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Review

The Orchids of Wetland Vegetation in the Central Balkans

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Abstract: Wetland ecosystems are important habitats for the growth and survival of numerous terrestrial orchids in Europe. This study reviews the current knowledge on the orchids of wetland vegetation in the Central Balkans. The orchid flora was analyzed from taxonomic, phytogeographical, ecological and conservation aspects. The most important taxa include the two Balkan endemics (*Dactylorhiza cordigera* subsp. *bosniaca* and *D. kalopissi* subsp. *macedonica*) and the three subendemics of the Balkans and the Carpathians (*Dactylorhiza cordigera* subsp. *cordigera*, *D. maculata* subsp. *transsilvanica* and *Gymnadenia frivaldii*), as well as a considerable number of Central European, Eurasian and boreal orchid representatives. Several orchid taxa occurring in the wet meadows and fens of the Central Balkans have a southern limit of their distribution in this part of Europe, suggesting that wetlands are important refuges for them. In total, 33 orchid taxa were recorded in plant communities from five classes, 10 orders and 17 alliances. Most orchid taxa grow in the following wetland vegetation types: wet meadows (class *Molinio-Arrhenatheretea*, order *Molinietalia caeruleae*, alliances *Molinion caeruleae*, *Deschampsion cespitosae* and *Calthion palustris*); fens (class *Scheuchzerio palustris-Caricetea fuscae*, order *Caricetalia fuscae*, alliance *Caricion fuscae*); tall-herb vegetation along mountain streams and springs (class *Mulgedio-Aconitetea*); marshes and herb-land vegetation of freshwater or brackish water bodies (class *Phragmito-Magnocaricetea*). This study highlights the importance of serpentine and silicate wetland vegetation types as important habitats for the survival of terrestrial orchids. In addition, detailed taxonomic, ecological and chorological studies of the wetland orchids of the Central Balkans need to be carried out in order to establish a successful plan for their conservation.

Keywords: Orchidaceae; species diversity; wet meadow; fens; mires; vegetation; ecology; Balkan Peninsula

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1. Introduction

The orchid family (Orchidaceae) is one of the largest and most diverse families in the plant kingdom, with approximately 28,000 species and 880 genera [1]. Because of their germination limitation, mycorrhizal specificity and pollinator specialization, orchids are particularly vulnerable to changes in ecosystem balance, especially changes in moisture content, light regime, nutrient availability and competition levels [2,3]. Habitat changes or their complete destruction have led to the extinction or decline in abundance and distribution of many orchids and, consequently, many species are protected by laws and/or are included in Red Data Books [4]. Therefore, knowledge of the habitats and ecological preferences of orchids is a prerequisite for their appropriate conservation.

Orchids are known to occur in almost all terrestrial ecosystems, while they are absent or less abundant in extremely dry deserts, salt marshes and agricultural lands [5,6]. Terrestrial orchids in Europe occur in forests and scrubs, grasslands, meadows, heaths, tall-herb vegetation as well as in mires, bogs, fens, marshlands and even in anthropogenic

vegetation [7]. Studies have often pointed out that orchid species occur in different vegetation types in different geographic regions and that the greatest differences occur when comparing the center and the edge of their range [8,9]. According to the "abundant-centre hypothesis", species at the edges of their range occur primarily in a limited number of plant communities, while species at the center of their range usually inhabit a wide variety of vegetation types [10].

Wetland ecosystems are important habitats for the growth and survival of numerous orchid species in Europe [6,7]. Due to climate change and global warming, these habitats are expected to decline or disappear in certain areas, especially near the Mediterranean. Therefore, the unique orchid flora of these areas can also be expected to decline or disappear. Knowledge of their spatial distribution and ecological characteristics is of great importance for conservation. So far, these habitats have been the main topic of several scientific papers. Some of them summarize the knowledge of habitats and phytocoenological affiliations of wetland orchids [11–16]. However, recent studies have examined the importance of wetland vegetation types as factors affecting the distribution and abundance of orchids [17,18]. In addition, over the past decades, numerous ecological studies have focused on the effects of wetland management (e.g., mowing) on orchid performance [19,20]. According to recent studies, orchids inhabiting wetlands in western and central Europe are most threatened [21–23]. On the other hand, knowledge about which wetland vegetation types are particularly rich in orchids, which orchids are specialists and which are generalists in wetland habitats, the impact of geological substrates as factors affecting the abundance and composition of orchids and the importance of these habitats for conservation in specific regions of Europe is still limited. Detailed insight into the preferences of wetland orchids will lead to a better understanding of conservation priorities and the application of conservation plans. In addition, this knowledge will allow predictions of species distribution and abundance in response to future changes in land cover and climate.

The Balkan Peninsula is an important center of orchid diversity, with the highest number of recorded species in the Mediterranean region, especially in the Aegean part of Greece [24,25]. Moreover, the Balkan Peninsula represents one of the most important centers of diversity of the genus *Dactylorhiza*, known for its numerous water-demanding representatives [26]. Although the area of the Central Balkans is insufficiently studied in terms of orchids, recent research indicates that wetland habitats in this area are important for many terrestrial orchids [15,18]. The orchids of the wetland vegetation in the Central Balkans have been studied mostly within the framework of extensive phytocoenological studies, which include a list of species with information on their abundance and sociality [27,28]. Given the strong influence of the humid climate in western Serbia, northern Montenegro, eastern Bosnia and Herzegovina, northern Albania and the northwestern part of North Macedonia, the significant presence of wet meadows, bogs, fens and marshes is understandable. In the Central Balkans, wetland vegetation can be divided into the following types: (a) submerged rooted herbaceous vegetation of brackish waters (*Ruppietea maritimae*); (b) salt marshes within the classes *Therosalicornietea* and *Festuco-Puccinellietea*; (c) freshwater aquatic vegetation (*Lemnetea*, *Charetea intermediae* and *Potamogetonetea*); (d) vegetation of freshwater springs, shorelines and marshes (*Montio-Cardaminetea*, *Isoëto-Nanojuncetea* and *Phragmito-Magnocaricetea*); (e) bogs and fens (*Oxycocco-Sphagnetea* and *Scheuchzerio palustris-Caricetea fuscae*); (f) wet meadows (some alliances within the class *Molinio-Arrhenatheretea*); and (g) tall-herb vegetation along mountain streams and water springs (some alliances within the class *Mulgedio-Aconitetea*) [27–32].

The present study represents a synthesis of knowledge on the orchids of the wetland vegetation of the Central Balkans, based on long-term personal field investigations, checking and revision of herbarium material and published sources. The study is based mainly on knowledge from Serbia, but also on some data from Bosnia, Montenegro and North Macedonia. The main objectives were: (i) to analyze the orchid flora of wetland vegetation from taxonomic, phytogeographical and life-form perspectives; (ii) to provide an overview of the classes, orders and associations of wetland vegetation in which orchids occur; (iii) to

determine the richness of orchid taxa in relation to wetland vegetation; (iv) to demonstrate the importance of geological substrates as factors affecting the distribution, abundance and composition of orchids; and (v) to identify the main threats to orchids of wetland vegetation and to draw basic conclusions for orchid conservation.

2. Overview of the Orchid Flora of Wetland Vegetation in the Central Balkans

The overall survey of orchid taxa occurring in the wetland vegetation of the Central Balkans given here (Table 1) is based on long-term personal field investigations, herbarium material and relevant published sources. The material in the herbarium of the University of Belgrade (BEOU) and in that of the Museum of Natural History in Belgrade (BEO) was reviewed and revised. The nomenclature and taxonomy in this study follow Djordjević et al. [33] and Euro+Med [34].

Table 1. Overview of orchid taxa of wetland vegetation in the Central Balkans with indication of their degree of representation and chorological groups and life forms. BOR—boreal, CE—Central European, CEM—Central European mountainous, CE-EUX-CAUC—Central European-Euxine-Caucasian, EAS—Eurasian, MED-SUBMED—Mediterranean-Submediterranean; R—rhizomatous orchids, I—intermediate type of orchids, T—tuberous orchids.

Taxon	Degree of Representation	Chorological Group	Life Form
Anacamptis coriophora (L.) R.M.Bateman, Pridgeon & M.W.Chase subsp. *coriophora*	3	CE	T
Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase subsp. *laxiflora*	1	MED-SUBMED	T
Anacamptis morio (L.) R.M.Bateman, Pridgeon & M.W.Chase subsp. *morio*	4	CE	T
Anacamptis palustris (Jacq.) R.M.Bateman, Pridgeon & M.W.Chase subsp. *palustris*	1	EAS	T
Anacamptis palustris subsp. *elegans* (Heuff.) R.M.Bateman, Pridgeon & M.W.Chase	1	EAS	T
Anacamptis pyramidalis (L.) Rich.	4	MED-SUBMED	T
Coeloglossum viride (L.) Hartm.	3	BOR	I
Dactylorhiza cordigera (Fr.) Soó subsp. *cordigera*	2	CEM	I
Dactylorhiza cordigera subsp. *bosniaca* (Beck) Soó	2	CEM	I
Dactylorhiza fuchsii (Druce) Soó subsp. *fuchsii*	3	BOR	I
Dactylorhiza incarnata (L.) Soó subsp. *incarnata*	1	BOR	I
Dactylorhiza kalopissii subsp. *macedonica* (J.Hölzinger & Künkele) Kreutz	1	MED-SUBMED	I
Dactylorhiza maculata (L.) Soó subsp. *maculata*	2	BOR	I
Dactylorhiza maculata subsp. *transsilvanica* (Schur) Soó	2	CE	I
Dactylorhiza majalis (Rchb.) P.F.Hunt & Summerh. subsp. *majalis*	1	CE	I
Dactylorhiza saccifera (Brongn.) Soó subsp. *saccifera*	3	MED-SUBMED	I
Dactylorhiza sambucina (L.) Soó	4	CE	I
Epipactis palustris (L.) Crantz	1	EAS	R
Gymnadenia conopsea (L.) R.Br.	3	EAS	I
Gymnadenia densiflora (Wahlenb.) A.Dietr.	2	EAS	I
Gymnadenia frivaldii Hampe ex Griseb.	1	CEM	I
Gymnadenia odoratissima (L.) Rich.	4	CE	I
Herminium monorchis (L.) R.Br.	2	EAS	T
Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase	3	CE	T
Neottia ovata (L.) Bluff & Fingerh.	3	EAS	R
Nigritella rhellicani Teppner & E.Klein	4	CEM	I

Table 1. *Cont.*

Taxon	Degree of Representation	Chorological Group	Life Form
Orchis mascula subsp. *speciosa* (Mutel) Hegi	4	CE-EUX-CAUC	T
Orchis militaris L. subsp. *militaris*	4	EAS	T
Platanthera bifolia (L.) Rich.	3	EAS	I
Platanthera chlorantha (Custer) Rchb.	3	CE	I
Pseudorchis albida (L.) Á.Löve & D.Löve subsp. *albida*	3	BOR	I
Spiranthes spiralis (L.) Chevall.	4	CE	T
Traunsteinera globosa (L.) Rchb.	3	CEM	T

In the overview of the orchid flora of wetland vegetation in the Central Balkans, we have particularly emphasized the degree of orchid presence in wetland vegetation types (Table 1):

1. species occurs exclusively in wetland vegetation types (at 100% of its sites, it is found in wetland vegetation types);
2. species grows mainly in wetland vegetation types and rarely occurs in other vegetation types (at 50–100% of its sites, it is found in wetland vegetation types);
3. species occurs in wetland vegetation types but mostly inhabits other vegetation types (at 10–50% of its sites, it is found in wetland vegetation types);
4. species rarely occurs in wetland vegetation types and mostly inhabits other vegetation types (at < 10% of its sites, it is found in wetland vegetation types).

2.1. Richness of Orchid Taxa and Taxonomic Analysis

The floristic composition of the orchid flora of wetland vegetation in the Central Balkans includes 33 species and subspecies classified in 14 genera (Table 1). Eight taxa occur exclusively in these vegetation types, while six taxa grow mainly in wetland vegetation types and rarely occur in other vegetation types (Table 1). On the other hand, there are 11 taxa that grow in wetland vegetation types but occur more frequently and with greater abundance in other vegetation types, while eight taxa very rarely occur in wetland vegetation types (Table 1). The most taxon-rich genera are *Dactylorhiza* (ten taxa), *Anacamptis* (six taxa) and *Gymnadenia* (four taxa). The genera *Orchis* and *Platanthera* are represented by two taxa, while nine genera (*Coeloglossum*, *Epipactis*, *Herminium*, *Neotinea*, *Neottia*, *Nigritella*, *Pseudorchis*, *Spiranthes* and *Traunsteinera*) are represented by a single taxon (Table 1).

The genus *Dactylorhiza* has the highest number of taxa within the total orchid flora of wetland vegetation in the Central Balkans (Figure 1), which is not surprising considering that wet habitats (fens, bogs, marshes and wet meadows) are typical habitats for representatives of this genus [26,35]. The occurrence of a large number of *Dactylorhiza* taxa can also be explained by the significant presence of silicate geological substrates in the study area, known for their high water-storage capacity, which is favorable for the growth and survival of numerous representatives of this genus [36]. The presence of the two Balkan endemics (*D. cordigera* subsp. *bosniaca* and *D. kalopissi* subsp. *macedonica*) and two Carpathian-Balkan subendemics (*D. cordigera* subsp. *cordigera* and *D. maculata* subsp. *transsilvanica*) is particularly important (Figure 1). *Dactylorhiza* × *serbica* (H.Fleischm.) Soó, a natural hybrid between *D. incarnata* subsp. *incarnata* and *D. saccifera* subsp. *saccifera*, which also inhabits the wetlands, was described in Serbia [33]. In addition, *D. maculata* subsp. *maculata*, *D. maculata* subsp. *trassilvanica*, *D. cordigera* subsp. *bosniaca* and *D. majalis* have a southern limit of their distribution in the Central Balkans [33], making their habitats of high conservation value in this region. The area of the Central Balkans is also a contact zone where *D. fuchsii* and *D. maculata* subsp. *maculata* from the west, north and northwest and *D. saccifera* from the south and southeast meet [37,38], so there is potential for their future taxonomic and phylogeographic research. Due to their complicated taxonomy, the *D. maculata* and *D. majalis* groups require detailed taxonomic and phylogeographic research in the Central Balkans.

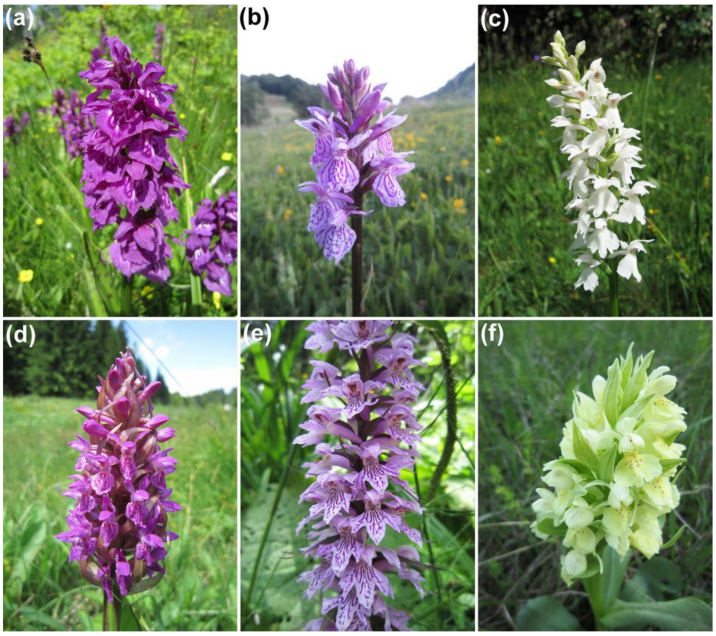

Figure 1. Some representatives of the genus *Dactylorhiza* of wetland vegetation in the Central Balkans: (**a**) *Dactylorhiza cordigera* subsp. *cordigera*, (**b**) *Dactylorhiza maculata* subsp. *maculata*, (**c**) *Dactylorhiza maculata* subsp. *transsilvanica*, (**d**) *Dactylorhiza incarnata* subsp. *incarnata*, (**e**) *Dactylorhiza saccifera* subsp. *saccifera*, (**f**) *Dactylorhiza sambucina* (photos V. Djordjević).

Three *Anacamptis* taxa that occur exclusively in wetland vegetation types are *Anacamptis laxiflora*, *A. palustris* subsp. *palustris* and *A. palustris* subsp. *elegans* (Figure 2). However, knowledge on the distribution of these taxa in the Central Balkans is insufficient, as these taxa are usually presented in the literature under their species rank for the flora of Serbia, i.e., as *Orchis laxiflora* Lam. [33]. Therefore, published data on the distribution and habitat preferences of these taxa in Serbia cannot be considered with any degree of certainty. Recent studies have shown that *A. palustris* subsp. *elegans* is the most widespread taxon, while *A. palustris* subsp. *palustris* is a rarer taxon, distributed mainly in the southern part of the Pannonian plain and very rarely in other parts of the Central Balkans [33,39–41]. Although *A. coriophora* subsp. *coriophora*, *A. morio* subsp. *morio* and *A. pyramidalis* occur in wet habitats, they are more common in other habitat types (mesophilous and xerophilous grasslands) [15].

Figure 2. Some representatives of the genus *Anacamptis* of wetland vegetation in the Central Balkans: (**a**) *Anacamptis palustris* subsp. *palustris*, (**b**) *Anacamptis palustris* subsp. *elegans*, (**c**) *Anacamptis laxiflora* ((**a**) photo I. Stevanoski; (**b**,**c**) photo S. Tsiftsis).

Among the *Gymnadenia* taxa, the Carpathian-Balkan subendemic *Gymnadenia frivaldii* (Figure 3a), which occurs exclusively in wetland vegetation types, should be emphasized.

The center of its distribution is on the mountains of the southeastern Dinaric Alps and on the mountains of the Scardo-Pindhian province, with a disjunction in the southeastern Carpathians [42–44]. This species has the southern and western limits of its distribution in the Central Balkans. Although *G. conopsea* is very common in wetland vegetation types in the Central Balkans, where it is often very abundant, this species also grows in other habitats such as mesophilous and xero-mesophilous meadows, as well as open woodlands [15].

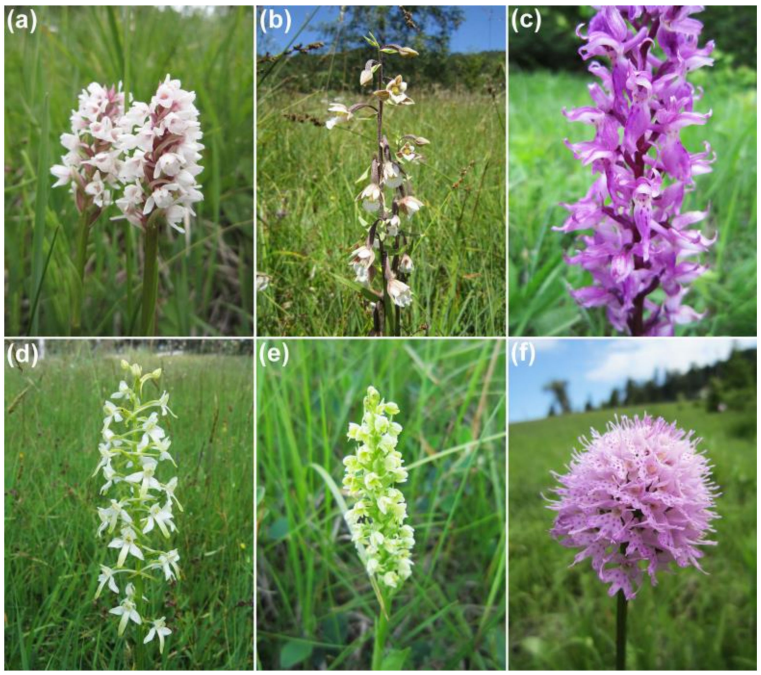

Figure 3. Some representatives of orchids of wetland vegetation in the Central Balkans: (**a**) *Gymnadenia frivaldii*, (**b**) *Epipactis palustris*, (**c**) *Orchis mascula* subsp. *speciosa*, (**d**) *Platanthera bifolia*, (**e**) *Pseudorchis albida*, (**f**) *Traunsteinera globosa* (photos V. Djordjević).

The orchid flora of the wetland vegetation of the Central Balkans includes a small number of representatives of the genera *Epipactis* and *Neottia*, known for their typical forest representatives. The species *Epipactis palustris* (Figure 3b), which occurs exclusively in wetland vegetation, is widespread throughout the Central Balkans [43]. *Neottia ovata*, on the other hand, is an ecologically very plastic species that grows in wetland vegetation as well as in other vegetation types, including forests [6,41,45]. The genus *Orchis* is also represented by only a few representatives, which is not surprising knowing that the species of this genus tend to grow in xerophilous and mesophilous habitats and often in forest ecosystems. Among the representatives of orchids, *Pseudorchis albida* (Figure 3e) and *Traunsteinera globosa* (Figure 3f) are of great importance, because these species have the southern limit of their distribution in the Central Balkans.

2.2. Phytogeographical Analysis

Chorological analysis of the orchid flora of wetland vegetation in the Central Balkans revealed the presence of six chorological groups (Figure 4). The chorological types for phytogeographical analysis were determined according to the principles defined by Meusel et al. [46,47], Meusel and Jäger [48], Stevanović [49] and Djordjević et al. [33]. The occurrence of orchids from different chorological groups can be explained by the fact that the Central Balkans is located in an area influenced by different floristic-vegetation regions due to historical, geological, geomorphological and climatic reasons and the considerable altitude differences in the study area.

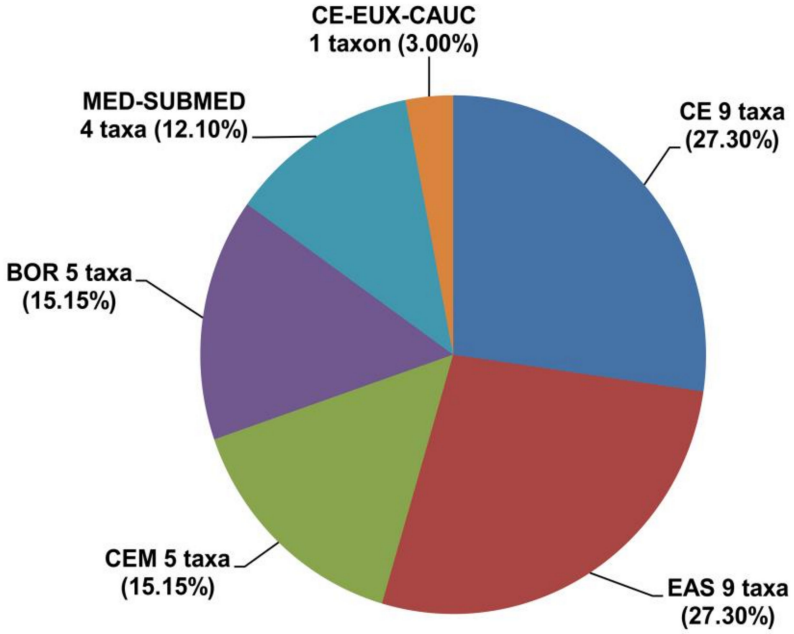

Figure 4. Spectrum of basic chorological groups of the orchid flora of wetland vegetation in the Central Balkans. CE—Central European; EAS—Eurasian; CEM—Central European mountainous; BOR—Boreal; MED-SUBMED—Mediterranean-Submediterranean; CE-EUX-CAUC—Central European-Euxine-Caucasian.

The chorological analysis of the orchid flora of wetland vegetation in Serbia indicates a pronounced dominance of orchids belonging to the Central European and Eurasian chorological groups (Figure 4). The Central European chorological group includes nine taxa from six genera (*Anacamptis*, *Dactylorhiza*, *Gymnadenia*, *Neotinea*, *Platanthera* and *Spiranthes*). The significant representation of Central European orchids is not surprising, considering that a large part of the Central Balkans has a temperate-continental climate and many different types of habitats where the majority of orchids of this chorological group occur. The Central European mountainous group is represented by five taxa from four genera (*Dactylorhiza*, *Gymnadenia*, *Nigritella* and *Traunsteinera*). Considering the numerous high-mountain areas in the Central Balkans, orchid representatives from this chorological group are expected.

The Eurasian chorological group includes nine taxa from seven genera (*Anacamptis*, *Epipactis*, *Gymnadenia*, *Herminium*, *Neottia*, *Orchis* and *Platanthera*) (Table 1). Many orchids of this chorological group are characterized by great ecological plasticity, which allows them to grow and survive in different habitats. *Gymnadenia conopsea*, *Neottia ovata* and *Platanthera bifolia* are among the least specialized and most widespread species [6,15,18].

The boreal chorological group has a significant presence—five orchid taxa from three genera (*Coeloglossum*, *Dactylorhiza* and *Pseudorchis*). Their occurrence in the Central Balkans can be explained not only by historical factors but also by favorable climatic conditions, adequate habitats as well as by the widespread presence of siliceous geological substrates. The fact is that most siliceous substrates, especially acidic and intermediate igneous rocks, have a high water-holding capacity, and siliceous substrates occupy large areas at higher altitudes suitable for many representatives of boreal orchids [36].

The Mediterranean-Submediterranean chorological group includes four taxa from two genera (*Anacamptis* and *Dactylorhiza*). While *A. laxiflora* is distributed mainly in the Mediterranean and Submediterranean regions and is less common in continental areas, *A. pyramidalis* and *D. saccifera* are species widely distributed throughout the Central Balkans [41]. However, the localities of *D. kalopissi* subsp. *macedonica* and *D. saccifera* in the Central Balkans represent their northern distribution limits in this part of Europe. In addition, *D. kalopissi* subsp. *macedonica* occurs in the Central Balkans only in North Macedonia but is

also distributed in Albania, Greece and Bulgaria [50]. *Orchis mascula* subsp. *speciosa* is the only taxon belonging to the Central European-Euxine-Caucasian chorological group.

2.3. Life Forms

The orchid representatives of wetland vegetation in the Central Balkans are terrestrial orchids that display characteristics of the geophyte life form [51,52]. However, we classified orchids according to the concept presented by Tsiftsis et al. [24], Averyanov [26], Štípková et al. [53] and Djordjević et al. [54]: (1) rhizomatous orchids; (2) "intermediate orchids" (intermediate in evolutionary history between rhizomatous orchids and orchids with spheroid tubers), i.e., orchids with palmate, fusiform, or stoloniferous tubers; and (3) tuberous orchids, i.e., orchids with spheroid tubers. The structure of life forms of orchids of wetland vegetation in the Central Balkans is shown in Figure 5.

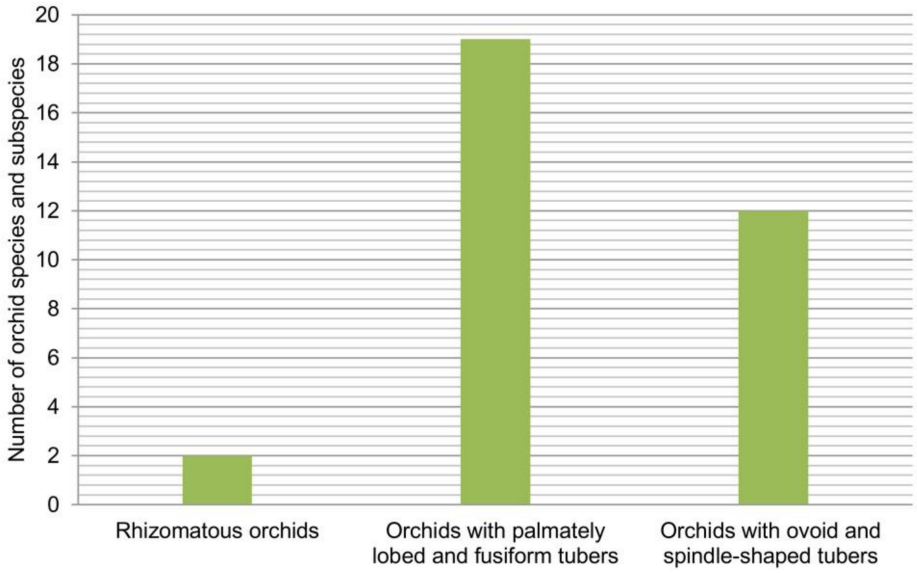

Figure 5. Structure of life forms of orchids of wetland vegetation in the Central Balkans.

The orchid flora of wetland vegetation in the Central Balkans is dominated by "intermediate orchids" (orchids with palmately lobed and fusiform tubers) (Figure 5). This group includes 19 orchid taxa from six genera (*Coeloglossum*, *Dactylorhiza*, *Gymnadenia*, *Nigritella*, *Platanthera* and *Pseudorchis*). Among these orchids, taxa of the genera *Coeloglossum*, *Dactylorhiza*, *Nigritella* and *Gymnadenia* have palmately lobed (finger-like) tubers, whereas species of the genus *Platanthera* are characterized by fusiform tubers. The significant presence of these orchids in the wetland vegetation of the Central Balkans is not surprising considering the origin and evolutionary development of orchids of this life form. The first occurrences of "intermediate orchids" have been associated with Alpine orogeny, i.e., the emergence of lower-temperature mountain habitats [26]. These orchids significantly expanded their range as a result of cooling at the end of the Neogene and in the Pleistocene and were able to colonize areas with plains where the degradation of the Tertiary thermophilic flora took place [26]. Therefore, they can be considered to have well-developed adaptations to the cold and wet conditions of the habitats.

The group having ovoid and spindle-shaped tubers includes 12 orchid species and subspecies classified into six genera (*Anacamptis*, *Herminium*, *Neotinea*, *Orchis*, *Spiranthes* and *Traunsteinera*). A lower proportion of orchids with spherical tubers in wetland vegetation is to be expected since these orchids usually inhabit dry and semi-dry habitats. Their tubers represent the final stage in the development of the underground organs of orchids, which enable many representatives to survive in habitats with dry and warm conditions [24]. However, *A. laxiflora*, *A. palustris* subsp. *palustris* and *A. palustris* subsp. *elegans* are taxa that represent exceptions to the rule and grow exclusively in wetland vegetation types.

There are only two orchids with rhizomes (*Epipactis palustris* and *Neottia ovata*). The smaller number of representatives of rhizomatous orchids is understandable because it is known that these orchids occur mainly in forest ecosystems [6,15].

3. Wetland Vegetation

Terrestrial orchids are widely represented in various types of wetland vegetation, including wet meadows, as well as bogs, fens and marshes [15,18,55,56]. In this section, an overview of the main wetland vegetation types with terrestrial orchids and literature sources is presented (Table 2). A total of 33 orchid species and subspecies were recorded in plant communities from five classes, 10 orders and 17 alliances (Table 2). The syntaxonomic nomenclature follows Mucina et al. [57] and Peterka et al. [58].

Table 2. Overview of wetland vegetation types with terrestrial orchids in the Central Balkans.

Vegetation Class	Vegetation Order	Vegetation Alliance	Orchid Species and Subspecies	Literature Sources
Molinio-Arrhenatheretea Tx. 1937	*Molinietalia caeruleae* Koch 1926	*Calthion palustris* Tx. 1937	*Anacamptis palustris* subsp. *elegans*, *Anacamptis morio* subsp. *morio*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza maculata* subsp. *transsilvanica*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza cordigera* subsp. *bosniaca*, *Dactylorhiza saccifera*, *Epipactis palustris*, *Gymnadenia conopsea*, *Neottia ovata*, *Platanthera bifolia*, *Traunsteinera globosa*	[15,18,41,59–62]
Molinio-Arrhenatheretea Tx. 1937	*Molinietalia caeruleae* Koch 1926	*Molinion caeruleae* Koch 1926	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis morio* subsp. *morio*, *Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*, *Anacamptis pyramidalis*, *Dactylorhiza fuchsii*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza maculata* subsp. *transsilvanica*, *Dactylorhiza majalis* subsp. *majalis*, *Dactylorhiza saccifera*, *Dactylorhiza sambucina*, *Epipactis palustris*, *Gymnadenia conopsea*, *Herminium monorchis*, *Neotinea ustulata*, *Neottia ovata*, *Orchis mascula* subsp. *speciosa*, *Orchis militaris*, *Platanthera bifolia*, *Platanthera chlorantha*, *Pseudorchis albida*, *Spiranthes spiralis*, *Traunsteinera globosa*	[15,18,41,60,63–70]
Molinio-Arrhenatheretea Tx. 1937	*Molinietalia caeruleae* Koch 1926	*Deschampsion cespitosae* Horvatić 1930	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis morio* subsp. *morio*, *Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza maculata* subsp. *transsilvanica*, *Dactylorhiza saccifera*, *Epipactis palustris*, *Gymnadenia conopsea*, *Neotinea ustulata*, *Neottia ovata*, *Platanthera bifolia*, *Traunsteinera globosa*	[15,18,40,41,60,62,66,71–74]
Molinio-Arrhenatheretea Tx. 1937	*Filipendulo ulmariae-Lotetalia uliginosi* Passarge 1975	*Mentho longifoliae-Juncion inflexi* T. Müller et Görs ex de Foucault 2009	*Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza saccifera*, *Epipactis palustris*, *Gymnadenia conopsea*, *Gymnadenia densiflora*, *Platanthera bifolia*	[15,18,41,75]
Molinio-Arrhenatheretea Tx. 1937	*Trifolio-Hordeetalia* Horvatić 1963	*Trifolion pallidi* Ilijanić 1969	*Anacamptis morio* subsp. *morio*, *Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*	[15,18,41,76–78]
Molinio-Arrhenatheretea Tx. 1937	*Trifolio-Hordeetalia* Horvatić 1963	*Trifolion resupinati* Micevski 1957	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis laxiflora*, *Anacamptis morio* subsp. *morio*, *Anacamptis palustris* subsp. *elegans*, *Gymnadenia conopsea*	[74,79–86]
Molinio-Arrhenatheretea Tx. 1937	*Trifolio-Hordeetalia* Horvatić 1963	*Molinio-Hordeion secalini* Horvatić 1934	*Anacamptis laxiflora*	[87]
Molinio-Arrhenatheretea Tx. 1937	*Potentillo-Polygonetalia avicularis* Tx. 1947	*Potentillion anserinae* Tx. 1947	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*, *Dactylorhiza incarnata* subsp. *incarnata*, *Orchis militaris*	[68,71,88]
Mulgedio-Aconitetea Hadač et Klika in Klika et Hadač 1944c 1944	*Adenostyletalia alliariae* Br.-Bl. 1930	*Cirsion appendiculati* Horvat et al. 1937	*Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza sambucina*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza saccifera*, *Gymnadenia frivaldii*, *Gymnadenia odoratissima*, *Gymnadenia conopsea*, *Nigritella rhellicani*	[74,89,90]
Phragmito-Magnocaricetea Klika in Klika et Novák 1941	*Phragmitetalia* Koch 1926	*Phragmition communis* Koch 1926	*Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza kalopissii* subsp. *macedonica*, *Epipactis palustris*, *Gymnadenia conopsea*	[15,18,41,60,91–93]

Table 2. *Cont.*

Vegetation Class	Vegetation Order	Vegetation Alliance	Orchid Species and Subspecies	Literature Sources
Phragmito-Magnocaricetea Klika in Klika et Novák 1941	*Magnocaricetalia* Pignatti 1953	*Magnocaricion elatae* Koch 1926	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis morio* subsp. *morio*, *Dactylorhiza incarnata* subsp. *incarnata*, *Gymnadenia conopsea*, *Traunsteinera globosa*	[15,41,60,94]
Phragmito-Magnocaricetea Klika in Klika et Novák 1941	*Magnocaricetalia* Pignatti 1953	*Magnocaricion gracilis* Géhu 1961	*Anacamptis palustris* subsp. *elegans*	[86,95]
Scheuchzerio palustris-Caricetea fuscae Tx. 1937	*Caricetalia davallianae* Br.-Bl. 1950	*Caricion davallianae* Klika 1934	*Dactylorhiza cordigera* subsp *cordigera*, *Dactylorhiza cordigera* subsp. *bosniaca*, *Epipactis palustris*, *Gymnadenia frivaldii*	[15,27,41,69]
Scheuchzerio palustris-Caricetea fuscae Tx. 1937	*Caricetalia fuscae* Koch 1926	*Caricion fuscae* Koch 1926	*Anacamptis coriophora* subsp. *coriophora*, *Anacamptis morio* subsp. *morio*, *Dactylorhiza cordigera* subsp. *bosniaca*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza kalopissii* subsp. *macedonica*, *Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza maculata* subsp. *transsilvanica*, *Dactylorhiza majalis* subsp. *majalis*, *Dactylorhiza saccifera*, *Epipactis palustris*, *Gymnadenia conopsea*, *Gymnadenia frivaldii*, *Herminium monorchis*, *Neottia ovata*, *Nigritella rhellicani*, *Platanthera bifolia*, *Pseudorchis albida*, *Traunsteinera globosa*	[15,18,27,41,59,62,74,89,93,96–103]
Scheuchzerio palustris-Caricetea fuscae Tx. 1937	*Caricetalia fuscae* Koch 1926	*Narthecion scardici* Horvat ex Lakušić 1968	*Gymnadenia frivaldii*, *Gymnadenia conopsea*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza cordigera* subsp. *bosniaca*, *Pseudorchis albida*	[27,90,102,104]
Scheuchzerio palustris-Caricetea fuscae Tx. 1937	*Caricetalia fuscae* Koch 1926	*Sphagno-Caricion canescentis* Passarge (1964) 1978	*Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza incarnata* subsp. *incarnata*, *Dactylorhiza maculata* subsp. *maculata*, *Dactylorhiza maculata* subsp. *transsilvanica*, *Epipactis palustris*	[15,27,41,103]
Montio-Cardaminetea Br.-Bl. et Tx. ex Klika et Hadač 1944	*Montio-Cardaminetalia* Pawłowski et al. 1928	*Cardamino-Montion* Br.-Bl. 1926	*Dactylorhiza cordigera* subsp. *cordigera*	[89]

Orchid richness in relation to vegetation classes, orders and alliances in the Central Balkans is presented in Figures 6–8. The greatest number of orchids was recorded in the class *Molinio-Arrhenatheretea* (28 taxa or 84.9% of the total analyzed orchid flora), followed by *Scheuchzerio palustris-Caricetea fuscae* (19 taxa), *Phragmito-Magnocaricetea* (nine taxa), *Mulgedio-Aconitetea* (eight taxa) and *Montio-Cardaminetea* (one taxon) (Figure 6).

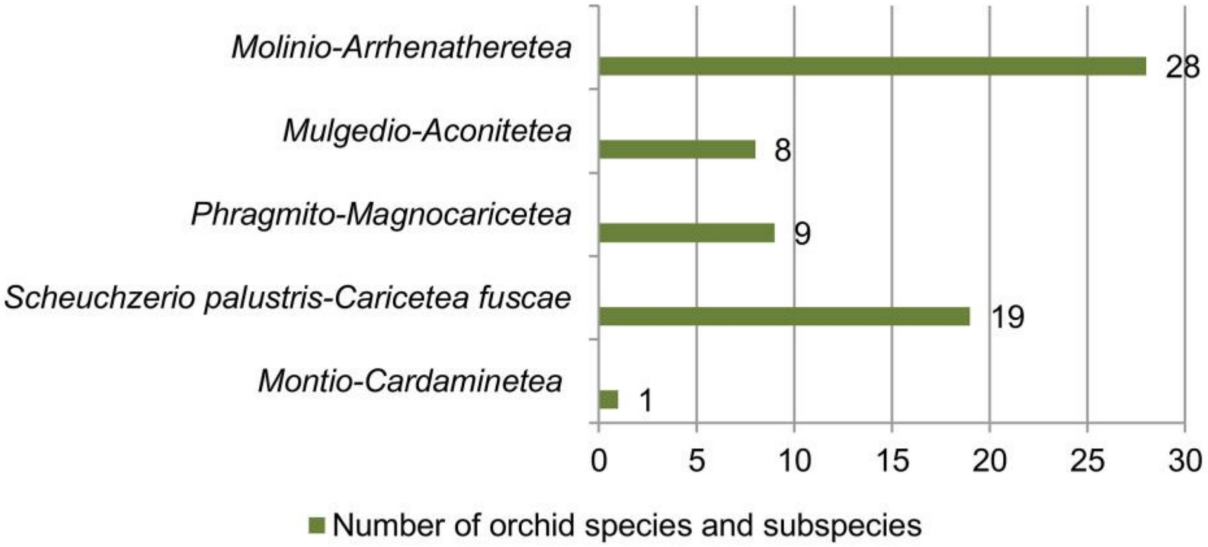

Figure 6. Richness of orchid species and subspecies in relation to vegetation classes.

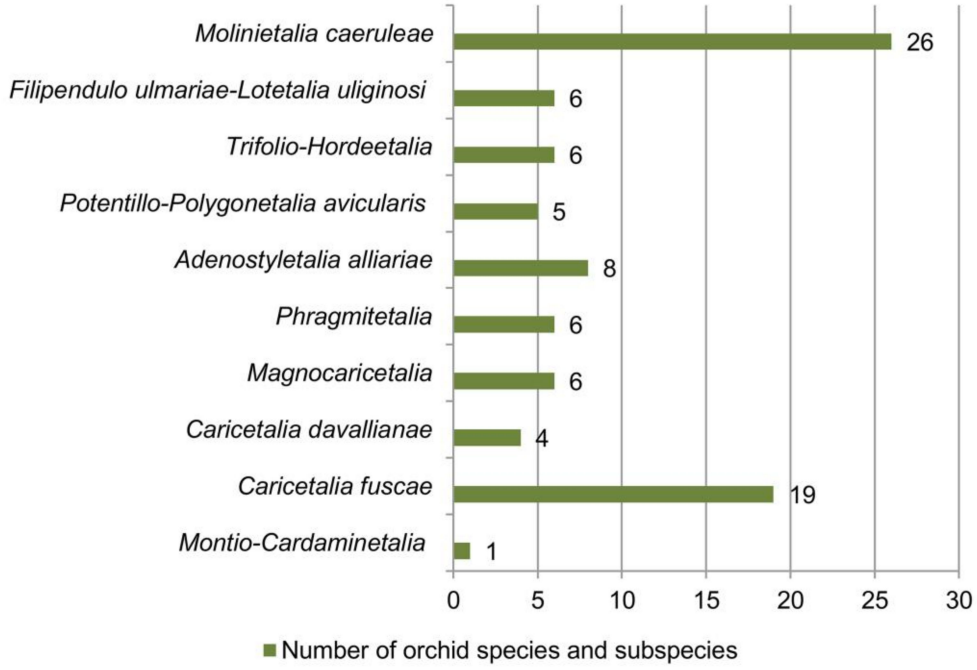

Figure 7. Richness of orchid species and subspecies in relation to vegetation orders.

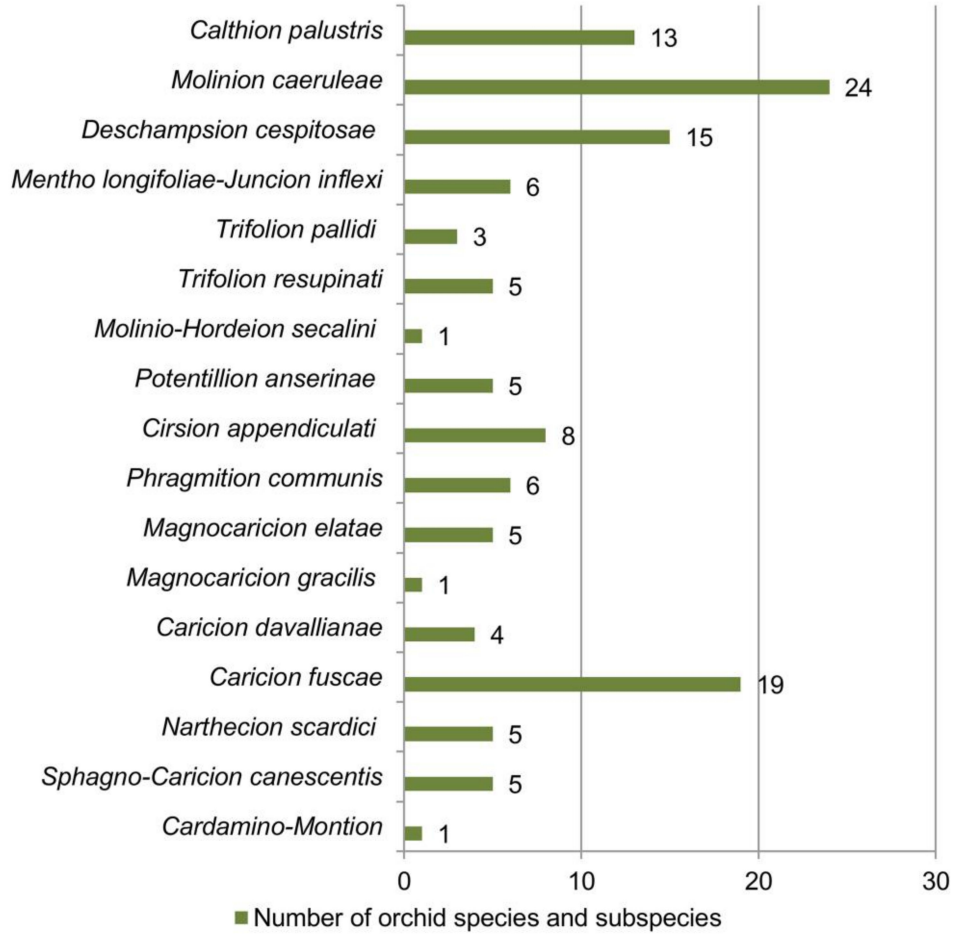

Figure 8. Richness of orchid species and subspecies in relation to vegetation alliances.

Concerning vegetation orders, the greatest number of orchids was recorded in the *Molinietalia caeruleae* (26 taxa or 78.8% of the total analyzed orchid flora), followed by

Caricetalia fuscae (19 taxa), *Adenostyletalia alliariae* (eight taxa), *Filipendulo ulmariae-Lotetalia uliginosi*, *Trifolio-Hordeetalia*, *Phragmitetalia*, *Magnocaricetalia* (six taxa each) and *Potentillo-Polygonetalia avicularis* (five taxa) (Figure 7). The smallest number of orchid taxa was found in the orders *Caricetalia davallianae* and *Montio-Cardaminetalia* (Figure 7).

Regarding the affiliation to vegetation alliances, the greatest number of orchid taxa was recorded in the *Molinion caeruleae* (24 taxa or 72.7%), followed by *Caricion fuscae* (19 taxa), *Deschampsion cespitosae* (15 taxa), *Calthion palustris* (13 taxa), *Cirsion appendiculati* (eight taxa), *Mentho longifoliae-Juncion inflexi*, *Phragmition communis* (six taxa each), and *Trifolion resupinati*, *Potentillion anserinae*, *Magnocaricion elatae*, *Narthecion scardici* and *Sphagno-Caricion canescentis* (five taxa each). The smallest number of orchid taxa was found in the alliances *Trifolion pallidi*, *Molinio-Hordeion secalini*, *Magnocaricion gracilis*, *Caricion davallianae* and *Cardamino-Montion* (Figure 8).

3.1. Wet Meadows

Orchids of the Central Balkans, which require hygrophilous and hygro-mesophilous habitat conditions, are particularly abundant in communities of the vegetation class *Molinio-Arrhenatheretea*. Many orchid taxa, including numerous taxa of the genus *Dactylorhiza*, were found in communities of the order *Molinietalia caeruleae* (mown meadows on mineral and peaty soils), especially in the alliances *Molinion caeruleae*, *Deschampsion cespitosae* and *Calthion palustris* (Table 2).

Recent studies from Serbia have shown that in the case of the alliance *Molinion caeruleae*, orchids are most abundant in stands of the communities *Molinietum caeruleae* W. Koch 1926 (Figure 9), *Molinio caeruleae-Deschampsietum cespitosae* Pavlović 1951 and *Lathyro pannonici-Molinietum caeruleae* Tatić et al. ex Aćić et al. 2013 [41]. Moreover, it has been shown that the composition of orchids in this vegetation type largely depends on the bedrock types. For example, *Molinion caeruleae* communities in Serbia on Quaternary sediments and carbonate clastites are particularly suitable for *Dactylorhiza incarnata* and *Anacamptis palustris* subsp. *elegans*, while *Molinion caeruleae* communities on serpentine support significant populations of *Platanthera bifolia* and *Dactylorhiza maculata* subsp. *transsilvanica* [18,105]. The importance of the order *Molinietalia caeruleae* as an important vegetation type for orchids has also been recognized in other European regions. The following orchid taxa have been recorded in *Molinion caerulae* communities in Europe: *Epipactis palustris*, *Dactylorhiza majalis*, *D. maculata* subsp. *maculata*, *Neotinea ustulata*, *Gymnadenia conopsea*, *G. densiflora* and *Neottia ovata* [11,13,45,106].

Figure 9. The association *Molinietum caeruleae* W. Koch 1926 (Serbia, photos V. Djordjević).

In the Central Balkans, a significant occurrence of orchids has been noted within the alliance *Calthion palustris*, which represents wet grasslands and tall herb communities that are often unmanaged and found on flat lands along streams or on saturated soils near headwaters. Orchids are most frequently recorded in communities of *Equiseto palustris-Eriophoretum latifolii* Petković ex Aćić et al. 2013, *Scirpetum sylvatici* Ralski 1931 (Figure 10), *Calthaetum palustris* s.l. and *Cirsietum rivularis* Nowiński 1927 (Figure 11). Previous studies in Europe have shown that *Dactylorhiza incarnata*, *D. maculata*, *D. majalis*, *D. praetermissa*, *D. saccifera*, *D. cordigera*, *Epipactis palustris*, *Gymnadenia conopsea* and *Neottia ovata* have significant populations in *Calthion palustris* communities [11,13,19,45,107–109].

Figure 10. The association *Scirpetum sylvatici* Ralski 1931 (Serbia, photo V. Djordjević).

Figure 11. The association *Cirsietum rivularis* Nowiński 1927 (Serbia, photo V. Djordjević).

In addition, many orchids occur in the Central Balkans in communities of the alliance *Deschampsion cespitosae*, which are mown temporarily wet meadows on heavy soils on floodplains in the forest and forest-steppe zones of (sub)continental Central and Eastern Europe. The orchids were most frequently recorded in the Central Balkans within the following communities: *Deschampsietum cespitosae* Horvatić 1930, *Agrostio stoloniferae-Juncetum effusi* Cincović 1959, *Junco articulati-Deschampsietum cespitosae* Petković ex Aćić et al. 2013 and *Rhinantho borbasii-Festucetum pratensis* Gajić ex Aćić et al. 2013 (Table 2). According

to earlier published data from Europe, *Dactylorhiza incarnata*, *D. saccifera*, *Epipactis palustris*, *Gymnadenia conopsea* and *Platanthera bifolia* are orchids commonly found in communities of this alliance [11,13,107].

Some orchids in the Central Balkans have significant representation within the vegetation order *Filipendulo ulmariae-Lotetalia uliginosi* (tall-herb wet meadow fringe vegetation on mineral soils) (Table 2). Within this order, *Epipactis palustris* and *Dactylorhiza incarnata* are among the most common species, especially abundant in *Mentho longifoliae-Juncion inflexi* communities [18,41].

Orchids are less prevalent in communities of the vegetation order *Trifolio-Hordeetalia* (Table 2). This vegetation type represents the wet meadows of the humid continental regions of the north-central Balkans, occurring on clayey, mesotrophic to eutrophic soils on riverside terraces and gentle slopes along the rivers [32,57,110]. *Anacamptis palustris* subsp. *elegans* is one of the most common taxa that have been recorded both in communities of the alliance *Trifolion resupinati* (vegetation of wet meadows of the subarid continental regions of the Southern Balkans) and in communities of the alliance *Trifolion pallidi* (vegetation of wet meadows of the humid continental regions of the north-central Balkans). *Anacamptis laxiflora* is especially common in communities of the alliances *Trifolion resupinati* (*Cynosuro-Caricetum hirtae* K. Micevski 1957, *Hordeo-Caricetum distantis* K. Micevski 1957 and *Trifolietum nigrescentis-subterranei* K. Micevski 1957) and *Molinio-Hordeion secalini* [79].

Some orchid taxa in the Central Balkans have been recorded in communities of the order *Potentillo-Polygonetalia avicularis* Tx. 1947 and the alliance *Potentillion anserinae* Tx. 1947 (Table 2). These are temporarily flooded and heavily grazed nutrient-rich pastures experiencing variable wet-dry or brackish-freshwater alternating conditions of temperate Europe [57,110,111].

3.2. Tall-Herb Vegetation along Mountain Streams and Springs

Representatives of the family Orchidaceae are less abundant in communities of the vegetation class *Mulgedio-Aconitetea* in the Central Balkans (Table 2). This vegetation represents tall-herb vegetation in nutrient-rich habitats moistened and fertilized by percolating water at high altitudes in Europe, Siberia and Greenland [57]. Within this vegetation class, certain orchid species were recorded in communities of the order *Adenostyletalia alliariae* (tall-herb vegetation on fertile soils at high altitudes of temperate and Mediterranean Europe) and the alliance *Cirsion appendiculati* (tall-herb vegetation on acidic soils along mountain streams and springs at high altitudes of the Eastern and Central Balkans) (Table 2).

3.3. Marshland Vegetation

In the Central Balkans, orchids also inhabit marsh communities of the class *Phragmito-Magnocaricetea* (reed, sedge bed and herb-land vegetation of freshwater or brackish water bodies and streams of Eurasia) (Table 2). Based on recent studies in the Central Balkans, it can be stated that especially *Dactylorhiza incarnata* and *Epipactis palustris* are significantly represented in the communities of *Magnocaricion elatae* (*Magnocaricetalia*) and *Phragmition communis* (*Phragmitetalia*) (Figure 12), whereas *Anacamptis palustris* subsp. *elegans* is recorded in the community of *Magnocaricion gracilis* (*Magnocaricetalia*). In Germany, *E. palustris* has also been recorded in communities of *Magnocaricion elatae* (marsh vegetation on oligotrophic to mesotrophic organic sediments of temperate Europe) [107]. In addition, *Dactylorhiza incarnata*, *D. majalis*, *Epipactis palustris*, *Hammarbya paludosa* and *Liparis loeselii* were found in the Czech Republic, Hungary and Germany in communities with *Phragmites australis* as a strongly represented species [109,112].

Figure 12. The association *Phragmitetum australis* Savič 1926 (Serbia, photo V. Djordjević).

3.4. Vegetation of Bogs and Fens

The vegetation class *Scheuchzerio palustris-Caricetea fuscae* (fens, transitional mires and bog hollows in the temperate, boreal and Arctic zones of the Northern Hemisphere) represents important vegetation types for many moisture-demanding orchid taxa in the Central Balkans (Table 2). This vegetation type has been estimated to occupy less than 0.001% of the total Serbian territory [18], so the existence of 19 orchid taxa in these wetland communities in the Central Balkans indicates its great conservation value. Moreover, recent studies in western Serbia indicated that four orchids (*Dactylorhiza cordigera* subsp. *cordigera*, *D. maculata* subsp. *maculata*, *D. saccifera* and *Gymnadenia frivaldii*) were significantly correlated with this vegetation class [18]. Orchids in the Central Balkans were recorded in communities of the order *Caricetalia fuscae* (sedge-moss vegetation of acidic fens in the boreal and temperate zones and in the supra-Mediterranean belt of mountains in Southern Europe) (Table 2). Within the order *Caricetalia fuscae*, orchids are significantly represented in the following communities: *Carici-Sphagno-Eriophoretum* R. Jovanović 1978, *Eriophoro-Caricetum paniculatae* R. Jov. 1983 (Figure 13), *Eriophoro-Caricetum echinatae* V. Randjelović 1998 (within the alliance *Caricion fuscae*), and *Sphagno-Caricetum nigrae* P. Lazarević 2016, *Molinio-Sphagnetum fusci* P. Lazarević 2016, *Sphagno-Caricetum rostratae* P. Lazarević 2016 (within the alliance *Sphagno-Caricion canescentis*) (Table 2).

Orchids belonging to the alliance *Carici-Nardion* V. Ranđelović 1998 at the national level are assigned to the alliance *Caricion fuscae* [57,58]. These are wet communities dominated by *Nardus stricta*, which are not well defined and for which research is still needed, not only in ecological terms but also in terms of nomenclature and classification. Some of the typical orchid taxa in these communities are *Anacamptis coriophora* subsp. *coriophora*, *Dactylorhiza sambucina*, *D. maculata* subsp. *maculata*, *D. maculata* subsp. *transsilvanica*, *D. cordigera* subsp. *bosniaca*, *D. cordigera* subsp. *cordigera*, *Gymnadenia conopsea*, *Platanthera bifolia* and *Traunsteinera globosa*. In addition, it should be noted that the separation of the alliances *Sphagno-Caricion canescentis* and *Caricion fuscae* in the area of the Central Balkans requires additional studies.

Figure 13. The association *Eriophoro-Caricetum paniculatae* R. Jov. 1983 (Serbia, photo V. Djordjević).

The specificity of the Central Balkans is the presence of orchids in the alliance *Narthecion scardici*, which represents relic oro-Mediterranean moderately-rich fens of the Balkans. Within this alliance, orchids are significantly represented in the community *Carici-Narthecietum* scardici Ht. 1953 [102]. The communities of this alliance have great conservation value, hosting significant populations of *Gymnadenia frivaldii*, *Dactylorhiza cordigera* subsp. *cordigera*, *D. cordigera* subsp. *bosniaca* and *Pseudorchis albida*. Orchids in the Central Balkans are less prevalent in communities of the vegetation alliance *Caricion davallianae* (sedge-moss calcareous mineral-rich fen vegetation of Europe and Western Asia) within the order *Caricetalia davallianae* (Table 2).

Communities of the class *Scheuchzerio palustris-Caricetea fuscae* are considered important for the growth and survival of numerous orchids in Europe. The following orchids have significant representation within this vegetation class in other European countries: *Anacamptis palustris* subsp. *palustris*, *Liparis loeselii*, *Dactylorhiza cordigera*, *D. maculata*, *D. majalis*, *D. fuchsii*, *D. incarnata*, *D. lapponica*, *D. russowii*, *D. traunsteineri*, *Epipactis palustris*, *Gymnadenia densiflora*, *G. frivaldii*, *G. conopsea*, *Malaxis monophyllos*, *Herminium monorchis*, *Hammarbya paludosa*, *Neottia ovata*, *Platanthera bifolia*, *Pseudorchis albida*, *Spiranthes aestivalis* and *S. sinensis* [11–13,19,45,57,112–117].

3.5. Vegetation of Springs

In the Central Balkans, orchids are less common in communities of the vegetation class *Montio-Cardaminetea* (vegetation of springs of Europe, the European Arctic archipelagos and Greenland) (Table 2). Within this vegetation class, only *Dactylorhiza cordigera* subsp. *cordigera* was found in communities of the order *Montio-Cardaminetalia* and the alliance *Cardamino-Montion* (vegetation of springs with cold and nutrient-poor water in the subalpine and alpine belts of mountains of central and southwestern Europe).

4. Geological Substrates

The geological substrates and soil properties represent important factors influencing the diversity patterns of terrestrial orchids [7,17,118,119]. Recent studies in the Central Balkans have shown that the bedrock type significantly affects the distribution, abundance and composition of orchids of wetland vegetation and that the greatest differences occur when comparing orchids in habitats on serpentine, carbonate and silicate bedrocks [18,36,105]. These studies underline the important role of bedrock types in separating niches of orchid taxa. Differences in the chemical and physical composition of geological substrates and soils also affect the size of orchid populations [105].

The carbonate geological substrates and soils are the most important for the growth and development of orchids in Central Europe [6,36,120,121]. The great representation of orchid taxa on carbonates in the Central Balkans is explained not only by the physical and chemical properties of the substrate but also by the considerable surface area of this substrate, considering that carbonate substrates are represented from lowlands to high-mountain areas [36]. However, many orchids, known to be characteristic species of carbonate habitats, have also been found on non-carbonate geological substrates in the study area. For example, *Epipactis palustris*, *Dactylorhiza fuchsii*, *Gymnadenia conopsea*, *Nigritella rhellicani* and *Neotinea ustulata* were found to grow in the Central Balkans on limestone-dolomite and carbonate clastites, as well as on various types of silicate substrates, whereas previous studies indicated that these species occur mainly or exclusively on carbonate substrates [6,11,13,122].

Recent studies on orchid ecological preferences suggest that wet habitats on serpentines are particularly important to the survival of numerous orchid species [18,36,105]. Orchids with large population sizes that are common in wet habitats on serpentines in the Central Balkans include *Gymnadenia conopsea*, *Platanthera bifolia*, *Dactylorhiza maculata* subsp. *transsilvanica*, *D. maculata* subsp. *maculata*, *D. sambucina*, *D. incarnata*, *Anacamptis coriophora* and *A. morio*, whereas *Coeloglossum viride*, *Traunsteinera globosa*, *Spiranthes spiralis*, *D. saccifera* and *A. pyramidalis* occur somewhat less frequently on these substrates [36,41]. The surprisingly large number of orchid taxa found in wet habitats can be explained by the physical and chemical properties of serpentine soils, especially their low nutrient content, as most orchid species are sensitive to increased phosphorus, nitrogen and potassium content in the soil [118,123–126]. It is known that serpentine substrates allow the development of open habitats with a generally low level of competition between plants, which enables the survival of low-competitive orchid taxa that have high light requirements [105]. In addition, mycorrhizal fungi are thought to play a key role in increasing tolerance to high levels of heavy metals in serpentine soils. Although serpentine soils are characterized by high concentrations of Ni, Cr and Co, an unfavorable ratio of Ca to Mg, and low content of macronutrients (N, P and K) [127], the impact of these specific characteristics is much lower when soils are moist and well developed, which is usually the case in wetlands on serpentine bedrock. This is one possible reason why many species characteristic of carbonate substrates are abundant in serpentine wetlands.

Orchids growing in wetland vegetation in the Central Balkans are very common on ophiolitic mélanges and sandstones from the Carboniferous and Permian periods, which include diabase, gabbro, spilite, cherts, sandstones, shales and marls of the Jurassic period, and sandstones from the Carboniferous and Permian periods. The great abundance of orchids on these geological substrates is due to their heterogeneous composition since these volcanogenic-sedimentary formations (the old name is "diabase-chert formation") usually contain diabase and cherts [128–130]. Orchids highly represented on ophiolitic mélanges and sandstones from the Carboniferous and Permian periods include the Carpathian-Balkan subendemics (*Dactylorhiza cordigera* subsp. *cordigera*, *D. maculata* subsp. *transsilvanica*, *Gymnadenia frivaldii*), as well as *Anacamptis morio*, *A. coriophora*, *A. pyramidalis*, *Epipactis palustris*, *Traunsteinera globosa*, *Neotinea ustulata*, *Platanthera bifolia*, *Pseudorchis albida*, *Dactylorhiza incarnata*, *D. maculata* subsp. *maculata*, *D. fuchsii* and *D. saccifera*. On the Stara planina mountain (eastern Serbia), on the substrate of the "red sandstone formation": conglom-

erates, sandstones and siltstones from the Permian period, significant populations of the following orchids were found in wetland vegetation: *Gymnadenia frivaldii*, *G. conopsea*, *Pseudorchis albida*, *Dactylorhiza cordigera* subsp. *cordigera*, *Dactylorhiza saccifera* and *Traunsteinera globosa* [131].

Many species inhabiting wetland vegetation in the Central Balkans have been found on metamorphic rocks (schists, gneisses and phyllites) [18,36]. Among them, those that occur mainly in high-altitude areas and are rare in the study area stand out. For example, *Gymnadenia frivaldii* and *Nigritella rhellicani* are very common on phyllites on Golija Mountain in western Serbia [41]. A recent study revealed that these two orchids are indicator species of schists, gneisses and phyllites [18]. Orchids are found very often on this bedrock type in western Serbia and on Kopaonik mountain, Mts Šar-Planina and Vlasina Plateau [62,99,132]. Other orchid taxa that have a large presence on schists, gneisses and phyllites in the Central Balkans are *Dactylorhiza maculata* subsp. *maculata*, *D. incarnata*, *D. saccifera*, *Gymnadenia conopsea*, *Anacamptis morio*, *Platanthera bifolia*, *Traunsteinera globosa* and *Epipactis palustris* [18,36,41,62,99,132].

Some orchid taxa of wetland vegetation in the Central Balkans have been recorded on acidic igneous rocks [18,36,41]. Orchids that occur to a considerable extent on quartz latites are *Dactylorhiza incarnata*, *D. maculata* subsp. *maculata*, *D. saccifera*, *D. sambucina*, *Nigritella rhellicani*, *Gymnadenia conopsea*, *Coeloglossum viride* and *Traunsteinera globosa*, while the orchids that are particularly abundant on granodiorites are *D. cordigera* subsp. *cordigera*, *D. cordigera* subsp. *bosniaca*, *D. saccifera*, *G. conopsea*, *G. frivaldii* and *T. globosa* [18,36,41,62,99,132]. Furthermore, orchid taxa of herbaceous wetlands were found growing on intermediate igneous rocks (andesite, dacite and porphyrite) [18,36,41]. Among these species, the following should be highlighted: *Anacamptis morio*, *A. laxiflora*, *Dactylorhiza incarnata*, *Epipactis palustris*, *Gymnadenia conopsea*, *Platanthera bifolia* and *Traunsteinera globosa*.

In the Central Balkans, numerous water-demanding orchids have been found on Quaternary sediments that include proluvial and alluvial deposits, eluvial-deluvial sediments and fluvial terraces. *Anacamptis palustris* subsp. *palustris*, *Anacamptis palustris* subsp. *elegans*, *A. morio*, *A. pyramidalis*, *Dactylorhiza incarnata*, *D. saccifera*, *Epipactis palustris*, *Gymnadenia conopsea*, *Neottia ovata*, *Orchis militaris* and *Traunsteinera globosa* grow on this type of substrate [18,36,41]. The lowest number of orchid species in the wetlands of the Central Balkans was recorded on flysch, which is a series of sedimentary rocks where marls, clay shales, sandstones, conglomerates and limestones are the most common [133]. Among the species that occur on this type of substrate, the following are noteworthy: *Dactylorhiza maculata* subsp. *maculata*, *Anacamptis morio*, *Gymnadenia conopsea*, *Platanthera bifolia* and *Traunsteinera globosa* [18,36,41].

5. Threat Factors and Conservation Priorities

5.1. Threat Factors

Factors threatening orchids of wetland vegetation in the Central Balkans can be classified into several groups: (a) hydrologic regime alteration; (b) pollution; (c) uncontrolled urbanization, industrialization and construction of transport infrastructures; (d) grazing intensity, mowing time and frequency; (e) agriculture; (f) tourism; (g) invasive and non-native species; (h) collection of orchids; and (i) climate change.

Hydromelioration works, soil drainage, creation of hydroaccumulations, capture of springs, channelization of natural runoff, deepening and straightening of river courses and other forms of hydrologic regime alterations are the main factors threatening water-demanding orchids in the Central Balkans. In Peštersko polje (southwestern Serbia), significant changes in the hydrological regime were made when a system of canals, dams and levees was built to divert the water basin into the Uvac hydropower system [27]. It is assumed that due to the drainage of the central part of Peštersko polje, the groundwater level has decreased and the vegetation has developed from fen communities of the class *Scheuchzerio palustris-Caricetea fuscae* to wet and mesophilous meadows [27,41]. It is important to emphasize that uncontrolled water use at springs and in the headwaters of rivers,

especially in mountainous regions, affects the water balance of entire regions and poses a potential threat to many orchid species.

Various forms of physical, chemical and biological pollution, directly and indirectly, threaten orchids of wetland vegetation in the Central Balkans. A direct negative impact can be seen in the vicinity of agricultural land, rural households, transport routes, industrial plants and tourist facilities. Orchids are particularly threatened by wastewater discharge, municipal waste disposal and soil nitrification. Since orchids are particularly sensitive to increased levels of nitrogen and phosphorus in the soil [118], their lower occurrence has been observed in wet meadows and fens near farms that use artificial or natural fertilizers and pesticides. One of the examples is Divčibare (northwestern Serbia), where waste oil, fuel oil and fecal water are occasionally discharged into the upper reaches of the river from restaurants and hotels. This polluted the soil, surface and groundwater and directly affected the degradation of this part of the mire area [41].

Uncontrolled urbanization, industrialization and construction of transport infrastructures without ecologically oriented spatial planning pose a significant threat to orchids of the Central Balkans. Urbanization and road construction have destroyed many wet habitats of orchids, especially in lowland areas and near tourist centers. Roads cut through natural ecosystems, disrupt or prevent communication between coenobionts, increase the erosion process and affect water and soil pollution, threatening orchids directly and indirectly. Incidentally, based on studies that included over 8,000 plant species, it was found that representatives of the family Orchidaceae have the highest risk of disappearing from the immediate vicinity of cities [134]. Among the many negative consequences of urbanization, the above authors pointed out in particular the decline of orchid populations and competition with invasive species. A particularly sharp decline in orchid populations due to a high degree of urbanization was observed in the northern areas of Western Europe (northern France, Belgium and Luxembourg) [5,22].

Intesive grazing and mowing in lowland, mountain and high-mountain areas of the Central Balkans negatively affect orchid taxa in wetland vegetation. Extensive animal husbandry leads to the intensification of erosion processes, damage to soil structure and quality, and thus to negative zoo-anthropogenic selection of plant cover. Grazing by cattle and sheep leads to the spread of the species *Nardus stricta* L. and the degradation of many mires and wet meadow ecosystems. Livestock management is the greatest threat to the survival of endangered plant species in Europe [135]. The negative consequences are not only due to direct grazing, but the impoverishment of the floristic composition of plant species is mainly due to nitrification and soil compaction. Early mowing of wet meadows has a negative impact, especially, on orchids that complete their reproductive phase (seed formation) by the time of mowing. The negative effects of this factor are mainly seen in the reduction of cross-pollination. It is important to note that the complete abandonment of traditional activities such as mowing or grazing would threaten the survival of many orchid species, as open habitats would thus be threatened by the development of forest and shrub vegetation [135]. Without the above-mentioned traditional activities, mires and wet meadows are particularly at risk due to the establishment of forest vegetation [27]. Previous studies have shown that mowing to some extent reduces competition between plants in the habitat and thus has a beneficial effect on the development of orchid populations. Regular annual mowing, when carried out in seasons when orchids do not appear above ground, has been shown to be beneficial to the optimal development of many species of the genus *Dactylorhiza* [19,20].

The spreading of arable land at the expense of natural ecosystems (wet meadows, fens and marshes) threatens orchids in the Central Balkans. In addition to the direct loss of natural habitats where orchids grow, the negative effects of the formation of agroecosystems can be seen in the fragmentation of habitats, fertilization of the soil and pollution of the soil with chemical substances, especially pesticides.

Uncontrolled tourism development is another important factor threatening orchids in the wetlands of the Central Balkans. Tourism has a negative impact on the status

of orchid populations, especially in the mountain tourist areas of the Central Balkans. The negative effects of this factor are manifested in the fragmentation and destruction of wet habitats where orchids grow, disruption of the water balance, ruderalization of ecosystems and pollution of air, water and soil [136]. The most severe impacts of tourism have been found in the mountains of Zlatibor and Kopaonik (Serbia), where many wet habitats have been destroyed or degraded. Previous research has shown that orchids in tourist areas are threatened primarily by habitat loss, picking by individuals, trampling of areas and ecosystem disturbance by motor vehicles and bicycles, as well as horseback riding [136–138].

Invasive and non-native species also threaten orchids in the Central Balkans. The negative impacts due to the disruption of cenotic relationships and reduction of biodiversity are most evident in lowland areas, near roads, agricultural lands, rural households and tourist centers, where many wet meadows are ruderalized and under the strong influence of invasive and non-native species (*Erigeron annuus*, *Conyza canadensis*, *Ambrosia artemisiifolia*, *Ailanthus altissima*, *Robinia pseudoacacia* and others) [41]. However, the negative impacts of non-native and invasive species in high-altitude areas have not been observed. In North America, invasive and non-native species threaten especially orchids of mire habitats [5].

Although orchid collecting is the most important threat to orchids on the global IUCN Red List [139], this factor does not pose a significant threat to wetland orchids in the Central Balkans. The consequence of picking orchids is a decrease in reproductive success, considering that they are prevented from cross-pollination and reproduction by seed [139]. The aboveground parts of orchids are harvested for their decorative flowers, especially in tourist areas. The use of orchid tubers for the production of the drink salep has been noted in the Pešter region (southwestern Serbia) and North Macedonia [140]. From a survey in the Pešter area, it appears that the locals use mainly *Anacamptis morio* and *Gymnadenia conopsea* for the production of the drink salep [41]. The production of salep threatens the survival of many orchid species, especially in the eastern Mediterranean countries, where salep is traditionally used as a food, tonic and aphrodisiac [141].

Climate change is another factor threatening the survival of orchids of wetland vegetation in the Central Balkans. Considering that the global temperature has increased in the last century (1.1 °C warming since 1850–1900) and that an average warming of 1.5 °C or more is expected in the next 20 years [142], drought is expected to lead to a decrease in the distribution of wetlands and consequently of orchids, and many species will be restricted altitudes. Thus, orchids in lowland and mid-altitude areas are more at risk than at higher altitudes due to higher temperatures. Orchids that grow exclusively in wetland vegetation types are most at risk, while orchids that are generalists, i.e., orchids that inhabit other habitats (dry and semi-dry grasslands and forest habitats), are less at risk. From a recent study on the effects of climate change on the distribution of *Traunsteinera globosa* and its pollinators, it appears that the distribution of *T. globosa* may decline significantly as a result of global warming, and pollinators of this orchid will also face a loss of habitat [143]. As a warmer climate makes growing seasons longer and warmer, increases productivity and decreases water levels, these effects increase the duration and intensity of interspecific competition, encourage competing species and force the niches of specialized wetland species towards narrower pH ranges [144]. This means that orchids known to be weakly competitive will face stronger competition, and the question for future research is how climate change will affect orchids with different ecological preferences for soil pH.

In addition to the factors already mentioned, the internal factors affecting the distribution and abundance of orchids are natural factors that operate during the belowground (need for mycorrhizal association) and aboveground (need for successful pollination) stages of orchid development [2,3]. It is important to emphasize that for most terrestrial orchids, the presence and effectiveness of mycorrhizae in the soil have a greater influence on survival than other factors.

5.2. Conservation Priorities

The conservation priorities defined in this study are based on the degree of representation of orchids of wetland vegetation (Table 1), the marginality and breadth of the species' niches [18], the size of their populations, the rarity and conservation status of their habitats, as well as the extent of their geographical distribution.

Special attention should be paid to orchid taxa that occur exclusively or mainly in wet habitats (Table 1). These orchids have the highest level of habitat specialization [18], the highest requirements for soil moisture, and their habitats (especially the fens) are the rarest and most threatened habitats in the study area [27,41]. Moreover, both the study area and the entire Balkan Peninsula represent one of the most important centers of evolution, diversity and endemicity of the genus *Dactylorhiza*, to which most specialists belong [17,18,26,35]. Conservation of these orchids requires ensuring adequate water supply in wet meadows, fens and marshes, while the optimal performance of many *Dactylorhiza* taxa can be achieved by regular annual mowing [19,20].

Special priority should be given to orchids whose southernmost range falls within the study area (e.g., *Dactylorhiza maculata* subsp. *maculata*, *D. maculata* subsp. *transsilvanica*, *D. cordigera* subsp. *bosniaca*, *D. fuchsii*, *D. majalis* and *Traunsteinera globosa*). Biomonitoring of these taxa in light of global warming is necessary because they are expected to respond rapidly to climatic changes [35].

One of the conservation priorities relates to wet habitats occurring on serpentine in the study area. Because the wet serpentine habitats of the Central Balkans are less used for agriculture, they could be considered as potential orchid reserves, especially considering that orchids are very common in these habitats and have large population sizes. In addition, wetland vegetation types at higher altitudes, occurring on silicate rocks known for their water-holding capacity, harbor numerous representatives of orchids and can be considered the most important habitats for specialized orchids, including an endemic taxon of the Balkans (*Dactylorhiza cordigera* subsp. *bosniaca*) and subendemic taxa of the Balkans and Carpathians (*Dactylorhiza cordigera* subsp. *cordigera*, *D. maculata* subsp. *transsilvanica* and *Gymnadenia frivaldii*).

6. Conclusions

The presence of 33 orchid species and subspecies was established in the wetland vegetation types of the Central Balkans. *Dactylorhiza* is the most taxon-rich genus (with ten taxa), followed by *Anacamptis* (six taxa) and *Gymnadenia* (four taxa). The phytogeographical analysis shows that representatives of the Central European and Eurasian chorological groups dominate, followed by orchids of the Central European mountainous and boreal groups. The analysis of life forms revealed that representatives with palmately lobed and fusiform tubers are dominant, followed by orchids with ovoid and spindle-shaped tubers and orchids with rhizomes.

According to the degree of occurrence in wetland vegetation types, eight taxa were found to occur exclusively in these vegetation types, six taxa grow mainly in wetland vegetation types and rarely occur in other vegetation types, 11 taxa grow in wetland vegetation types but occur more frequently in other vegetation types, while eight taxa occur very rarely in wetland vegetation types. Most of the orchid taxa were found in communities of the classes *Molinio-Arrhenatheretea* and *Scheuchzerio palustris-Caricetea fuscae*; the orders *Molinietalia caeruleae* and *Caricetalia fuscae* and the alliances *Molinion caeruleae*, *Caricion fuscae*, *Deschampsion cespitosae* and *Calthion palustris*.

Serpentine and silicate bedrock types and their wet habitats in the Central Balkans are important for many orchids, suggesting that they may play an important role in orchid conservation. The study highlights the importance of establishing biomonitoring for orchids that have southern limits of their distribution in the Central Balkans, in the face of global warming. Future detailed taxonomic, chorological and ecological studies of orchids of wetland vegetation in the Central Balkans are necessary to conduct their successful conservation.

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