cpDNA: cpSSRs	Spain	[233]

	16. *Pinus heldreichii*	
nDNA: nEST-SSRs	Belgrade parks, Belgrade, Serbia	[231]
cpDNA: cpSSRs	Bulgaria	[234]
	17. *Pinus mugo*	
Isozymes cpDNA: cpSSRs	Poland, Germany, Austria, Italy	[235]
cpDNA: *matK*, *rbcL*, *trnH-psbA*, *trnL-trnF*, *rpl20-rps18*, *trnV*, *ycf1*, *ycf2*	Dendrological Garden of the Poznan University of Life Sciences, Poland	[191]
cpDNA: cpSSRs RAPDs	Czech Republics, Poland, Germany, Austria, Italy	[236]
cpDNA: cpSSRs	Germany, Austria, Italy, Slovenia, Ukraine, Romania, Bosnia and Herzegovina, Montenegro, Poland, Slovakia, Bulgaria,	[237]
cpDNA: cpSSRs	France, Austria,	[238]
Isozymes cpDNA: *trnL-trnF*	Peat bog reserve "Bor na Czerwonem", Poland	[239]
Allozymes	Bulgaria, Poland	[240]
CMA and DAPI heterochromatin	Slovenia, Bosnia and Herzeovina, Kosovo, Croatia, Montenegro, Austria	[241]
nDNA: nSSRs	Poland, Italy, Germany, Austria, Slovenia, Romania, Bosnia and Herzegovina, Montenegro, Bulgaria	[242]
allozymes	Ukrania, Switzerland	[243]
dhn1, dhn2, dhn4, dhn9, ef, lea, abaR, phytP, gia, gib, chcs, rpS10, eph, phy cpDNA: trnF-trnL, trnV intron mtDNA: nad7-1	Poland, Slovakia, Ukraine, Romania	[244]
nDNA: nEST-SSRs	Belgrade parks (Serbia), Belgrade, Serbia	[231]
RAPDs	Italy, France	[245]
	18. *Pinus nigra*	
cpDNA: cpSSRs mtDNA: nad1-2, nad5-4, nad7-1	Serbia	[246]
Karyotype analysis	Bosnia and Herzegovina	[241]
nDNA: nSSRs	Bulgaria	[247]
cpDNA: cpSSRs	Albania, Austria, Bosnia and Herzegovina, Bulgaria, Crimean Peninsulas, Cyprus island, Spain, France, Greece, Croatia, Italy, Morocco, North Macedonia, Romania, Serbia, Montenegro, Russia, Turkey	[248]
cpDNA: cpSSRs mtDNA: nad1-2, nad5-1, nad7-1	Spain, Morocco	[177]
cpDNA: cpSSRs	France, Spain, Italy, Slovenia,	[249]
cpDNA: cpSSRs	Bulgaria (provenance test „Siracovo")	[250]
RAPDs	Austria, Turkey, Croatia	[251]
ISSRs	Spain, Morocco	[252]
nDNA: nSSRs cpDNA: SSRs, matK, rbcL, trnH-psbA mtDNA: nad5–4	Italy, Turkey, Croatia, Algeria, Cyprus, France, Serbia, Austria, Romania, Ukraine, Russia, Spain	[158]
nDNA: nEST-SSRs	Belgrade parks (Serbia), Croatia	[231]
cpDNA: cpSSRs	Turkey	[218]

cpDNA: trnV-trnH	Greece	[219]
RAPDs	Turkey	[253]
cpDNA: cpSSRs	Spain	[233]
cpDNA: cpSSRs	Albania, Austria, Bosnia and Herzegovina, Bulgaria, Crimean Peninsulas, Cyprus island, Spain, France, Greece, Croatia, Italy, Morocco, North Macedonia, Romania, Serbia, Montenegro, Russia, Turkey	[254]
SNPs cpDNA: cpSSRs	Albania, Austria, Bosnia and Herzegovina, Bulgaria, Crimean Peninsulas, Cyprus island, Spain, France, Greece, Croatia, Italy, Morocco, North Macedonia, Romania, Serbia, Montenegro, Russia, Turkey	[157]
	19. *Pinus peuce*	
nDNA: nEST-SSRs	Serbia	[231]
	20. *Pinus pinaster*	
Dehydrin	Spain	[255]
cpDNA: cpSSRs mtDNA: nad1-2	Spain, Morocco	[177]
cpDNA: psaA-trnS mtDNA: nad1-2	No data	[256]
nDNA: nEST-SSRs	Croatia	[231]
cpDNA: cpSSRs	Spain	[233]
	21. *Pinus pinea*	
Dehydrin	Spain	[255]
nDNA: nSSRs	Portugal, Spain, Morocco, France, Tunisia, Italy, Lebanon, Israel, Cyprus, Greece, Turkey	[230]
nDNA: nEST-SSRs	Croatia	[231]
ISSRs RAPDs	Turkey, Syria	[215]
cpDNA: trnV-trnH	Greece	[219]
Isozymes	Spain, Greece, Italy, Lebanon, Portugal, Turkey, France	[257]
cpDNA: cpSSRs	No data	[258]
cpDNA: cpSSRs	Spain	[233]
	22. *Pinus sylvestris*	
cpDNA: *matK*, *rbcL*, *trnH-psbA*, *trnL-trnF*, *rpl20-rps18*, *trnV*, *ycf1*, *ycf2*	Dendrological Garden of the Poznan University of Life Sciences, Poland	[191]
cpDNA: cpSSRs	France	[238]
Isozymes cpDNA: *trnL-trnF*	Peat bog reserve “Bor na Czerwonem”, Poland	[244]
allozymes	Ukrania, Switzerland	[243]
dhn1, dhn2, dhn4, dhn9, ef, lea, abaR, phytP, gia, gib, chcs, rpS10, eph, phy cpDNA: trnF-trnL, trnV intron mtDNA: nad7-1	Poland, Slovakia, Ukraine, Romania	[244]
nDNA: nEST-SSRs	Belgrade parks, Belgrade, Serbia	[231]
SNPs	Austria	[228]
cpDNA: cpSSRs	Turkey	[218]
cpDNA: trnV-trnH	Greece	[219]
RAPDs	Romania	[259]

RAPDs	Botanical Garden of Vilnius University, Lithuania	[260]
Allozymes RAPDs	Sweden	[261]
RAPDs	Sweden	[262]
cpDNA: cpSSRs	Spain	[263]
cpDNA: cpSSRs	Spain	[233]
SNPs	Across Scandinavia into western Russia	[264]
SNPs	Entire geographic distribution of species	[265]
	23. *Pinus uncinata*	
cpDNA: *matK*, *rbcL*, *trnH-psbA*, *trnL-trnF*, *rpl20-rps18*, *trnV*, *ycf1*, *ycf2*	Dendrological Garden of the Poznan University of Life Sciences, Poland	[191]
cpDNA: cpSSRs	Italy, Spain, France, Andorra	[237]
cpDNA: cpSSRs	Spain, France, Switzerland, Italy	[238]
CMA and DAPI heterochromatin	Spain	[241]
RAPDs	Italy, France	[245]
cpDNA: cpSSRs	Spain	[233]

Over the past few decades, a large number of molecular markers have been developed that show a relatively high degree of intraspecies polymorphism, which is suitable for population-genetic studies of Gymnospermae. At the nuclear genome (nDNA) level, frequently used markers are RFLP (Restriction Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), and AFLP (Amplified Fragment Length Polymorphism) ([168,171,174,176,178,182], etc.). However, the most common type of molecular markers widely used in population-genetic research not only in Gymnospermae, but also in Angiospermae, are microsatellites or SSRs (Single Sequence Repeats) ([28,154,165–168,177], etc.). They are characterized by their hypervariability, co-dominant nature, specificity, simple application, etc., which have led to their very wide application in research in different groups of plants. In addition to microsatellites, sequences of selected regions of chloroplast (cpDNA) and mitochondrial (mtDNA) genomes are widely used in the population genetics of Gymnospermae ([154,155,161–163,167,177], etc.). They are characterized by a lower mutation rate compared to microsatellites, but they represent a very powerful tool for the detection of population differentiation, considering that haploid genomes are more sensitive to the effects of genetic drift compared to the nuclear genome.

Conifers, in general, are characterized by an extremely high degree of genetic diversity in populations and species as a whole, as well as a low degree of genetic differentiation of populations due to effective gene flow through seed and pollen dispersal and a high connectivity of populations. However, some widespread Pinaceae species, where high levels of genetic diversity are expected, have been observed to be genetically monomorphic or poorly variable. One of the best-known examples is the stone pine *Pinus pinea*, which is distributed along almost the entire Mediterranean and is characterized by an almost complete absence of genetic diversity at the level of allozymes [257], nuclear [230], and chloroplast microsatellites [258]. It is believed that during the Pleistocene glaciations, xerothermic European conifers experienced an extremely strong bottleneck effect, given that, during the LGM, they could survive exclusively in the southernmost points of the refugium where there were favorable ecological conditions for their survival. This resulted in a drastic reduction in effective population size (Ne), as well as a loss of genetic diversity. Since genetic variability is considered a prerequisite for the successful adaptation of a species to new environmental conditions, the fact that *Pinus pinea* maintained such a low level of genetic diversity during the later expansion of its range is particularly interesting. As possible explanations, Vendramin et al. [258] suggested the following: 1. expansion that started relatively recently, that is, at least 3000 years ago when people started intensive cultivation; 2. the species survived the LGM in at least two separate refugia (southern Spain and southeastern France); 3. during the bottleneck phase, there was a mass extinction of specific parasites; and 4. successful adaptation to new environmental conditions primarily depends on the variability of phenotypic traits and not on the diversity of genetic markers. On the other hand, it has been shown that some European Pinaceae species with an extremely small current distribution area, such as *Picea omorika*, can show not only an extremely high level of genetic diversity but also a high genetic differentiation of populations [156]. This genetic profile of *P. omorika* is explained by the long-term survival of this species in a localized refugium on the Balkan Peninsula.

The above examples indicate the extremely great importance of historical factors in modeling the level of genetic diversity and genetic differentiation of tthe Pinaceae species, as well as the fact that the current genetic profile of each species is the result of the combination of elemental properties of the species and historical factors.

7. Conclusions

While the analysis of morpho-anatomical traits of conifer needles was a hallmark of 20th century research, these studies are still used at the population level [264], frequently in conjunction with climatic factors [265]. These variable sets of morpho-anatomical data suggest that new varieties or forms could be selected in future. This review paper provides a detailed examination of the terpene composition of European Pinaceae species. However, the list of references would be even longer if we included data on their biological activity [266,267] and other attributes.

In the tabular presentation of the most abundant *n*-alkanes, it seems that all species are similar and that no chemotaxonomic conclusions can be drawn from them, which is nevertheless possible when they are examined at the population level.

Based on the review of the published results of the genetic diversity of European species of the genus *Pinus* and the applied genetic markers, we can say that thermophilic Mediterranean pines such as *P. brutia*, *P. halepensis*, and *P. pinea* show low levels or even absence of genetic diversity, and *P. pinaster* has an intermediate position, while the frigoriphilous species, *P. nigra*, *P. silvestris*, and *P. uncinata*, are characterized by the highest degree of genetic diversity [156,177,233,249,258,263], respectively. Thus, this result supports the hypothesis that during the Pleistocene glaciations, frigophilic species, due to their better adaptation to colder conditions, could often maintain higher effective population sizes and genetic variability.

It is well known that the examined features are very variable between species. This is confirmed in the tabular displays. On the other side, one can see from the tables that some species have not been examined yet in some features, and this fact is very important information for further investigations.

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