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FIRST RECORDS OF THREE *Epipactis* TAXA (Orchidaceae) IN THE VOJVODINA PROVINCE

ABSTRACT**:** In recent decades, many new species of the genus *Epipactis* have been described across Europe. Many of these species were initially thought to be narrowly localized with small ranges. However, intensified research, particularly in well-preserved forests, has revealed these taxa in new and often distant locations from where they were initially described. Similarly, over the last 15 years, several new *Epipactis* taxa have been discovered in Serbia, primarily in the western regions of Central Serbia. Since 2018, our floristic research has recorded three *Epipactis* taxa, previously known only from Central Serbia, in the Vojvodina Province on Fruška Gora Mt. *Epipactis helleborine* subsp. *distans* was found at two, *E. leptochila* subsp. *neglecta* at one, and *E. purpurata* at two sites. These findings span three different UTM squares (10×10 km), with all three taxa occurring only in square 34TDR00. They were recorded in deciduous forests or their edges, primarily in beech-linden habitats. At these sites, negative habitat changes, primarily caused by the cutting of older trees, have been noted, resulting in shifts in community structure between 2018 and 2025. Considering the ongoing discovery of new *Epipactis* taxa in Serbia and its neighboring countries, it is likely that Fruška Gora Mt. still harbors overlooked species.

KEYWORDS: *Epipactis helleborine* subsp. *distans*; *Epipactis leptochila* subsp. *neglecta*; *Epipactis purpurata*; Fruška Gora Mt.; Serbia; Srem

INTRODUCTION

The genus *Epipactis* Zinn belongs to the subfamily Epidendroideae Lindl. within the family Orchidaceae Juss. (Wood, 2005). It exhibits a predominantly Eurasian distribution, primarily confined to temperate and sub-Medi-

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terranean zones, with extensions into the tropical and subtropical regions of Southeast Asia and East Africa (Delforge, 2006; Kühn et al., 2019).

High morphological plasticity, influenced by habitat conditions, along with frequent obligate or facultative autogamy and cleistogamy, has led to the description of numerous taxa with limited ranges and small populations in recent decades. This emergence occurs alongside the well-established taxa that are characterized primarily by relatively large distribution areas (Delforge, 2006). It is now considered that autogamous species, which tend to be spatially localized, evolved from ancestral widely distributed allogamous species (Tsiftsis & Antonopoulos, 2017).

The number of species within the genus varies significantly due to the aforementioned reasons. According to the Plants of the World Online database (POWO, 2025), 54 accepted species, including 12 subspecies, are recognized across the entire range of the genus. Other authors (Kühn et al., 2019) report 16 species and 11 subspecies for Europe and the Mediterranean region, whereas Delforge (2006) identifies as many as 59 species for a similar geographic area. According to Delforge, the genus can be divided into two sections – *Arthrochilium* (Irmisch) Beck, which comprises only two species, and section *Euepipactis* Irmisch, which contains seven species groups: E. phyllanthes, E. leptochila, E. purpurata, E. helleborine, E. atrorubens, E. tremolsii, and E. albensis.

Species of the genus *Epipactis* predominantly inhabit various forest ecosystems, including forest margins and glades, as well as shrublands, grasslands, dune slacks, road verges, swampy meadows, fens, bogs, and riparian zones (Kühn et al., 2019). In Europe, their presence is closely associated with relict deciduous forests, particularly those dominated by beech (Delforge, 2006).

Within the territory of Serbia, 11 taxa of the genus *Epipactis* have been documented to date: *E. atrorubens* (Hoffm.) Besser, *E. exilis* P. Delforge, *E. helleborine* (L.) Crantz subsp. *helleborine*, *E. helleborine* subsp. *distans* (Arv.-Touv.) R. Engel & P. Quentin, *E. leptochila* (Godfery) Godfery subsp. *neglecta* Kümpel, *E. microphylla* (Ehrh.) Sw., *E. muelleri* Godfery subsp. *muelleri*, *E. palustris* (L.) Crantz, *E. pontica* Taubenheim, *E. purpurata* Sm. and *E. tallosii* A. Molnár & Robatsch (Diklić, 1976; Djordjević et al., 2018, 2023; Süveges et al., 2019).

This study presents the first confirmed records of three *Epipactis* taxa – *E. helleborine* subsp. *distans*, *E. leptochila* subsp. *neglecta*, and *E. purpurata*, from Fruška Gora Mt., simultaneously representing their first documented presence in northern Serbia (Srem region, Vojvodina Province). The objectives of this research were: (i) to present the distribution of the newly recorded taxa in Vojvodina Province and analyze their geographic positions relative to previously known localities of these taxa in Central Serbia; (ii) to describe the ecological preferences and habitat conditions of the newly recorded taxa on Fruška Gora Mt. and critically compare the obtained data with existing information on their habitats in other parts of Serbia and Europe; (iii) to determine the population size by counting the actual number of ramets of each taxon in the study area; and (iv) to identify potential threats to the survival of populations of the newly recorded taxa on Fruška Gora Mt. Taken together, these objectives also have practical relevance for conservation planning, as the updated eco-

logical and distributional data can support management of these taxa and inform future assessments for The red data book of flora of Serbia.

MATERIALS AND METHODS

Floristic field surveys targeting representatives of the Orchidaceae family were conducted within the broader area of Fruška Gora Mt. (Srem region, Vojvodina Province) over the period from 2018 to 2025. The surveys encompassed all vegetation seasons and a wide variety of natural habitat types, including grasslands, shrublands, and forests, as well as habitats subject to varying degrees of anthropogenic degradation. Furthermore, a revision of the Orchidaceae herbarium specimens at the BUNS Herbarium (Thiers, 2025) was performed.

Taxonomic identification was carried out following relevant literature sources (Buttler, 1996; Delforge, 2006; Kühn et al., 2019; Tsiftsis & Antonopoulos, 2017; Vlčko, 2023). Nomenclature generally adheres to the Plants of the World Online database (POWO, 2025), except *E. helleborine* subsp. *distans*, for which a broader taxonomic consensus is lacking; its nomenclature was therefore established based on the aforementioned references. For each taxon, one voucher specimen comprising the above-ground plant parts was collected and deposited in the BUNS Herbarium.

Geographical coordinates and altitudinal data were recorded using a handheld GPS device. The spatial distribution of the recorded taxa within Vojvodina Province was mapped utilizing a 10×10 km UTM grid system (Lampinen, 2001). Habitat classification followed the national habitat typology guidelines (Anonymous, 2010). Geological substrates were identified based on the 1:100.000-scale geological map of Serbia (Čičulić-Trifunović & Rakić, 1976), while the soil cover was assessed according to the 1:50.000-scale pedological map of Vojvodina (Nejgebauer et al., 1971). Population censuses of the newly recorded orchid taxa were conducted *in situ*, employing ramets as the unit of enumeration (Jacquemyn & Hutchings, 2010). Documented conservation threats observed during fieldwork are detailed for each taxon.

RESULTS AND DISCUSSION

During floristic field surveys conducted from 2018 to 2020, supplemented by additional fieldwork up to 2025 in the Fruška Gora Mt. wider area, the presence of three orchid taxa was confirmed: *E. helleborine* subsp. *distans*, *E. leptochila* subsp. *neglecta*, and *E. purpurata* (Figure 1). These taxa represent new records for this mountain, as well as for the Srem region and the entire Vojvodina Province. For each taxon, comprehensive data are presented regarding their distribution, habitat characteristics, ecological preferences, population sizes, flowering phenology, and potential threats impacting their persistence within the study area.

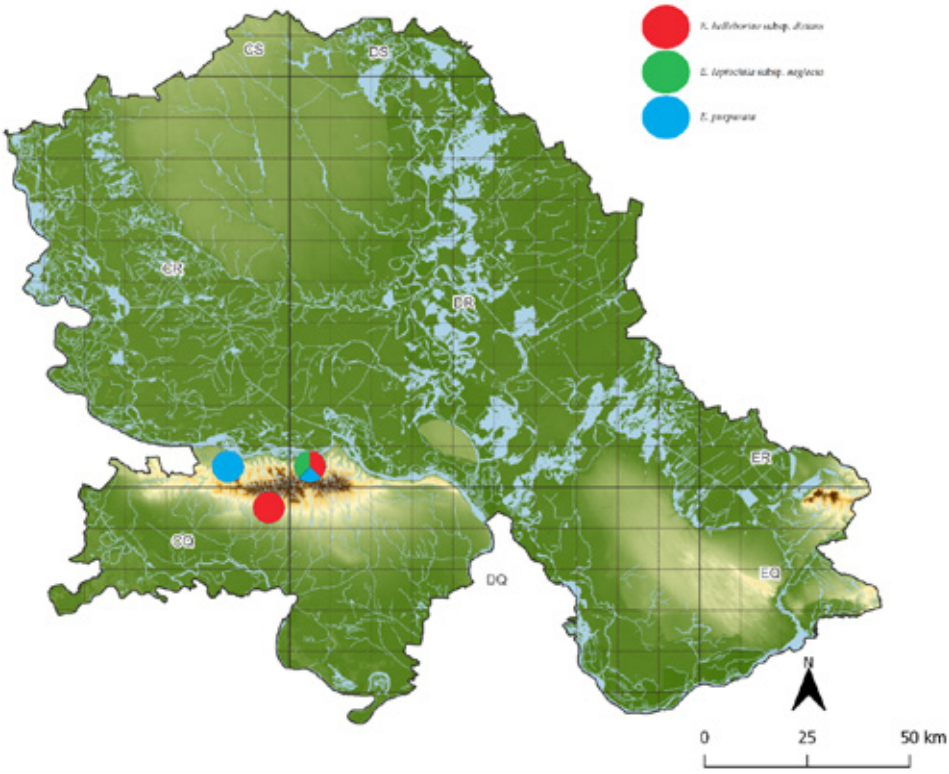

Figure 1. Distribution of newly registered orchid taxa in Vojvodina Province

Epipactis helleborine (L.) Crantz subsp. *distans* (Arv.-Touv.) R. Engel & P. Quentin, *Orchidophile* (Asnières) 124: 205 (1996)

Synonyms: *E. distans* Arv.-Touv., *E. helleborine* var. *orbicularis* (K. Richt.) Verm., *E. helleborine* subsp. *orbicularis* (K. Richt.) E. Klein

General distribution

The range of *E. helleborine* subsp. *distans* extends from northeastern Spain through southern France and northern Italy to Central Europe, and eastwards to Crimea. The southernmost distribution limit is in the mountainous regions of northern Greece on the Balkan Peninsula, while isolated populations occur in northern Europe, including northern Germany, Poland, the Baltic states, and southern Sweden (AHO, 2018; Dolinar, 2015; Kreutz & Fateryga, 2012; Tsiftsis & Antonopoulos, 2017).

Within the Balkan Peninsula, this taxon has been recorded in Slovenia (Dolinar, 2015), Croatia (AHO, 2018), Bosnia and Herzegovina (Šabanović et al.,

2021), Serbia (Djordjević et al., 2016), Montenegro (Radak et al., 2025), Romania (Paucâ & Morariu, 1972), Bulgaria (Стоянов, 1964), and Greece (Tsiftsis & Antonopoulos, 2017).

Distribution in Vojvodina Province

Fruška Gora Mt., Popovica, N45 10.928, E19 49.896, UTM 34TDR00, 301 m a.s.l., 04 July 2020, coll. B. Radak, A. Vlku, J. Peškanov, det. B. Radak (BUNS 25688); Fruška Gora Mt., Letenka, N45 08.173, E19 41.020, UTM 34TCQ99, 436 m a.s.l., 09 July 2020, coll. et det. B. Radak & J. Peškanov (BUNS 25689)(Figure 2); Fruška Gora Mt., Letenka, N45 08.172, E19 41.014, UTM 34TCQ99, 437 m a.s.l., 19 August 2025, B. Radak & J. Peškanov (field obs.).

Figure 2. Epipactis helleborine subsp. *distans*

Photograph by B. Radak (09 July 2020, Serbia, Fruška Gora Mt., Letenka)

Previously, this taxon had been reported in Serbia only within two 10×10 km UTM grid squares in Southwestern Serbia (Đorđević, 2021). The findings from Fruška Gora Mt. constitute the first records for the Srem region and Vojvodina Province, marking the northernmost known occurrences of this taxon in Serbia. The nearest known Serbian localities, Jabuka and Kamena Gora (Đorđević, 2021), are approximately 200 km distant from Fruška Gora Mt.

Habitat and ecology

Epipactis helleborine subsp. *distans* was first recorded on Fruška Gora Mt. on 4 July 2020, in the vicinity of Popovica, at the forest edge of the beech and silver linden community *Tilio-Fagetum submontanum* (M. Janković & Mišić 1960, Mišić 1972; Code A3.228 of the national habitat classification), near a forest path. At the site where ramets of this taxon developed, herbaceous vegetation and forest litter were absent. The geological substrate consists of conglomerates, sandstones, limestones, clays, and tuffs, while the soil is classified as gray-brown podzolic. The ramets developed under semi-shaded conditions at an elevation of 301 m a.s.l.

A few days later, the same taxon was observed at an additional site close to the road near Letenka on Fruška Gora Mt. The ramets were found between the margin of a mixed deciduous forest (*Hypoglosso-Querco-Carpinetum serbicum* M. Jank. 1980; Code A2.61 of the national habitat classification) and an asphalt road. All ramets were situated one to three meters from the road. The upper tree layer consisted of *Quercus petraea* (Matt.) Liebl. and three *Tilia* L. species: *T. cordata* Mill., *T. platyphyllos* Scop., and *T. tomentosa* Moench. The shrub layer included *Acer campestre* L., *A. platanoides* L., *Carpinus betulus* L., *Crataegus monogyna* Jacq., *Fraxinus ornus* L., and *Staphylea pinnata* L. The forest litter was well-developed, whereas the herbaceous layer had low coverage and was composed of species such as *Campanula persicifolia* L., *C. trachelium* L., *Euphorbia amygdaloides* L., *Geum urbanum* L., *Hedera helix* L., *Helleborus odorus* Waldst. & Kit. ex Willd., *Lapsana communis* L., *Pulmonaria officinalis* L., *Ruscus hypoglossum* L., *Stellaria holostea* L., as well as seedlings of woody plants. The geological substrate here consists of sericitic and albite-chlorite schists, sericitic quartzites, and phyllites. The pedological substrate is gray-brown podzolic soil. Ramets at this site developed under semi-shade conditions at 436 m a.s.l. A follow-up field survey conducted on 19 August 2025 at the same site revealed significant habitat degradation resulting from anthropogenic impacts. Extensive logging of tall trees resulted in increased light penetration, transforming the habitat from semi-shade to highly illuminated conditions, with many areas losing continuous forest canopy cover. This led to the colonization of non-forest species, such as *Clinopodium vulgare* L., *Erigeron annuus* (L.). Desf., *Hypericum perforatum* L., *Urtica dioica* L., and *Verbena officinalis* L. The herbaceous layer, formerly sparse, now covers nearly the entire ground surface. Additionally, a single ramet of *E. helleborine* subsp. *distans* was recorded on the opposite side of the

road along the edge of the beech-linden forest, which was also affected by degradation processes. The spread of this taxon to the edge of the beech-linden forest is likely due to increased light availability.

The habitat conditions of *E. helleborine* subsp. *distans* observed on Fruška Gora Mt. correspond to those reported in the literature. This taxon develops from full sun to semi-shade environments, including sunny forest clearings (Dolinar, 2015), shrubby slopes (G.I.R.O.S., 2009), thermophilic pine forests (Delforge, 2006; Kreutz & Fateryga, 2012; Tsiftsis & Antonopoulos, 2017; Vlčko et al., 2003), and open habitats within spruce zones (Radak et al., 2025; Tomović et al., 2021), ranging from lowland to 2200 m a.s.l. (Delforge, 2006; Dolinar, 2015). This orchid primarily prefers thermophilic habitats and, when present in cooler forests, it typically occurs at the forest margins. Such a situation was documented on Fruška Gora Mt., where one subpopulation was found at the edge of a light mixed oak-linden-hornbeam forest and another along a forest path in a light area at the margin of a beech-linden forest. *Epipactis helleborine* subsp. *distans* generally develops on calcareous soils (Dolinar, 2015; Vlčko et al., 2003). The geological substrate at the Popovica site includes limestone, which aligns with the general ecological preferences of this taxon. However, *E. helleborine* subsp. *distans* has also been recorded on transitional geological substrates and those characterized by silicates, such as cherts (Tomović et al., 2021) and marly soils (Delforge, 2006). Therefore, the second Fruška Gora Mt. record (Letenka), found on a predominantly silicate geological substrate, corresponds with its ecological preferences.

In Serbia, *E. helleborine* subsp. *distans* has previously been documented only in meadow communities and at the margins of spruce forests on limestone at altitudes between 1196 m and 1246 m (Đorđević, 2021). Thus, the communities and geological substrates where it was recorded on Fruška Gora Mt., provide novel data on the ecological and habitat preferences of this taxon within Serbia. Furthermore, these Fruška Gora Mt. localities occur at considerably lower altitudes (301 and 436 m) than previous Serbian records. The substantial difference in recorded altitudes on Fruška Gora Mt., combined with the distinct habitat types compared to previously known localities in Serbia, which are also separated by a considerable distance (approximately 200 km), suggests that this taxon may have a much wider distribution within the country, and that additional occurrences can be expected.

Population size and flowering time

At the Popovica locality, five ramets of *E. helleborine* subsp. *distans* were recorded in just 2 m², with three being in bud and two not forming buds at all during the field survey on 4 July 2020. During the first visit to Letenka locality (9 July 2020), 13 ramets of this taxon were recorded, growing in eight separate groups over an area of 84 m². At that time, the plants were in the early stages of flowering. These data correspond with the recorded flowering period of this taxon throughout its range (Delforge, 2006; Dolinar, 2015; Vlčko

et al., 2003), as well as with observations from southwestern Serbia, where it was found to flower from early to late July (Đorđević, 2021). During the second visit to Letenka locality (19 August 2025), a decline in population size was observed compared to the 2020 record. At that time, eight ramets were recorded, growing in five separate groups. Moreover, a noticeable spatial expansion of the population was noted, as one ramet was found at the edge of the neighboring beech-linden forest, where this orchid was not present five years earlier, increasing the area occupied by the ramets of this taxon to 120 m².

Conservation status

This taxon is protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2025) and is listed in Appendix II. *Epipactis helleborine* subsp. *distans* is considered Endangered in Slovakia (Vlčko et al., 2003) and the Czech Republic (Grulich, 2017). In Serbia, *E. helleborine* subsp. *distans* is not legally protected, and its conservation status has been assessed as Critically Endangered (Djordjević et al., 2016). At the Letenka locality, there is a potential risk of population destruction due to its proximity to an asphalt road, which raises the possibility of plants being picked during flowering, as well as risks from road maintenance works. During the latest road renovation, large amounts of stones, soil, and other materials were dumped directly next to the plants. Additionally, intensive logging of larger trees was observed at the site. This does not necessarily have to lead to the destruction of this taxon population, as increased light availability and habitat illumination are preferred by it; however, the immediate danger comes from the physical destruction of plants due to machinery access and tree felling.

Epipactis leptochila (Godfery) Godfery subsp. *neglecta* Kümpel, Mitt. Arbeitskreises Heimische Orchideen 11: 30 (1982)

Synonyms: *E. leptochila* var. *neglecta* (Kümpel) Gévaudan, *E. neglecta* (Kümpel) Kümpel

General distribution

Epipactis leptochila subsp. *neglecta* is primarily distributed across Central Europe, ranging from France in the west to Romania in the east, and from Germany in the north to northeastern Italy and the mountains of northern Greece in the south (Kühn et al., 2019; POWO, 2025).

Within the Balkan Peninsula and the southern part of the Pannonian plain, *E. leptochila* subsp. *neglecta* has been recorded in Hungary (Molnar, 2011), Slovenia (Dolinar, 2015), Croatia (Nikolić et al., 2025), Serbia (Djordjević et al., 2016), Montenegro (Radak et al., 2025), Greece (Antonopoulos & Tsiftsis, 2012), and Romania (Ardelean et al., 2018).

Figure 3. Epipactis leptochila subsp. *neglecta*

Photograph by B. Radak (22 July 2020, Serbia, Fruška Gora Mt., Popovica)

Distribution in Vojvodina Province

Fruška Gora Mt., Popovica, N45 10.909, E19 49.700, UTM 34TDR00, 343 m a.s.l., 13 July 2018, coll. et det. B. Radak (BUNS 25686); Fruška Gora Mt., Popovica, N45 10.917, E19 49.678, UTM 34TDR00, 343 m a.s.l., 04 July 2020, B. Radak, A. Vlku, J. Peškanov (field obs.); Fruška Gora Mt., Popovica, N45 10.929, E19 49.639, UTM 34TDR00, 340 m a.s.l., 22 July 2020, coll. et det. B. Radak, A. Vlku, J. Peškanov (BUNS 25687)(Figure 3).

Epipactis leptochila subsp. *neglecta* was first documented in Serbia in 2016, with occurrences recorded on Golija Mt., in the vicinity of Ivanjica, on Pobijenik Mt., near Priboj, and in the area surrounding Nova Varoš. Subsequent observations have confirmed its presence on Tara Mt., Zvijezda Mt., and Jadovnik Mt. (Đorđević, 2021). To date, all known records of this taxon within Serbia have been restricted to the Western and Southwestern regions of the country. The recent discovery of *E. leptochila* subsp. *neglecta* in the area near Popovica on Fruška Gora Mt. represents the first confirmed record for the Srem region and the Vojvodina Province. This finding also constitutes the northernmost documented occurrence of this taxon in Serbia, situated approximately 130 km north of its closest known localities in Western Serbia.

Habitat and ecology

Epipactis leptochila subsp. *neglecta* was recorded at a single locality on Fruška Gora Mt., specifically in the area near Popovica. The population of this taxon developed within a beech-linden forest (Code A3.228 of the national habitat classification), belonging to the *Tilio-Fagetum submontanum* (M. Janković & Mišić, 1960) Mišić 1972 community. The upper tree layer consisted of only two species: *Fagus moesiaca* (K. Malý) Czeczott and *T. tomentosa*, while the understory layer of small trees and shrubs included, in addition to these two species, *A. campestre*, *A. platanoides*, *C. betulus*, *F. ornus*, and *S. pinnata*. During the initial recording year, the upper tree layer was composed approximately equally of beech and silver linden. However, in subsequent years, due to logging activities, primarily targeting large beech trees, this community underwent significant structural changes, resulting in nearly pure stands of silver linden in some parts of the area. Depending on the specific microhabitat where ramets of *E. leptochila* subsp. *neglecta* were observed, the herbaceous layer cover ranged from very sparse to almost absent. The recorded herbaceous species included *Asarum europaeum* L., *Galium odoratum* (L.) Scop., *R. hypoglossum*, *H. helix*, *Mercurialis perennis* L., as well as another orchid species recently recorded for Fruška Gora Mt., *E. purpurata*. The preference of *E. leptochila* subsp. *neglecta* for sites with poorly developed herbaceous layers has also been confirmed in other parts of its distribution range (Ardelean et al., 2018; Molnar, 2011; Petrova & Venkova, 2006). The geological substrate of the locality consists of conglomerates, sandstones, limestones, clay, and tuffs, while the soil type is classified as gray-brown podzolic. At the time of flowering, the substrate was moderately moist with a thick layer of forest litter, and the ramets grew under deep shade at an elevation of 340–343 meters a.s.l.

In Europe, *E. leptochila* subsp. *neglecta* develops in medium to deep shade within beech and oak-hornbeam woodlands, thermophilous oak-hornbeam forests, and other mesophilous deciduous or coniferous forests on dry to moist calcareous soils, up to an altitude of 1500 m (Delforge, 2006; Kühn et al., 2019; Tsiftsis & Antonopoulos, 2017; Vlčko et al., 2003). The habitat of this taxon on Fruška Gora Mt., beech-linden forest, deep shade, and moderately moist substrate, almost completely corresponds to its habitat preferences throughout the rest of its range. The only deviation concerns the geological substrate, which other authors report as exclusively calcareous, whereas at the Popovica locality, a mixture of carbonate and silicate rocks was recorded. Such a situation has already been documented in Western and Southwestern Serbia, where this taxon grows on limestone-dolomite, ophiolitic mélange, Carboniferous and Permian sandstones, Quaternary sediments, and schists-gneisses-phyllites (Đorđević, 2021). In the mentioned regions of Serbia, this orchid has been recorded in beech and spruce forests, as well as mixed beech and fir forests, beech and spruce, and beech, fir, and spruce forests, at elevations ranging from 762 to 1404 m a.s.l. (Đorđević, 2021). Considering these data, the ecological

range of *E. leptochila* subsp. *neglecta* in Serbia is significantly expanded by the findings from Fruška Gora Mt., where it was found at altitudes approximately half as high and within a community where it had not previously been recorded.

Population size and flowering time

This taxon was first recorded in the Fruška Gora Mt. area on 13 July 2018, when only three ramets were registered within an area of 56 m², all in the initial flowering stage. Upon a subsequent field visit (04 July 2020), 20 ramets were found, at which time the flower buds were formed, but flowering had not yet commenced. A later field survey (22 July 2020) included an adjacent forest area not covered during the previous visit, during which 21 flowering ramets and four in bud were recorded. Considering the two surveyed areas in July 2020, the total recorded population of *E. leptochila* subsp. *neglecta* amounted to 45 ramets over an area of 7597 m². The observed increase in population size, from three ramets in 2018 to 45 in 2020, is primarily attributable to the larger survey area in the latter year. As only a small subset of the surveyed area was investigated in 2018, it cannot be concluded whether the population truly increased during this period.

Across the entire range of *E. leptochila* subsp. *neglecta*, flowering occurs from June to early August (Delforge, 2006; Kühn et al., 2019), while in Serbia it has been recorded to flower from early July to early August (Đorđević, 2021), which is consistent with the flowering period observed on Fruška Gora Mt.

Conservation status

This taxon is protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2025) and is listed in Appendix II. *Epipactis leptochila* subsp. *neglecta* is considered Endangered in Slovakia (Vlčko et al., 2003), Critically Endangered in the Czech Republic (Grulich, 2017), and Near Threatened in Hungary (Molnar, 2011). In Serbia, it is not legally protected, and its conservation status has been assessed as Endangered (Djordjević et al., 2016).

In the Fruška Gora Mt., this orchid develops more deeply within the forest, away from forest trails frequently used by tourists and hikers, thus reducing the risk of collection. However, in recent years, intensive logging of large trees, primarily beech, has been observed in the Popovica area, which has already led to changes in the community structure, resulting in increasingly light-exposed habitats. These conditions are not favorable by this taxon. Similar negative impacts of inadequate forestry practices on the decline of its populations have also been reported in Slovakia (Vlčko et al., 2003).

Epipactis purpurata Sm., Engl. Fl. 4: 41 (1828), nom. cons.

Synonyms: *E. latifolia* var. *bracteis-longioribus* Lindl., *E. latifolia* var. *purpurata* (Sm.) Nyman, *E. latifolia* subsp. *purpurata* (Sm.) K. Richt., *Helleborine purpurata* (Sm.) Druce

General distribution

The range of the species broadly encompasses the temperate zone of Western and Central Europe, whereas it is rare in the Atlantic region. To the west, it occurs from southern England and France, extending eastward to Ukraine and Moldova. The northernmost limits of its distribution are found in Denmark and Lithuania. To the south, its range descends to northern Spain (Pyrenees Mts.), southern Italy (Pollino Mt.), and northwestern Greece (Grammos Mt. and Ioannina) (AHO, 2018; Buttler, 1996; Delforge, 2006; Kühn et al., 2019; Tsiftsis & Antonopoulos, 2017).

On the Balkan Peninsula, as well as in the southern parts of the Pannonian plain, this taxon is present in Hungary (Molnar, 2011), Slovenia (Dolinar, 2015), Croatia (Nikolić et al., 2025), Bosnia and Herzegovina (Šabanović et al., 2021), North Macedonia (Teofilovski, 2023), Greece (Tsiftsis & Antonopoulos, 2017), Romania (Sârbu et al., 2021), and Bulgaria (Petrova, 2011).

Distribution in Vojvodina Province

Fruška Gora Mt., Mačkovac, N45 09.315, E19 33.947, UTM 34TCR80, 329 m a.s.l., 02 July 2018, coll. B. Radak, A. Vlku, M. Prodanović, det. B. Radak (BUNS 25691); Fruška Gora Mt., Popovica, N45 10.907, E19 49.709, UTM 34TDR00, 344 m a.s.l., 13 July 2018, coll. et det. B. Radak (BUNS 25692) (Figure 4); Fruška Gora Mt., Popovica, N45 10.907, E19 49.709, UTM 34TDR00, 344 a.s.l., 22 July 2020, B. Radak, A. Vlku, J. Peškanov (field obs.).

The first record of *E. purpurata* in Serbia was on Maljen Mt. (Djordjević et al., 2010) in Western Serbia. This species was later documented at numerous localities in Northwestern, Western, and Southwestern Serbia (Đorđević, 2021). Subsequently, it was also recorded on Radan Mt. (Sabovljević et al., 2021) and Kopaonik Mt. and Željin Mt. (Sabovljević et al., 2023) in Central Serbia, as well as on Miroč Mt. (Sabovljević et al., 2024) in Northeastern Serbia. The findings from the Mačkovac and Popovica sites represent the first records for the Srem region and Vojvodina Province, where this taxon has been documented in two different UTM 10×10 km squares. Additionally, these are the northernmost distribution points of *E. purpurata* in Serbia, located approximately 115 km from Jablanik Mt., the closest known locality of this taxon within the country (Đorđević, 2021).

Figure 4. Epipactis purpurata

Photograph by B. Radak (13 July 2018, Serbia, Fruška Gora Mt., Popovica)

Habitat and ecology

Epipactis purpurata was recorded for the first time in the Vojvodina Province at the Mačkovac site on Fruška Gora Mt. Here, it develops in an almost pure stand of *T. tomentosa*. Near this locality, other species, such as *C. betulus* and *Robinia pseudoacacia* L., were recorded. At a somewhat greater distance, communities with *F. moesiaca* and *Quercus* spp. were noted. Considering that pure stands of linden on Fruška Gora Mt. are of secondary origin, the community in which *E. purpurata* was recorded probably originated as a result of degradation, i.e., the cutting of beech-linden or mixed forests of linden, beech, sessile oak, and hornbeam (Janković & Mišić, 1980). The stand where the orchid was found was floristically very poor; the shrub layer was almost undeveloped, and in the herbaceous layer only *H. helix* was present. Additionally, forest litter was absent. The geological substrate consists of conglomerates, sandstones, clays, and coal, while the pedological substrate was brown forest soil. Ramets of *E. purpurata* developed under conditions of complete shade at an altitude of 329 m a.s.l. This taxon was also recorded at the Popovica locality, where it developed within the *Tilio-Fagetum submontanum* community, under identical conditions as *E. leptochila* subsp. *neglecta*, for which this habitat was initially described. The only difference appears at the microhabitat

level, where ramets of *E. purpurata* consistently developed in areas without any herbaceous vegetation, but with a thick layer of forest litter.

This taxon most commonly inhabits shady deciduous beech and hornbeam forests, often their barest parts, as well as mixed or rarely coniferous forests (e.g., *Pinus nigra* J. F. Arnold subsp. *nigra*), from sea level up to 1600 m a.s.l. (Antonopoulos & Tsiftsis, 2012; Buttler, 1996; Delforge, 2006; Kühn et al., 2019). It develops mainly on deep, heavy, moist to moderately moist, acidic to neutral substrates, primarily on clay and chalk (Buttler, 1996; Delforge, 2006; Dolinar, 2015; Kühn et al., 2019; Vlčko et al., 2003), but also on serpentine substrates (Antonopoulos & Tsiftsis, 2012), as well as on sands and gravels, though particularly associated with clays (Harrap, 2016). The habitats in which *E. purpurata* was found on Fruška Gora Mt., beech-linden forests and degraded linden forests on a geological substrate composed of both carbonate and silicate and metamorphic rocks, in deep shade, fully correspond to the habitat preferences of this species throughout its range.

Epipactis purpurata has so far been recorded in Serbia in beech forests, mixed forests of beech and fir, spruce forests, mixed forests of spruce, beech, and fir, as well as oak forests, at altitudes ranging from 516 to 1413 m a.s.l. (Đorđević, 2021). It has been found on very diverse geological substrates – limestones, dolomites, and ophiolitic mélange (diabases, spilites, and dolerites; gabbros; sandstones, clays, marls, and hornfels from the Jurassic period), flysch (sandstones, siltstones, and marls), and harzburgites (Đorđević, 2021; Sabovljević et al., 2023). Considering these data, *E. purpurata* was recorded for the first time in Serbia on Fruška Gora Mt. within the *Tilio-Fagetum submontanum* community, as well as in pure communities of silver linden forests of secondary origin. Furthermore, the altitudes recorded on Fruška Gora Mt. (329 and 344 m), where this taxon occurs, are the lowest measured so far in Serbia.

Population size and flowering time

Among the three newly recorded taxa for the region of Vojvodina and Fruška Gora Mt., *E. purpurata* exhibits the smallest population. This taxon was first recorded in the mentioned area on 2 July 2018 at the Mačkovac locality, where two ramets in the budding stage were found. Considering that they grew only 20 cm apart, they likely belong to the same individual. At the second locality (Popovica) during both field visits on 13 July 2018 and 22 July 2020, two flowering ramets were recorded each time, spaced two to three meters apart, suggesting that they may belong to two different plants (genets).

E. purpurata primarily flowers from July to September (Buttler, 1996; Delforge, 2006; Dolinar, 2015; Kühn et al., 2019), thus the flowering period of this taxon in the Fruška Gora Mt. region aligns with that of the rest of its range. In rare cases, in the United Kingdom, flowering has been recorded as early as late June and as late as late September (Harrap, 2016), whereas in Greece, flowering is limited to August (Tsiftsis & Antonopoulos, 2017).

Conservation status

Epipactis purpurata is protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2025) and is listed in Appendix II. Its conservation status on the global IUCN Red List is assessed as Least Threatened (Rankou, 2011). In Bulgaria, it is classified as Endangered (Petrova, 2011); in Slovakia, as Vulnerable (Vlčko et al., 2003); and in the Czech Republic and Hungary, as Near Threatened (Grulich, 2017; Molnar, 2011). In Serbia, it is not legally protected, and its conservation status is assessed as Critically Endangered (Djordjević et al., 2010). Across its range, the species is primarily threatened by negative forestry practices, logging, and forest management (Molnar, 2011; Vlčko et al., 2003), which in some countries have led to drastic declines in population size or occupied area (Harrap, 2016).

In recent years, at the Popovica locality on Fruška Gora Mt., older trees, mainly beech, have been cut, altering the character of the community. The ground layer has also been physically disturbed due to timber extraction.

CONCLUSION

This paper presents the first confirmed records of three taxa of the genus *Epipactis* (*E. helleborine* subsp. *distans*, *E. leptochila* subsp. *neglecta*, and *E. purpurata*) on the Fruška Gora Mt., thereby expanding their known range to the northern part of Serbia, specifically the Srem region, Vojvodina Province. It was determined that these taxa occur in specific types of forest communities, primarily beech-linden and mixed sessile oak forests, which is consistent with their known preferences in other parts of their range. However, new habitat types and geological substrates where these orchids occur have also been recorded in this part of Serbia. During the study period, a negative change in habitat quality was observed due to the logging of older trees. This emphasizes the importance of conducting further detailed research and continuously protecting natural habitats in this area to preserve floristic diversity and achieve a more comprehensive understanding of the region's biodiversity. Although this study focused on Fruška Gora Mt., these *Epipactis* taxa may also occur in other forested areas of Vojvodina, including the Vršac Mts. Future surveys in these regions are needed to verify their presence and better understand their distribution and habitat preferences across the Vojvodina Province.

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ОРИГИНАЛНИ ЧЛАНАК
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ПРВИ НАЛАЗИ ТРИ ТАКСОНА РОДА *Epipactis* (Orchidaceae) ЗА ВОЈВОДИНУ

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РЕЗИМЕ: Током последњих деценија, значајан број нових врста рода *Epipactis* описан је широм Европе. Многе од тих врста познате су по уском ареалу распрострањења. Међутим, са интензивирањем истраживања, пре свега у добро очуваним шумама, ови таксони су проналажени на новим локалитетима, често веома удаљеним од места са којих су првобитно откривени. У последњих петнаест година, присуство неколико нових таксона рода *Epipactis* забележено је и у Србији, пре

свега у западном делу централне Србије. Овај рад представља прве налазе три таксона рода *Epipactis*: *E. helleborine* subsp. *distans*, *E. leptochila* subsp. *neglecta* и *E. purpurata* са Фрушке горе, чиме је по први пут потврђено њихово присуство у северној Србији (Аутономна Покрајина Војводина). У раду је приказана дистрибуција ових новооткривених таксона у Војводини, њихове еколошке и станишне преференције, као и упоредна анализа у односу на постојеће еколошке податке из других делова Србије. Такође је приказана величина њихових популација на Фрушкој гори и потенцијални фактори угрожавања који би могли утицати на њихов опстанак у том подручју. Теренска истраживања, с циљем мапирања представника породице Orchidaceae, спроведена су на ширем подручју Фрушке горе (Срем, Војводина) у периоду од 2018. до 2025. године, обухватајући све вегетационе сезоне и све типове станишта. Идентификација новооткривених таксона извршена је коришћењем релевантне литературе, а по један ваучер примерак сваког таксона депонован је у хербаријуму BUNS-a. Сви таксони су забележени у укупно три различита UTM квадрата величине 10×10 km, при чему су заједно присутни једино у квадрату 34TDR00. *Epipactis helleborine* subsp. *distans* је регистрована на локалитетима Поповица и Летенка, где расте уз ивице буково-липових шума и мешовитих шума китњака са грабом и липом, респективно. *Epipactis leptochila* subsp. *neglecta* забележена је искључиво у близини Поповице, унутар буково-липове шуме. Овај таксон има највећу популацију међу новооткривенима, са 45 цветајућих изданака забележених 2020. године. Трећи таксон, *E. purpurata*, регистрован је на два локалитета – на Мачковцу и у близини Поповице. Ова врста има најмању популацију међу новооткривеним таксонима, са само четири цветајућа изданка забележена 2018. године на два различита локалитета. Врста је пронађена у буково-липовим шумама, као и у чистим липовим састојинама. Еколошке преференције свих новооткривених таксона одговарају онима из других делова њихових ареала, иако су у поређењу са остатком Србије забележени нови типови заједница, геолошких подлога или надморских висина на којима се јављају. На свим истраживаним локалитетима примећена је деградација станишта, првенствено изазвана сечом старијих стабала, што је довело до промена у карактеру појединих биљних заједница у периоду од 2018. до 2025. године, када су истраживања спроведена. С обзиром на то да се нови таксони рода *Epipactis*, као и нови локалитети већ познатих, и даље откривају широм Србије и околних земаља, оправдано је претпоставити да Фрушка гора и даље скрива њихове нове локалитете.

КЉУЧНЕ РЕЧИ: *Epipactis helleborine* subsp. *distans*; *Epipactis leptochila* subsp. *neglecta*; *Epipactis purpurata*; Фрушка гора; Србија; Срем

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FLORA AND VEGETATION OF DELIBLATO SANDS (SERBIA): A REVIEW OF FLORISTIC AND VEGETATION RESEARCH THROUGH THE CENTURIES

ABSTRACT: Due to its unique natural characteristics, Deliblato Sands (Deliblatska peščara) has always attracted numerous researchers who study its flora and vegetation. The first written data on the botanical study of this area date back to 1800 and contains valuable information about the flora. In a 225-year-long tradition, researchers and inspiration have not disappeared until today. 365 publications have been published on the topic of studying some aspects of the flora or vegetation of the Deliblato Sands. Most of the publications presented some specific taxa or group of taxa in the Deliblato Sands as a part of the wider research area (159). Most of the first finds of plant taxa were recorded in the research period 1951–2025. In the same period the highest number of publications analyzing the flora or

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vegetation of the Deliblato Sands were published 253 in total. Most productive author contributing with floristic data of the Deliblato Sands was Melanija Obradović (and collaborators) with 19 publications. The largest number of publications or researchers were from Serbia, more precisely the former republic of Yugoslavia (238). Researchers from Hungary, Austria and the Czech Republic have contributed throughout history, also. This review indicates that the Special Nature Reserve "Deliblatska peščara" continues to be an inexhaustible source of inspiration for science, given that the number of publications is growing by years, both by national and international researchers.

KEYWORDS: Banat; Banater Sandwüste; Banatska peščara; Belo Brdo; Bielobrdo; Delibláti-homokpuszta; Deliblatska peščara; historical overview; Vojvodina

INTRODUCTION

Due to their exceptionality, the Pannonian sandy areas have always attracted the attention of geographers, as well as biologists. Sand dunes in Pannonian plain are oases of biodiversity, especially considering that they are inhabited by special organisms adapted to specific conditions. Successive stages of vegetation on inland sand dunes change rapidly and they are usually under the strong influence of human activities (Chytrý, 2007; Ćuk et al., 2023).

As a unique phenomenon in Europe and one of the largest continental deposits of sand, the Deliblato Sands was attractive for fundamental and experimental research. This is evidenced by the fact that over 600 different publications have been published about this area (Butorac & Habijan-Mikeš, 1997).

Deliblato Sands is a unique geomorphological phenomenon located in the south-eastern Banat (Figure 1), in the Northern Serbian province of Vojvodina. The Sandy area spreads over 34,829 ha and extends in southeast and northwest direction. It is characterized by specific geological structure – thick layers of silica-carbonate sand originating from Pleistocene. The wind Košava has shaped expressive dune relief, ranging between 70 and 200 meters a.s.l. (Ćuk, 2019). The interplay of the region's distinctive relief and mobile soils, a moderately continental climate, the absence of surface waters, and the combined effects of natural processes and human activities has shaped the development of unique sand, steppe, steppe-forest, forest, and meadow plant communities.

Deliblato Sands is an example of a large and long-term human commitment to overcoming natural processes. This commitment is reflected in the actions of preventing the movement of sand mass from Deliblato Sands to the fertile agricultural soils of the Pannonian Basin-by afforestation (Ćuk et al., 2023; Milenković et al., 2018).

Over the past 200 years, the Deliblato Sandhills have undergone intensive afforestation. The stabilization of formerly active sand areas was most successful with black locust (*Robinia pseudoacacia* L.) (Ćuk et al., 2023). However, the use of this invasive species has transformed much of the landscape into forest (Ćuk, 2019). Consequently, the expansion of forest vegetation fragments grassland, steppe, and sandy habitats, which, without active protection, are at risk of collapse (Janssen et al., 2016).

Figure 1. Position of Serbia (red) in Europe (left) and the Deliblato Sands (red) in Serbia (right)

HISTORY OF FLORISTIC RESEARCH

Early floristic surveys and first records of species

In the period of 225 years (1800–2025), the area of Deliblato Sands attracted numerous researchers with its uniqueness. During this period, a total of 365 scientific publications were published on the flora of the Deliblato Sands. The first botanical data from this area were published by Waldstein and Kitaibel in their overview of rare plants of Hungary (*Descriptiones et icones plantarum rariorum Hungariae*, published in periods 1799–1802 and 1803–1805, Figure 2a). Their publication includes descriptions of approximately fifteen species from the Deliblato Sands, collected during an excursion in May 1800. These data represent the first published records of the flora of the Deliblato Sands. Part of the results of the research by Waldstein and Kitaibel (142 species) was published later, by Gombocz (Gombocz, 1945).

Anton Rochel carried out his field research in the area of Deliblato Sands in 1815 and 1835 and published the results in 1828 and 1838. He points to species that are present in Deliblato Sands, and at the same time are unique to the Pannonian Plain. Rochel´s colleague and disciple physician Johann Heuffel continued his work for 30 years (1827–1857). Heuffel (1858) gives the first overview of the flora of the wider area (Banat), without using the toponym "Deliblatska peščara", but with general locality names according to the parts of the then active Banat military border that covered military regiments: German (teutonico), Serbian (illyrico) and Romanian (valachico). Records of taxa related to the area of Deliblato Sands are mostly marked with "*illyrico*", often

specified with the expression "*in arena mobili*", i.e. on mobile sands. Heuffel summarized all botanical data and take into account publications and results of Wierzbicki (1840; 1842a; 1842b; 1845).

Figure 2. a) Rindera umbellata (Waldst. & Kit.) Bunge – new species for science described on Deliblato Sands by Waldstein and Kitaibel in 1805;

b) Fritillaria degeniana Wagner was first described in 1906 by Wagner from Deliblato Sands as a new species for science, now considered as synonym for *F. montana* Hoppe ex W. D. J. Koch

Intensive floristic research began with the intensive afforestation process in 1818. This period lasted throughout the second half of the 19th and the beginning of the 20th century (Ćuk et al., 2023). The study of the flora of the area and the techniques of afforestation was initiated by Bachofen (in 1833 – Krendl, 2003) and Wessely (1873). Illes (1884) and Mahr (1891) discuss the techniques of successful afforestation of the Deliblato Sands, but they also discuss the plant species that should be used in this process. Ajtay (1902; 1907; 1912; 1917a; 1917b; 1931), Kiss (1913) and many others also dealt with a similar topic – afforestation and binding of the sand, with special attention to selection of species, taxonomy and hybridization of used plant material (Appendix 1).

Many botanists visited and surveyed the area of Deliblato Sands, where they recorded new taxa for the area. Josif Pančić visited the Deliblato Sands in 1867 and included discovered flora in his publication from 1868; Borbás was one of the most productive scientists when it comes to the flora of the Deliblato Sands – since 1876 he published 17 different scientific articles with

results from this area (see Appendix 1). He worked under Alexander Braun in Berlin and Anton Kerner von Marilaun in Innsbruck, whose guidance had a lasting impact on his taxonomic and phytogeographical work. Kerner's influence was particularly significant in shaping his understanding of the ecology and vegetation of the sands of the Pannonian Plain. Borbás' works primarily focus on individual species or species groups, often documenting them as previously unrecorded for the area, while frequently also describing processes of sand stabilization. Other botanist who published results about flora of the Deliblato Sands were: Janka (1867); Sonklar (1870); Simkovics (1878); Degen (his results are mentioned in: Domin, 1907; Polatschek, 2013; Szujkó-Lacza, 1981; Szabó, 1910a); Fiek and Wetschky (Fiek, 1895); Bernátsky (1902; 1904; 1908) Javorka, Lengyel, Magocsy Simonkai and Thaisz (their results mentioned in Szujkó-Lacza, 1981); Murr (1912); Tuzson (1915); Pevalek (Lőkös, 1988); Rummelspacher (1965).

Wagner visited this area in the period 1894–1903 and published results in 1898, 1906, 1913 and 1914. He gave a significant and perhaps the first detailed overview of the complete flora of the Deliblato Sands, as well as the vegetation. According to Wagner, the flora of Deliblato Sands is so diverse that "no one can find an area larger than half a cadastral area with the same uniform flora". In his overview, Wagner classified flora according to origin and habitats.

Španović (1936) presents detailed observations on the floristic composition and distribution of plant communities and also addresses the issues of afforestation and sand stabilization, but in his publication, he relies significantly on the work of Wagner (Wagner, 1898; 1906; 1913; 1914).

In the period between the two World Wars, the research activity was less pronounced, because it was considered that the sand was under control.

Overviews of the flora

After Wagner (1914), and Broz (1953a), one of the more detailed analyzes of the flora of the Deliblato Sands was carried out between 1955 and 1980 by Sigunov (1961; 1962; 1970; 1976; 1979), who mentioned in his publications about 651 taxa. Sigunov (1976) states that the list of flora consists of a total of 759 taxa. He believes that some previously recorded species have disappeared or are currently retreating (*Viola* × *neményana* Wagner 1913, *V. ajtayana* Wagner 1913, *Aconitum lycoctonum* L., *Atropa bella-donna* L.).

Panjković (1977) published an overview of the phytogeographical characteristics of the flora of the Deliblato Sands based on previous literature data and own research.

Obradović & Panjković (1980) published the prodromus of ferns and other plants of Deliblato Sands.

Gajić et al., in 1983, gave a comprehensive overview of the flora of this area, with 891 taxa.

After such a detailed list, next review of the flora was given by Ćuk (Ćuk, 2019). In this dissertation, 1072 taxa are presented within the flora of the Deli-

blato Sands, which represents almost 1/3 of the plant diversity of the Republic of Serbia (Figure 3).

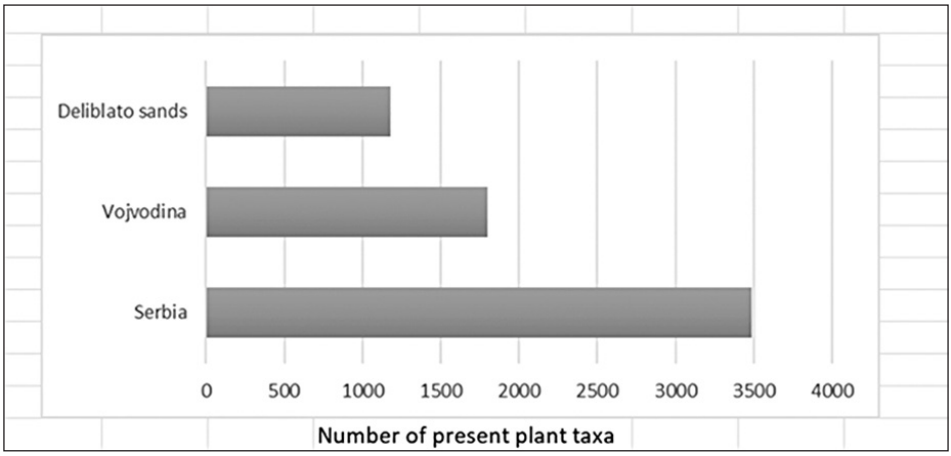

Figure 3. Numerical ratio of the total diversity of the flora of Deliblatska peščara, Vojvodina and Serbia (Ćuk, 2019)

A common feature of all detailed surveys of the flora of the Deliblato Sands is the inclusion of all species recorded previously, including those with limited populations or questionable taxonomic status since their first discovery in the area. This approach has generated a large volume of repeated data, often without a critical assessment or verification of the taxa's actual presence in the field. In order to analyze the publications about the flora of the Deliblato Sands throughout history, all references are divided into four groups, in relation to the period from which they originate:

- Group I – the first findings of plant taxa originating from the period 1800–1850;
- Group II – the first findings of plant taxa originating from the period 1851–1900;
- Group III – the first findings of plant taxa originating from the period 1901–1950;
- Group IV – the first findings of plant taxa originating from the period 1951–2025.

If all research periods are compared (Figure 4), the largest number of plant species living on Deliblato Sands was mentioned for the first time in the interval 1951–2025. The largest number of new finds in the flora of the Deliblato Sands was recorded until 1983. In the last 40 years, only 8 new taxa have been recorded for this area.

During the floristic research of Deliblato Sands, a notable challenge arose due to the lack of access to original data for the taxa gathered in the past (her-

barium material is missing, or localities are described too widely). However, that did not prevent the repetition of data in each subsequent review of the flora. This suggests that once floristic data debut in literature, they remain static throughout the research periods, posing a significant obstacle in delineating the temporal fluctuations in the Deliblato Sands flora.

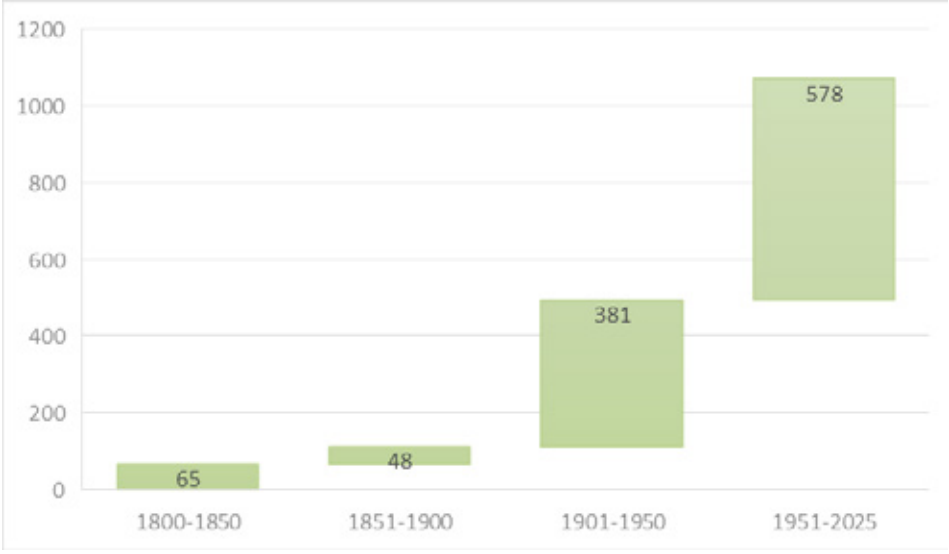

Figure 4. Overview of the first findings of plant taxa for four research periods in the last 225 years

Research in sense of conservation of the area

Intensive research of the flora of the Deliblato Sands in sense of conservation lasted from 1951 to 1995, when this area was completely protected for the first time. Grozdanić (1956) and Čolić & Broz (1969) worked on the first proposals for the protection of the reserve. An overview of the condition and protection of the sandy habitats of the entire country, including the Deliblato Sands, was given by Butorac & Habijan-Mikeš (1997), Habijan-Mikeš (1998), Butorac et al. (2002) and Butorac & Panjković (2013).

Within the rich history of studying the flora and vegetation of the Deliblato Sands, many researchers have published results providing arguments for improving or planning the protection of the area (Kuzmanović, 1994; Stojšić et al., 1995; Stevanović et al., 1999; Medarević et al., 2004; Tomović et al., 2007; Grdović et al., 2012; Lazarević et al., 2012; Andrašev et al., 2014; Đorđević et al., 2017; Puzović & Panjković, 2015; Amižić et al., 2017; Čavlović et al., 2017; Sedlak, 2019; Ivajnšič & Devetak, 2020; Jakovljević et al., 2020; Jenačković et al., 2020; Kalinić et al., 2020; Ho et al., 2025; Novaković et al., 2025).

Various thematic research that supplemented the knowledge of flora

After World War II, some thematic research also included the area of the Deliblato Sands. Non-native and invasive species in Vojvodina or Serbia, including in the area of Deliblato Sands were analyzed by Petrović (1951), Radulović (1952), Šajinović & Koljadžinski (1978), Ivković et al. (1980), Ivković & Čapaković (1981), Panjković et al. (2006), Anačkov et al. (2013) and many others (Tucović et al., 2004; Andrašev et al., 2014; Popov et al., 2016; Ćuk, 2019; Kalinić et al., 2020, Anđelović et al., 2016; 2022; Avramov et al., 2024). The study of medicinal plants on Deliblato Sands was the research focus of Tucakov (Tucakov, 1953; 1958; Šajinović & Mihajlov, 1979), Šljivovački (1966), Živanović (1979), Obradović et al. (1984), Popović et al. (2012; 2014). Particularly significant are the recent publications that include chemical profiling of medicinal plants from the Deliblato Sands area and explore the possibilities of their practical application (Chalchat et al., 2004; Pejin et al., 2012; Rajčević et al., 2016; Nađpal et al., 2018; Krstić et al., 2019; 2021 and 2025; Čutović et al., 2022; Jadranin et al., 2023; Todorović et al., 2023; Batinić et al., 2024; Jovanović et al., 2024).

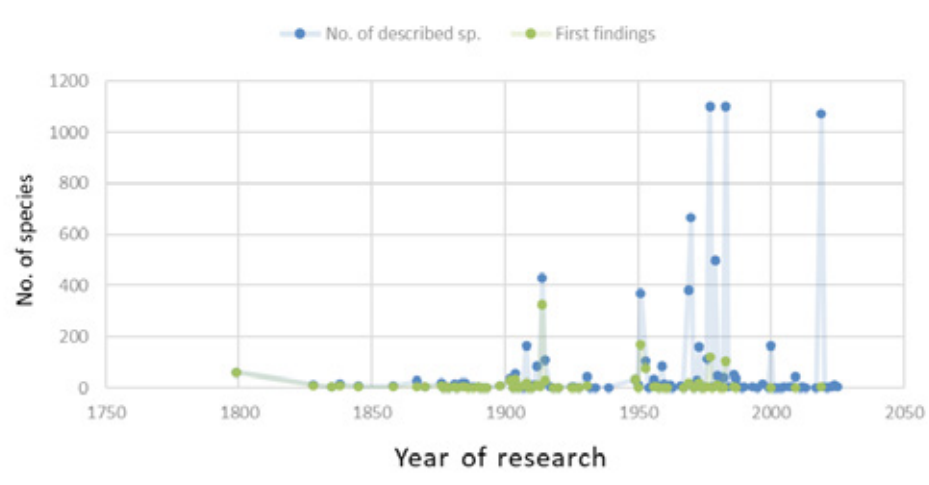

Figure 5. Findings of plant taxa recorded on the Deliblato Sands in the period 1800–2025

blue – finds of all taxa
green – taxa recorded for the first time for the area of Deliblatska peščara; On the x-axis, the years of publication are shown, while the y-axis represents the number of recorded/mentioned taxa.

In addition, individual results from certain localities or researches concerning individual taxa were published also: Obradović – who gave the highest number of publications with data about some aspects of flora of Deliblato Sands

(see Appendix 1: 1962; 1975; 1979a; 1979b; 1981), Obradović & Panjković (1980; 1988), Obradović & Budak (1980a; 1980b), Obradović & Boža (1981), Obradović et al. (1982; 1983; 1984; 1986; 1988; 1989; 1990), Ehrendorfer (1964), Diklić (1967), Diklić & Nikolić (1974; 1980), Diklić & Obratov-Petković (2002), Stevanović (1972), Borisavljević (1974; 1976), Gajić (1975; 1982), Ivković (1978; 1981; 1982), Gajić et al. (1981), Gajić & Olđa (1982), Popović et al. (1983a; 1983b), Igić (1986), Stevanović (1999), Vukov et al. (2000), Dinić et al. (2002), Tomović et al. (2003; 2007), Ćurić et al. (2010), Vuleta et al. (2010; 2011), Španiel et al. (2011), Lazarević & Stojanović (2012), Polatschek (2013) and many other (see the Appendix 1). The taxa that have received the most attention in individual studies are *Iris pumila* L. (a total of 20 publications) and *Paeonia tenuifolia* L. and *Paeonia officinalis* L. (a total of 10 studies).

A substantial number of publications build upon previously published floristic data, integrating them with new findings and thus providing comprehensive overviews of the floristic diversity of the Deliblato Sands (Figure 5, blue dots), while most botanical studies focus on specific, smaller groups of species or on individual taxa. However, noteworthy share of publications has revealed the floristic diversity of the Deliblato Sands for the first time in scientific literature (Figure 5, green dots). (Appendix 1).

Herbarium collections

In addition to scientific publications, a substantial number of plant material collections also include representatives of the flora of the Deliblato Sands. Among these, herbarium collections are by far the most numerous. Specimens from this unique area are preserved in national herbaria of the Republic of Serbia, including the Herbarium of the University of Novi Sad (BUNS), the Herbarium of the Institute for Nature Conservation of Vojvodina Province (PZZP), the Natural History Museum – Herbarium in Belgrade (BEO), and the Herbarium of the Institute of Botany and Botanical Garden "Jevremovac" and others. Moreover, herbarium specimens originating from the Deliblato Sands are also housed in numerous European collections, such as the Herbarium Kitaibelianum of the Hungarian Natural History Museum in Budapest, the Botanischer Garten und Botanisches Museum Berlin, and the Naturhistorisches Museum Wien, as well as in historical collections in Paris, London, and several other major herbaria across Europe. Today, with the existence of global aggregation databases such as GBIF, JSTOR Global Plants, and JACQ, many specimens from Serbia, including localities in the Deliblato Sands, are easily accessible, as they are indexed in these databases. This also confirms the wide distribution of herbarium material from Deliblato, with numerous duplicates preserved in various European and international collections.

However, there are also smaller, local collections specifically dedicated to representing the flora of the Deliblato Sands. Notable examples include the collections of the National Museum in Vršac and the Teodor Soška collection.

The oldest significant collection of the flora of Deliblato Sands in Serbia is stored in the natural history department of the National Museum in Vršac (Sučević, 1954). The botanical collection from the area of Deliblato Sands was collected from 1910 to 1911 and contains altogether 313 specimens with 171 taxa. The creator of the collection was Bernátsky (1873–1945), assistant professor at the University of Budapest, who was born in Vršac. The herbarium was partly damaged, both by the war in Serbia and by the ravages of time, and in 1952 it was restored for the first time. It consists of 29 volumes. The material comes from five localities, some of them outside of the Deliblato Sands and outside of Serbia: Vršac Mountains, Marila, Oravica (Romania). From Deliblato Sands, main localities were: Dupljaja (46 species), Šušara (55 species). This collection is significant because it represents one of the oldest collections of plant taxa from the Deliblato Sands.

Teodor Soška collected 380 taxa from Deliblato Sands in his herbarium in 1943 and 1944. The localities where specimens were collected include: Flamunda, Rošijana, Kajtasovo, Kravan, Vrelo, Grebenac, Korn, Čoka, Devojački bunar, Keja Lakuluj, Šusara. The majority of specimens are from Flamunda, because at that time it was considered that this was the central part of Deliblato Sands, with the most typical climatic characteristics. Soška collected mosses and lichens from this area (Broz, 1951). The list of flora based on this collection was published after his death (Broz, 1951) and includes, in addition to the vascular flora, 19 species of mosses and 12 species of lichens. After working on the results of Teodor Soška's research, Broz (1953a) gave an overview of the complete flora of this area.

HISTORY OF VEGETATION RESEARCH

Publications on the vegetation of the Deliblato Sands remain relatively scarce. Only five papers provide a comprehensive overview of all vegetation types in the Deliblato Sands region (Wagner, 1914; Stjepanović-Veseličić, 1953; 1979; Parabućski, 1980; Ćuk, 2019). Three additional studies focus on specific vegetation types within the area or its surroundings (Polić, 2008; Ćuk, 2019a; Jovanović, 1986). Sixteen publications examine particular aspects of certain vegetation types, without covering the overall diversity, while 19 place vegetation data from the Deliblato Sands in a broader context, considering sandy habitats or regional and national scales (Appendix 1). For a vegetation research period of about 160 years, there are four publications before the development of classical phytocoenology (Braun-Blanquet, 1928; 1964; Horvat et al., 1950) that analyze the plant communities of this area. After the development of classical phytocoenology, five more publications were published with an overview of the present plant communities on the Deliblato Sands.

Vegetation research of the Deliblato Sands before Braun-Blanquet

In the period before Braun-Blanquet approach, the study of vegetation was based on the descriptive observations of the authors. This was first given by Kerner (1863, in Conrad, 1951), who described the vegetation of the sands between the Danube and the Tisa/Tisza based on dominant species and defined three formations: *Chrysopogon gryllus* (L.) Trin. formation – on humus sand; formation of *Stipa pennata* L. – *Stipa capillata* L. – transition phase and formation of annual plants (*Bromus* L., *Bassia* All., *Corispermum* L.).

Vegetation research of the sands of Serbia was carried out by Adamović (1904). He provides an extensive ecological study of the flora and vegetation of sands in eastern Serbia, which he says has many similarities with Deliblato Sands, not only in origin, but also in the biology and ecology of the species. In his research, Adamović divided the vegetation into formations (and them into facies), based on physiognomic-ecological characteristics, and often also the seasonal dynamics of the vegetation. He listed characteristic species for each of the formations and facies, accompanying those which occur sporadically, as well as rarely. Adamović divides plant species according to origin into Pontic, Eurasian, Mediterranean, American and cosmopolitan. He selected out typical psammophytes from Serbian sands, but also other psammophilic and indifferent species. Main formations of vegetation by Adamović (1904) are: flying sand dunes formation, formation of sandy steppes or puszta, formation of willows on the sand, formation of sand meadows, formation of thickets, forest formation, formation of riparian forests and cultivated areas, with ruderal and segetal vegetation.

Tuzson (1915) and Wagner (1913) divides the plant cover of the Deliblato Sands in a similar way, based on physiognomy, but also on the type of habitat. Main formations by Wagner (1913) are: vegetation of loose sand and blown surfaces (pioneer formations), deserts (multiple subtypes, based on dominant species), meadows with different types (untouched, uniform (with *Festuca wagneri* (Degen, Thaisz & Flatt) Krajina)) or colorful (with several species); pastures; rites), then aquatic vegetation, vegetation of low trees and bushes, park-type forests, forests, weeds of arable land and ruderal plants.

Period of classical phytocoenology

The first overview of the vegetation diversity of the Pannonian Basin sands, and consequently of the Deliblato Sands, following the then-new, and still highly significant, Braun-Blanquet methodology, was provided by Reszo Soó (Soó, 1940; 1957). His research provides a division of the vegetation of the Pannonian Basin sands, based on previous botanical research, and singles out the following associations:

1) Communities of herbaceous plants: *Brometum tectorum* Soó 1938, *Festucetum vaginatae* (Rapaics ex Soó 1929) Borhidi 1996, *Festucetum sulcatae* Soó 1938, *Festuca pseudovina-Potentilla arenaria* community. At the

same time, each of the associations has four geographical variants *danubiale* (located between the Tisza and the Danube), *tibescense* (in the Nyírség region), *arrabonicum* (in the Raab area) and *deliblaticum* (on the Deliblato Sands).

2) Forest communities – initial or degradation stages (with *Juniperus communis* and *Populus alba*) and forests (*Quercetum roboris festucetosum* Soó 1940 and *Quercetum roboris convallarietosum* Soó 1934).

The pioneering and first comprehensive phytocoenological study of the Deliblato Sands vegetation was conducted by Stjepanović-Veseličić (1953), with a monographic edition published in 1979, marking a foundational contribution to the understanding of this unique vegetation types. Stjepanović-Veseličić published the first phytocoenological overview of the area, with collected relevés according to the Braun-Blanquet method, as part of her doctoral dissertation. Vegetation data from the sands of Serbia were collected in 1948, 1949, 1952 and 1953. Stjepanović-Veseličić described the most important types of natural vegetation on Serbian sands and determined the direction of vegetation succession. On Deliblato Sands, Stjepanović-Veseličić describes sand-dune vegetation (with two described associations), the sand-steppe vegetation (three associations), the sand-swamp vegetation (two associations) and the forest vegetation on the sand (one association). She mentioned some types of ruderal vegetation and fragments of natural poplar forests also.

Panjković & Butorac (2013) provide a theoretical overview of the sand-dune vegetation of Vojvodina and Deliblato Sands, from the class *Festucetea vaginatae* Soó 1968.

As a part of her doctoral dissertation, Ćuk (2019; 2019a) provided an overview of the vegetation of the Deliblato Sands at the level of associations and subassociations. This work included a revision of the phytocoenology based on contemporary phytocoenological studies, while also presenting newly recorded associations. It represents the most recent published overview of the vegetation of the area. Ćuk sampled natural vegetation – pioneer sand dune vegetation, steppe vegetation, shrubs, forests, but also planted forests (black locust and pine forests). According to Ćuk (2019; 2019a), the vegetation of the Deliblato Sands can be classified into six classes and orders, seven alliances and 13 associations: *Bassio laniflorae-Brometum tectorum* (Soó, 1938) Borhidi 1996, *Alysso gmelini-Festucetum vaginatae* Stjepanović-Veseličić (1953) 1956, *Koelerio macranthae-Festucetum wagnerii* Stjepanović-Veseličić 1953, *Adonido vernalis-Chrysopogonetum grylli* (Stjepanović-Veseličić, 1953) Aćić et al., 2014; *Festuco-Potentilletum arenariae* Stjepanović-Veseličić 1953; *Molinietum coeruleae* Koch 1926; *Salicetum rosmarinifoliae* Stjepanović-Veseličić 1953; *Holochoeno-Calamagrostietum epigejos* Popescu et Sanda 1978; *Pruno spinosae-Cratagetum* (Soó, 1927) Hueck 1931; *Querco-Tilietum tomentosae* Stjepanović-Veseličić 1953; *Junipero-Populetum albae* (Zólyomi ex Soó, 1950) Szodfridt 1969, *Bromo sterilis-Robinietum pseudoacaciae* Pócs 1954 and pines plantations.

ANALYSES OF PUBLISHED RESEARCH ABOUT FLORA AND VEGETATION OF DELIBLATO SANDS

Analyzing the publication history on the flora and vegetation of the Deliblato Sands reveals a gradual increase in the number of studies over time. During the most recent research period (1951–2025), the highest number of publications focusing on the flora or vegetation of the Deliblato Sands was recorded, totaling 253 (Figure 6).

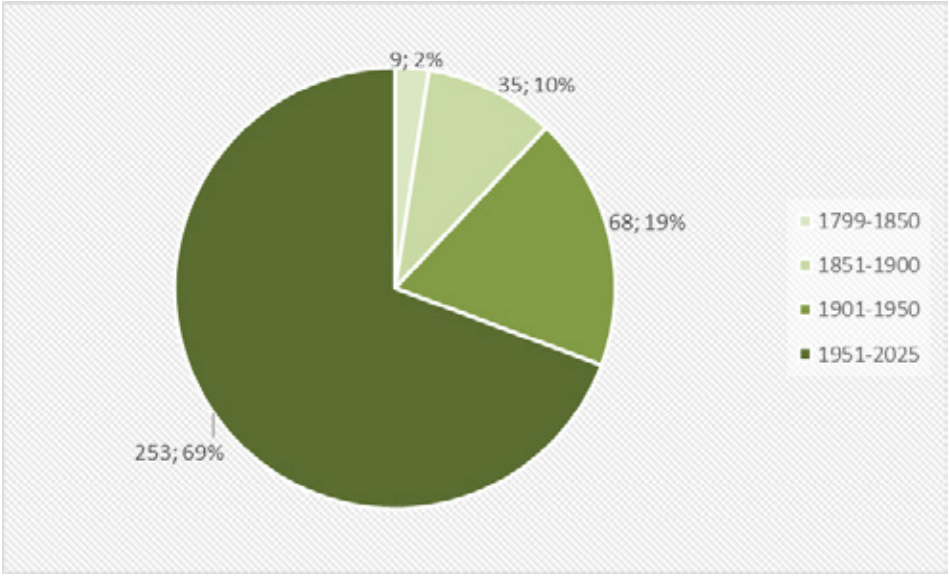

Figure 6. Overview of publication periods on the flora and vegetation of the Deliblato Sands in the last 224 years

Most of the studies published for the area of Deliblato Sands and analysed in this paper dealt with a broader analysis of the flora (at regional, national or international level) where data from the Deliblato Sands are also presented (159). Furthermore, there are many different surveys analysing some specific taxa from Deliblato Sands (morphological, genetical, physiological or other studies: 74). From the field of forestry and afforestation of sand using different methods and plant species so far, 45 scientific papers were published (Figure 7).

The largest number of publications or researchers analysed in this paper orginating from the former republic of Yugoslavia (65%). Then the most numerous publications are from Hungary (26%), especially for the period up to 1950. Researchers from Austria and the Czech Republic have contributed throughout history, also (Figure 8).

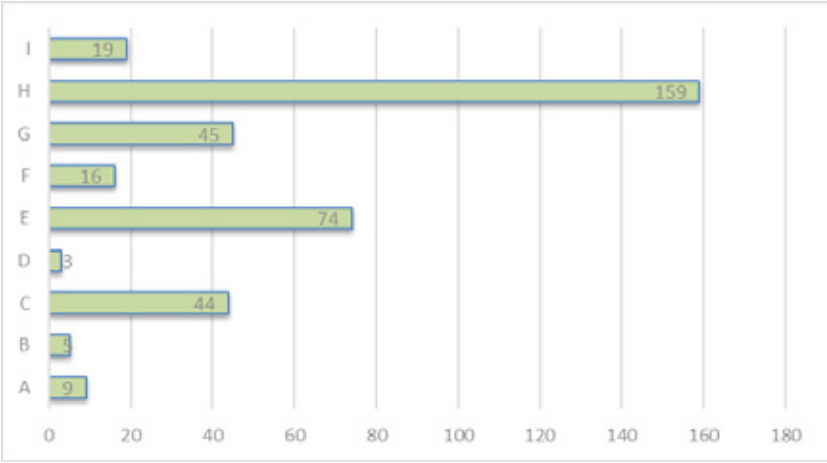

Figure 7. Different types of flora or vegetation survey of Deliblato Sands: A – Overview of the flora of Deliblato Sands; B – Overview of the vegetation of Deliblato Sands; C – Discovery of new taxa (or group of taxa) on Deliblato Sands; D – Discovery and description of new syntaxa in the area of Deliblato Sands; E – Various botanical studies that include individual taxa from Deliblato Sands; F – Analyses of characteristics of vegetation types on Deliblato sands; G – Various researches in the field of forestry; H – A broader analysis of the flora (regional or national level) where data from the Deliblato Sands are also presented; I – A broader analysis of the vegetation (regional or national level) where data from the Deliblato Sands are also presented

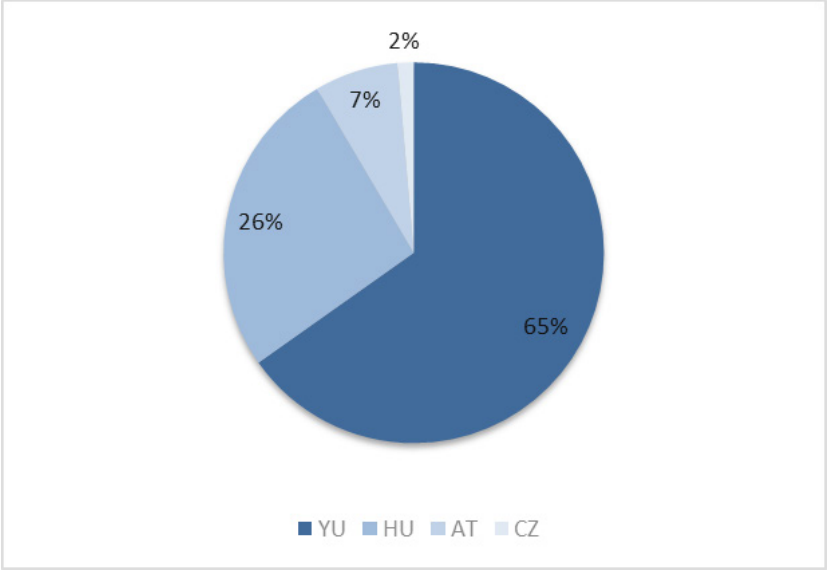

Figure 8. Origin of the publications: YU – former republic Yugoslavia; HU – Hungary; AT – Austria; CZ – Czech Republic

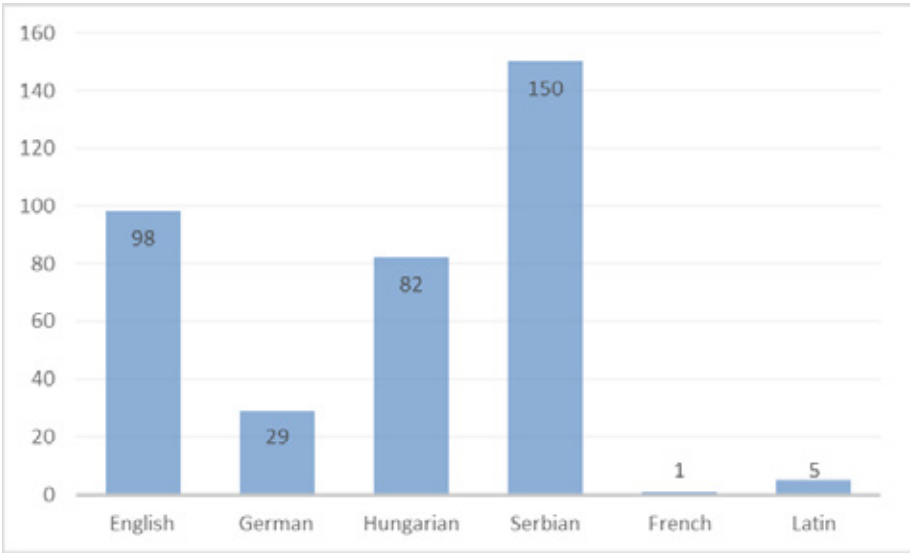

Figure 9. Languages of the publications about flora and vegetation of Deliblato Sands

According to this (Figure 9), the highest number of the publications are written in Serbian language (150), and also in English (98) and Hungarian (82). The latest publications are written in English.

From 365 publications about flora and vegetation of Deliblato Sands, 303 of them are articles or short reports in scientific journals. All these publications are published in 82 different scientific journals (Appendix 2). The highest number of articles is published in Matica Srpska Journal for Natural Sciences (Zbornik Matice srpske za prirodne nauke) – 26.

CONCLUSION

As a site of interest, Deliblato Sands were explored by many scientists, especially in the area of floristical and taxonomical research. Many researchers gave comprehensive overviews of present flora, and some of them gave details about specific taxa or group of taxa. Vegetation analyses were less published than surveys of flora or some aspects of plant taxa from Deliblato Sands. Despite the numerous floristic and several vegetation surveys on Deliblato Sands, there are still many unanswered questions and there is room for the contribution of future researchers.

In this sense, it is very important to resolve the status of taxa and syntaxa that have questionable presence or syn/taxonomical status.

It is especially important to direct the future research focus to the needs of protection of certain syntaxons, i.e. habitat types, and consider specific proposals for their preservation.

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Appendix 1: The list of publications of the flora and vegetation of Deliblato Sands, according different types of survey: A – Overview of the flora of Deliblato Sands; B – Overview of vegetation of Deliblato Sands; C – Discovery of some taxa on Deliblato Sands; D – Description of some syntaxa in the area of Deliblato Sands; E – Various botanical studies that include individual taxa from Deliblato Sands; F – Analyses of characteristicis of some vegetation types on Deliblato Sands; G – Various researches in the field of forestry; H – A broader analysis of the flora (regional or inter/national level) where data from the Deliblato Sands are also presented; I – A broader analysis of the vegetation (regional or inter/national level) where data from the Deliblato Sands are also presented

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2. Aćić S, Šilc U, Petrović M, Tomović G, Dajić-Stevanović Z (2015): Classification, ecology and biodiversity of Central Balkan dry grasslands. *Tuexenia* 35: 329–353.									X
3. Adamović L (1904): *Die Sandsteppen Serbiens*. Leipzig: Verlag von Wilhelm Engelmann. 617 p.									X
4. Ajtay J (1902): A deliblati futóhomokról. *Erdészeti Lapok* 41(1): 26–46.							X		
5. Ajtay J (1907): A boróka (*Juniperus communis*) bogyójának értékesitéséről. *Erdészeti Lapok* 46(4): 228–230.							X		
6. Ajtay J (1912): A delibláti kincstári homokpuszta ismertetése. *Erdészeti Lapok* 51(1): 25–42.							X		
7. Ajtay J (1914): Die Aufforstung der ärarischen Sandpusta Deliblat. In: L. Fekete und T. Blattny: *Die Verbreitung der forstlich wichtigen Bäume und Sträucher in ungarichem Staate*. Selmecbánya. 150p.							X		
8. Ajtay J (1917a): A szappangyökér termelése a deliblati homokpusztán. *Erdészeti Lapok* 56(1–2): 25–27.							X		
9. Ajtay J (1917b): A szappangyökér termelése a deliblati homokpusztán. *Erdészeti Lapok* 56(13–14): 327–329.							X		
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Appendix 2. List of scientific journals selected by researchers for publishing results of floristic and vegetation surveys on Deliblato Sands.
Journals with the highest number of published articles with tis topics are green highlighted

1. Acta biologica Iugoslavica, serija D – Ekologija	3
2. Acta Biologica Szeged	1
3. Acta biologica. Acta literarum ac scientarum regiae universitatis hungaricae Francisco-Josephinae, sectio A) biologica scientarum naturalium	1
4. Acta Botanica Croatica	1
5. Acta Botanica Hungarica	2
6. Acta Botanica Scientiarum Hungaricae	1
7. Acta Herbologica	2
8. Acta Veterinaria Beograd	1
9. Advanced Technologies	1
10. Allelopathy	2
11. Allgemeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie	2
12. Annalen des Naturhistorischen Museums in Wien	2
13. Annales Musei Nationalis Hungarici ~ Természetrajzi Füzetek	11
14. Applied Ecology and Environmental Research	2
15. Aquatic invasions	1

16. Arhiv bioloških nauka ~ Archives of Biological Sciences	17
17. Biologica Nyssana	1
18. Botanica Serbica	3
19. Botanikai közlemények ~ Növénytani közlemények	9
20. Bulletin of the Natural History Museum in Belgrade ~ Glasnik Prirodnjačkog muzeja u Beogradu, serija B – Biološke nauke	20
21. Central European Journal of Biology	1
22. Cryptogamie, Bryologie	1
23. Czech Journal of Animal Science	1
24. Deliblatski pesak. Zbornik radova 1-6.	12
25. Diversity	1
26. Ecography	1
27. Erdészeti Lapok	17
28. Feddes Repertorium	1
29. Flora oder allgemeine botanische Zeitung (Regensburg)	5
30. Folia Geobotanica	1
31. Food Chemistry	1
32. Forests	2
33. Genetika	1
34. Georgikon for Agriculture	1
35. Glasnik Instituta za botaniku i Botaničke bašte Univerziteta u Beogradu	2
36. Glasnik Prirodnjačkog muzeja u Beogradu, serija C – Šumarstvo i lov	2
37. Glasnik Republičkog zavoda za zaštitu prirode i prirodnjačkog muzeja u Titogradu	1
38. Glasnik Šumarskog fakulteta	15
39. Global Ecology and Conservation	1
40. Hemijska Industrija	1
41. Horticulturae	1
42. Indian Journal of Traditional Knowledge	2
43. Journal of Essential Oil Research	1
44. Journal of Forest Science	1
45. Journal of Plant Ecology	1
46. Journal of the Serbian Chemical Society	1
47. Journal of Vegetation Science	1
48. Land	1
49. Magyar Botanikai Lapok	16
50. Magyar Növénytani Lapok	2
51. Mathematikai és Természettudományi közlemények	15
52. Mollecules	1
53. Neobiota	1

54. Nova Acta Leopoldina	1
55. Österreichische botanische Zeitschrift	4
56. Pharmaceuticals	2
57. Phytologia Balcanica	1
58. Plant, Cell & Environment	1
59. Plant Systematics and Evolution	1
60. Plants	2
61. Saudi Pharmaceutical Society Journal	1
62. Scientific Reports	1
63. Selekcija i semenarstvo	1
64. Studia botanica hungarica	4
65. Šumarski glasnik	1
66. Šumarski list	4
67. Šumarstvo	11
68. Természettudományi közlöny; Pótfüzetek a Természettudományi közlönyhöz	9
69. Thaiszia Journal of Botany	1
70. Tiszia	1
71. Topola	2
72. Tuexenia	3
73. Unija bioloških naučnih društava Jugoslavije, serija G – Biosistematika	8
74. Univerzitet u Novom Sadu, Zbornik radova Prirodno-matematičkog fakulteta, serija za biologiju.	10
75. Verhandlungen des zoologisch-botanischen Vereins in Wien	1
76. Willdenowia	1
77. Wulfenia	1
78. Zaštita bilja	1
79. Zaštita prirode	7
80. Zbornik Matice srpske za prirodne nauke	26
81. Zbornik radova Instituta za šumarstvo i drvnu industriju	1
82. Zootaxa	1

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ИСТОРИЈАТ ФЛОРИСТИЧКИХ И ВЕГЕТАЦИЈСКИХ ИСТРАЖИВАЊА ДЕЛИБЛАТСКЕ ПЕШЧАРЕ

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РЕЗИМЕ: Због својих јединствених природних карактеристика, Делиблатска пешчара је одувек привлачила бројне истраживаче који се баве проучавањем флоре и вегетације. Први писани подаци о ботаничком проучавању овог подручја датирају из 1800. године и садрже вредне податке о флори. У традицији дугој 225 година, инспирација и истраживачи нису нестали до данас. Објављено је 365 публикација на тему проучавања неког аспекта флоре или вегетације Делиблатске пешчаре. Већина публикација представља неке специфичне таксоне или групе таксона у Делиблатској пешчари као део ширег истраживачког подручја (159). Већина првих налаза биљних врста забележена је у периоду истраживања 1951–2025. У истом периоду објављено је највише публикација које се баве анализом флоре или вегетације Делиблатске пешчаре, као ужег подручја (укупно 253). Најпродуктивнији аутор са највећим доприносом у флористичким подацима Делиблатске пешчаре је Меланија Обрадовић, која је са сарадницима објавила 19 публикација о флори овог подручја. Највећи број публикација или истраживача био је из Србије, тачније бивше републике Југославије (238). Кроз историју су допринели и истраживачи из Мађарске, Аустрије и Чешке. Овај рад указује да Специјални резерват природе „Делиблатска пешчара” наставља да буде непресушан извор инспирације за ботаничке науке, с обзиром да број публикација расте из године у годину, како домаћих тако и страних истраживача.

КЉУЧНЕ РЕЧИ: Банат; Banater Sandwüste; Банатска пешчара; Бело брдо; Биелобрдо; Deliblâti-homokpuszta; Делиблатска пешчара; историјски преглед; Војводина

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EFFECTS OF TOURISM ON LITTORAL PLANTS OF LAKE PROVALA AND BEGEČKA JAMA

ABSTRACT: Wetlands are characterized by a unique combination of ecological factors and are currently facing significant threats, particularly to plant diversity. In 2023, the influence of sports and recreational tourism on plant diversity in the littoral zones of Lake Provala and the Nature Park Begečka Jama was investigated. The diversity of plant species and physical and chemical characteristics of water were analyzed. The results revealed that at sites under pressure, a smaller number of plant species was recorded compared to the control site. According to the PERMANOVA analysis, there is no statistically significant difference between pressured and non-pressured locations. Since sports and recreational tourism is permitted in the studied areas, the findings confirm that they do not have a significant impact on plant diversity.

KEYWORDS: diversity; macrophytes; permanova; recreational tourism; sports tourism; wetlands

INTRODUCTION

In the history of ecological research, biodiversity loss has been identified as a major problem, primarily resulting from the modification of natural habitats due to anthropogenic influences (Sodhy et al., 2006). The International Union for Conservation of Nature (IUCN) has emphasized the importance of ephemeral and small water basins, recognizing them as priority habitats in wetland protection and management systems due to the unique communities of aquatic organisms they support (Radulović and Teodorović, 2011).

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Wetlands are characterized by a unique combination of ecological factors, including hydrological, pedological, microclimatic and mesoclimatic influences, as well as distinctive vegetation (Valk, 2006). These ecosystems rank first in the value of their services among all ecosystems, contributing 47% of the global ecosystem service value, making them one of the most important and productive ecosystems on Earth (Ting Xu et al., 2019).

However, wetlands face significant threats, particularly to plant diversity, which is globally endangered. Rare and threatened species are at high risk of extinction if these threats are not addressed. As 21% of native plant species are specialist in aquatic habitats, the loss of natural wetland ecosystems could have severe consequences for vascular plant diversity (Richardson et al., 2015). Contemporary freshwater ecosystems can be characterized as biodiversity hotspots (Haase et al., 2023), essential for biodiversity conservation. Without enhanced protection, many endangered aquatic species may vanish before the century's end (Williams and Dodd, 1978). Wetlands also provide critical ecosystem services, including climate regulation, flood prevention, soil erosion control, nutrient recycling, biomass production and opportunities for recreation and tourism. These services highlight the vital role wetlands play in maintaining ecological balance and supporting human well-being (Keddy et al., 2009).

The flora of wetlands is essential for numerous reasons. Beyond its role in the food chain, wetland phytocoenoses exhibit high levels of primary production and provide critical habitats for various groups, including periphyton, epiphytic bacteria, macroinvertebrates, fish, and birds (Cronk et al., 2001). Aquatic macrophytes function as bioaccumulators, absorbing nutrients, heavy metals and pesticides from the water. Additionally, they serve as bioindicators, reflecting the state and quality of the environment (Santos et al., 2022).

Wetland flora is threatened by the same factors that endanger ecosystems globally, such as anthropogenic activities including desiccation, degradation, pollution, changes in hydrological regimes, invasive species and tourism development. Sports tourism encompasses recreational activities like sport fishing, boating, swimming and diving (Liddie et al., 1980). Fishing tourism is particularly prominent in these areas due to their favorable fish habitats (Lazić et al., 2008). In addition, lake recreational activities cause physical alterations of the shoreline zone leading to endangerment of natural habitats and littoral communities.

The impact of sports and recreational tourism on freshwater ecosystems is evident in the decline of biodiversity, degradation of flora caused by boat propellers, discharge of wastewater and introduction of non-native species. Therefore, the objective of this study is to examine the effects of sports and recreational tourism on plant diversity in the littoral zones of lakes.

MATERIALS AND METHODS

Field research was carried out in May and June 2023 at two locations, at Lake Provala and Begečka Jama Nature Park. Both researched areas are natural ecosystems, with the exception that Provala Lake is not the protected area,

while Begečka Jama was declared as Nature park – a protected area of the third category (Galamboš, 2011).

Study area

The first research site, Lake Provala, is located on the left bank of the Danube River in the Vojvodina province, southwestern Bačka region, approximately 2 km southwest of Vajska and 2.5 km northwest of Bođani, within the Vajštansko-Bođanski Rit (Figure 1). Lake Provala was formed during a major flood in May 1924, when the water level of the Danube River reached an exceptionally high level. This lake represents a macrophytic type of ecosystem, with a flora comprising 65 plant species that primarily develop in the narrow coastal zone. The plant species are widely distributed, reflecting the relatively uniform conditions typical of aquatic ecosystems (Nikolić, 2005).

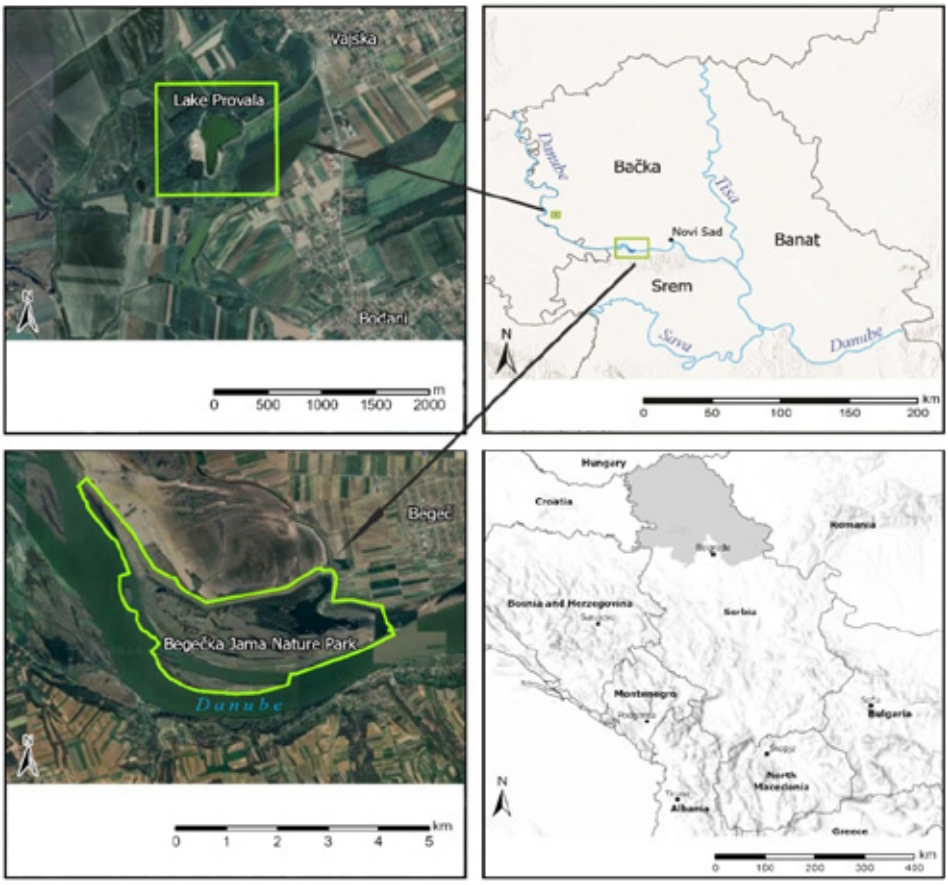

Figure 1. Locations of study area (based on LS, OS, NMA, Geodatastyrelsen, GSA, GSI, OpenStreetMap contributors, and the GIS User Community)

The second research site is the Begečka Jama Nature Park, also situated in the Vojvodina province, southern Bačka region, on the left bank of the Danube River, about 20 km west of Novi Sad. Within the boundaries of the Begečka Jama Nature Park, 125 taxa of higher plants have been recorded, many of which hold national and international significance. For instance, *Nymphaea alba* L. and *Potamogeton nodosus* Poir. are classified as strictly protected species, while *Acorus calamus* L., *Carex acuta* L., *Crataegus nigra* Waldst. & Kit., *Eleocharis acicularis* (L.) Roem. & Schult. and *Trapa natans* L. are listed as protected species (Anonymous, 2016).

Study design

In the littoral zones of each investigated area, two sites were selected: one experiencing pressure from sports and recreational tourism and a control site without such pressure (Figures 2–5). The sites under the pressure at both lakes were exposed to beach-related human activities, involving intensive trampling and sediment disturbance. Although the samples were taken at the beginning of the summer season, the impact of sports and recreational activities was already evident. At each site, the percentage cover of each plant species was determined by analyzing five plots (2 × 2 m), resulting in a total of 20 plots across all sites.

Figure 2. Lake Provala – locality with the influence of sports and recreational tourism (Photo D. Blagojević)

Additionally, the physical and chemical parameters of the water were measured during field research using specialized instruments. Temperature, oxygen saturation and dissolved oxygen levels were measured with a field oximeter, while pH values were determined using a portable pH meter.

Figure 3. Lake Provala – control locality (Photo D. Blagojević)

Figure 4. Begečka Jama Nature Park – locality with the influence of sports and recreational tourism
(Photo D. Blagojević)

Figure 5. Begečka Jama Nature Park-control locality (Photo D. Blagojević)

Data analysis

The Shannon-Weaver index was used to calculate species diversity across all study sites. To quantify dissimilarities in community composition between different sites, Permutational Multivariate Analysis of Variance (PERMANOVA) was employed, using the Bray-Curtis dissimilarity measure with 9999 permutations to test significance. Non-metric Multidimensional Scaling (NMDS) was applied to visualize patterns in community composition and assess the spatial relationships between sites. Additionally, Indicator Species Analysis was conducted to identify species significantly associated with specific sites. All analyses were performed in R version 4.2.2 (R Core Team, 2022), using the packages "vegan" (Oksanen et al., 2022), "ggplot2" (Wickham, 2016), and "indicspecies" (De Cáceres and Legendre, 2009). These methods provided valuable insights into ecological variations among the studied sites, highlighting key patterns in biodiversity and habitat specificity.

RESULTS

The mean values of dissolved oxygen, saturation and pH were highest at Lake Provala (Table 1). The average water temperature was also highest at Lake Provala, particularly in the area under pressure from sports and recreational tourism. However, the highest levels of dissolved oxygen and saturation were recorded at Lake Provala's control site. At Begečka Jama, the site under pressure exhibited a higher mean temperature compared to its control area. Despite these variations, no significant differences were observed in the physical and chemical characteristics of the water between the control and influenced sites.

Table 1. Physical-chemical characteristics of the investigated localities with mean values of physical-chemical water parameters

Measured parameters of the water	Provala Lake		Begečka Jama Nature Park	
	Locality with the pressure	Control locality	Locality with the pressure	Control locality
Temperature (°C)	25.8	25.4	25.1	24.6
Dissolved oxygen (mg/l)	10.11	10.62	10.02	9.18
Saturation oxygen (%)	120.88	129.8	120.0	114.0
pH	8.8	8.8	8.3	8.2

At sites under influence, a smaller number of plant species was recorded, including *Nymphoides peltata* (S. G. Gmel.) Kuntze, *Spirodela polyrhiza* (L.) Schleid., *Potamogeton crispus* L., *Ceratophyllum demersum* L. and *Stuckenia pectinata* (L.) Börner (Tab. 2). In the control area, in addition to these five species, the following were also detected: *Lemna minor* L., *Nuphar lutea* (L.) Sm., *Salvinia natans* (L.) All., *Rorippa amphibia* (L.) Besser and *Persicaria amphibia* (L.) Delarbre.

Table 2. Recorded species on control and influence sites

	Presence of the recorded plant species on the localities	
Plant species	Locality with the pressure	Control locality
Nymphoides peltata	+	+
Spirodela polyrrhiza	+	+
Potamogeton crispus	+	+
Ceratophyllum demersum	+	+
Stuckenia pectinata	+	+
Lemna minor	–	+
Nuphar lutea	–	+
Salvinia natans	–	+
Rorripa amphibia	–	+
Persicaria amphibia	–	+

The two-dimensional configuration of Non-metric Multidimensional Scaling (NMDS) provided a good representation of the community data, with a stress value of 0.07364 after 9999 iterations. This low stress value indicates that the NMDS ordination captured the main patterns of community composition well. The analysis of species composition using PERMANOVA revealed that there was no significant difference in plant structure across different site levels (Pseudo-F=1.8374, p=0.131), suggesting that plant composition did not differ significantly between the sampled sites (Figure 6). According to the Indicator Species Analysis, only one indicator species, *Lemna minor*, was identified for the control sites (p = 0.0108).

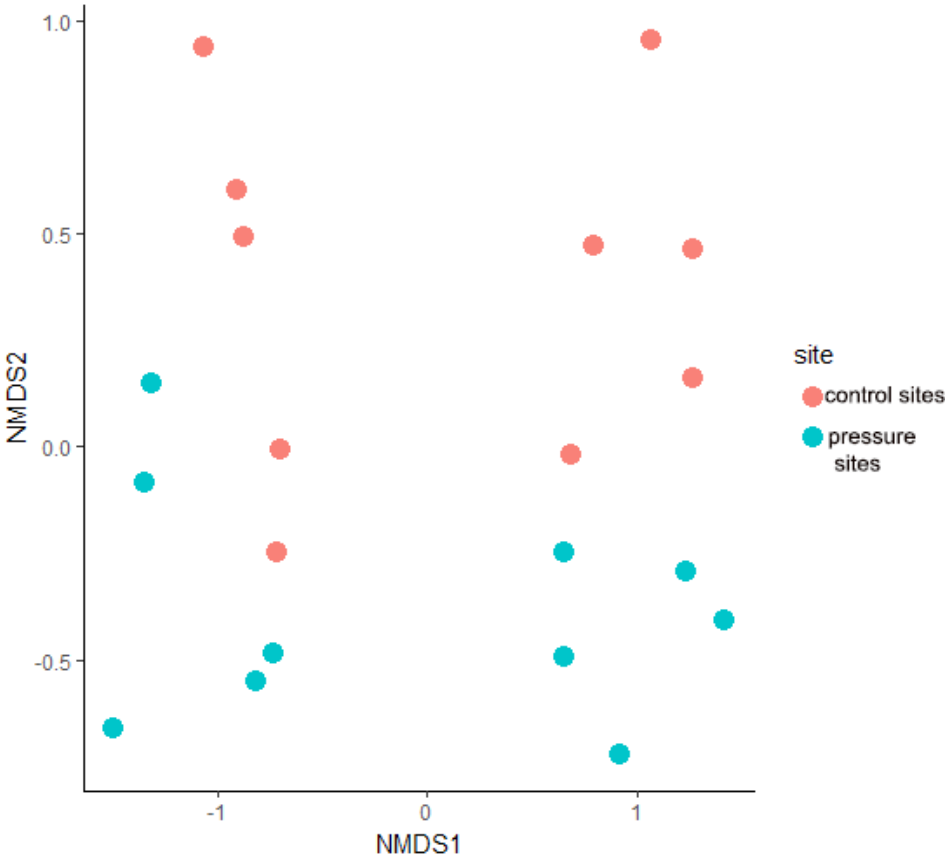

Figure 6. Graphic representation localities with and without influence

DISCUSSION

The presence of aquatic plants in ecosystems positively affects both the living organisms and the properties of water and sediment. They play a crucial

role in providing habitats for macroinvertebrates, fish and birds. Aquatic macrophytes act as bioaccumulators, absorbing various harmful substances and metabolically breaking them down through biodetoxification. For example, *E. canadensis*, *T. natans*, and *C. demersum* are known to accumulate elements such as Mn, Ni, Mo, Cu, Sr and Ba, while *C. demersum* also stores significant amounts of nitrogen. By accumulating and transforming harmful substances, aquatic macrophytes improve the physical, chemical and biological conditions of aquatic ecosystems, making them valuable for phytoremediation. Emergent vegetation also plays a vital role in biologically protecting shorelines from erosive processes. Furthermore, macrophytes contribute significantly to organic production (biomass), the formation of vegetation cover and the process of photosynthesis, which directly supports the functioning of the biosphere (Nikolić, 2005).

The research was conducted in the littoral zones of the lakes, as these are the most productive areas for aquatic plants. While the physical and chemical characteristics of the water showed no significant differences between the investigated sites, plant diversity was notably higher in the control areas (10 species) compared to the sites influenced by sports and recreational tourism (5 species). This suggests that anthropogenic impacts, such as vegetation removal, play a significant role in reducing plant diversity.

In the coastal areas under pressure, vegetation removal often leads to ecosystem degradation and conversion into arable or urban land. Sports and recreational tourism activities, such as commercial and recreational fishing, frequently involve biological, chemical and mechanical (physical) control of aquatic vegetation to increase fish stocks. For example, herbicides are used to create open spaces for fishermen, while mechanical removal of plants is conducted for various purposes (https://www.fao.org/4/X7580E/X7580E13.htm).

Based on the PERMANOVA method for the plant communities in the area of Lake Provala and Begečka Jama, there are no statistically significant differences between sites with pressure and sites without pressure, as confirmed by the *p* values. Furthermore, only one indicator species, *L. minor*, was identified for the control sites. This species typically occupies the early stages of habitat succession and is considered a natural habitat pioneer (Borhidi, 1995). This finding suggests that the control sites may also be impaired.

The research established that sports and recreational tourism did not affect plant diversity. This may be attributed to the fact that fishing is limited and strictly regulated, particularly in Begečka Jama, which is a protected area. Wetlands and aquatic plants serve as critical habitats for fish spawning and shelter. Additionally, coastal and inland wetlands provide essential breeding, nesting, migratory and non-breeding habitats for numerous species of waterfowl, wading birds, shorebirds, mammals, reptiles and amphibians (Nyman, 2011).

CONCLUSION

In this research, the impact of sports and recreational tourism on the diversity of plants in the littoral zones of Lake Provala and Begečka Jama was analyzed.

Greater plant diversity was recorded in the control areas of any investigated locality. Statistical analyses revealed no significant differences in plant diversity between locations exposed to anthropogenic pressure and those without such pressure. Given that sports-recreational tourism is permitted in the studied areas, the findings confirm that it has no significant impact on plant diversity. Recognizing the global importance of aquatic ecosystems is a vital step toward developing strategies for their conservation.

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УТИЦАЈ ТУРИЗМА НА БИЉНЕ ВРСТЕ ПРИОБАЛНИХ ПОДРУЧЈА ЈЕЗЕРА ПРОВАЛА И БЕГЕЧКА ЈАМА

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РЕЗИМЕ: Влажна станишта данас представљају једне од најугроженијих типова станишта, нарочито ако се посматра диверзитет биљака. У овом раду приказан је утицај спортско-рекреативног туризма на диверзитет биљака у литоралној зони језера Провала и Бегечка јама. Истраживања су вршена у периоду од маја до јуна 2023. године. На сваком локалитету, одабрана су места где постоји утицај спортско-рекреативног туризма и места где нема (контрола) и на њима су пописане биљне врста и утврђена је покровност биљног покривача. Такође, на датим местима одређене су физичко-хемијске карактеристике воде. Наши резултати су показали да контролна места имају већи број биљних врста (10) у поређењу са местима где постоји притисак (5). Статистички значајне разлике нису констатоване у физичко-хемијске карактеристике воде између места са притиском и без њега. Такође, применом PERMANOVA анализе потврђено је да не постоје статистички значајне разлике у структури биљних заједница између контроле и места под притиском. Наша истраживања су показала да спортско-рекреативни туризам нема утицаја на диверзитет биљних врста у литоралној зони ова два влажна екосистема.

КЉУЧНЕ РЕЧИ: диверзитет; макрофите; пермутациона мултиваријантна анализа варијансе (PERMANOVA); рекреативни туризам; спортски туризам; влажна подручја

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CADMIUM EFFECTS ON HIGHER PLANTS

ABSTRACT: Cadmium (Cd) is a heavy metal widely distributed in the biosphere. Environmental pollution with Cd is widespread throughout the world. At higher concentrations, it is very toxic to living organisms. Plants absorb Cd from the soil solution rather easily, and it enters the food chain mostly through them. The availability of Cd for plants depends primarily on the chemical properties of the soil. During the uptake of Cd, interaction with ions of other elements may occur. Plant species differ in the intensity of absorption and thus accumulation of Cd, which is absorbed in the form of ions or chelates. Cadmium mostly accumulates in the roots and may then be transported by xylem and phloem. Toxic concentrations of Cd can cause a variety of unfavorable changes in the anatomical and morphological features of plants, affect physiological and biochemical processes, their mineral composition and reduce growth. Cadmium may inhibit germination by hindering water uptake and mobilization of seed reserves. The effect of Cd on photosynthesis was studied in the most detail. Higher concentrations of Cd adversely affect the synthesis of chloroplast pigments, photosynthetic electron transport and the Calvin cycle more than other processes. Some substances can be used to mitigate the phytotoxic effect of Cd, such as silicon, boron and biochar etc. Cadmium-hyperaccumulating plant species possess specific mechanisms by which they can mitigate the toxicity of higher Cd concentrations.

KEYWORDS: accumulation; heavy metal; Cadmium (Cd); distribution; growth; plants; photosynthesis; seed germination; toxicity

INTRODUCTION

Cadmium is a soft silver-white metal, belonging to the group of heavy metals (HM). Together with zinc and mercury, it is included in the II B group of the periodic table. Cadmium was discovered by Sreomeyer in 1817. The atomic

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number of Cd is 48, atomic weight is 112.41 g/mol. It is found in nature but in the form of salts. The most famous salt is $CdSO_4$ and it is also found in the form of CdS, $CdCl_2$ and $Cd(NO_3)_2$. In the air, it quickly turns into CdO. Heavy metals are among the biggest environmental pollutants (Karahan et al., 2020). They can pollute soil, air, water and plants. They are very toxic to all living organisms, microorganisms, plants, animals and humans. Cadmium can cause toxic effects in living organisms even at low concentrations. It is one of the most toxic heavy metals due to its high solubility in water and non-degradability. It can enter the human body primarily through ingestion and partly through the respiratory tract. It concentrates in bones, kidneys and liver, causing numerous serious diseases (Altio and Tritscher, 2004). Therefore, significant attention is paid to this element both from a health and ecological point of view. According to the World Health Organization (WHO), the weekly tolerable exposure to Cd is 0.007 mg/kg of body mass (WHO, 2000). Terrestrial plants mostly absorb Cd from the soil and the concentration of Cd in the Earth's crust is on average 0.15 to 0.20 mg/kg. The average concentration of Cd in the surface layer of soil, based on a large amount of data in different soil types and countries, ranges from 0.06 to 1.1 ppm in dry matter (Kabata-Pendias and Pendias, 2000). Numerous human activities lead to environmental pollution with Cd: mining and metal refining, municipal sewage sludge, animal manure, compost, mineral fertilizers, pesticides, atmospheric fall-out, coal fly ash, cement factories, natural mobilization of Cd by weathering of rocks and volcanic activity, etc. (Bogdanović et al., 1997; Kabbata-Pendias and Pandias, 2000; Rizwan et al., 2017). Cadmium is a harmful non-essential element for plants, humans and animals. Owing to its good solubility in water and high mobility in the soil, plants absorb Cd easily and more intensively compared to some other HMs. It can affect numerous physiological, biochemical and metabolic processes of plants. Owing to its chemical similarity with some other divalent cations (like Ca^{2+} and Mg^{2+}), Cd can substitute them in the active part of the molecule of some proteins and thus cause a disturbance in their function. The phytotoxicity of Cd is based, among other things, on its ability to bind to histidyl, thiol and carboxyl groups of enzymes and structural proteins, thus preventing their original physiological and biochemical action (Huybrechts et al., 2019). For the above and other reasons, excessive accumulation of Cd in plants can cause numerous morphological, physiological and biochemical disorders, the ultimate effect of which is reduced production of organic matter or even death. Cadmium-stress adversely affects photosynthesis and reduces chlorophyll content (Zhou et al., 2024), negatively affects seed germination (Chanpiwat and Numprasanthai, 2024), causes oxidative stress, production of superoxide free radicals resulting in DNA damage and lipid peroxidation of the cell membrane system (Hossain et al., 2012; Haider et al., 2021) and affects leaf structure and root anatomy (Kovačević et al., 1999; Maksimović et al., 2007). Considering the numerous environmental pollutants containing Cd and its toxicity at higher concentrations for living organisms, it is understandable that there is a great interest in this element.

Uptake, transfer and accumulation of cadmium

Plants can absorb Cd through the roots and leaves, stems and seeds. The sources of Cd can be soil, air and water habitats. The most significant is its absorption from the soil, where it is found in different forms, primarily in soluble and exchangeable form. Bioavailability of Cd depends on numerous chemical and physical properties of the soil, pH value, capacity of cation exchange, organic matter content, presence of ions of other elements, temperature, humidity and soil texture (Wei et al., 2023; Huang et al., 2021). The pH value of the soil is of particular importance for the bioavailability of Cd, since it decreases significantly in an alkaline environment. Acidic soils enhance Cd solubility, whereas liming immobilizes Cd. Soil organic matter binds Cd but can also form soluble complexes that increase mobility. Microbial activity modifies Cd bioavailability through siderophore production, root exudates, and mycorrhizal associations. Biochar and phosphate amendments have shown promise in reducing bioavailable Cd pools (Guan et al., 2025).

Cadmium enters roots via multiple transporter families: ZIP (ZRT/IRT-like proteins), NRAMPs, HMAs (heavy metal ATPases), and Ca^{2+} channels. The high-affinity Fe^{2+} transporter, IRT1, is a major Cd entry route in Arabidopsis (Tao et al., 2022). Once inside the root symplast, Cd is either bound by phytochelatins or exported into xylem vessels by HMA2/HMA4. Vacuolar sequestration is mediated by ABC transporters and HMA3. Transpiration stream largely drives Cd accumulation in leaves, whereas phloem mobility is relatively restricted, though grains of rice and wheat still accumulate Cd to toxic levels (Yu et al., 2024).

Due to the chemical similarity and charge characteristics between Cd and Ca, Fe(II), Zn and Mn, there is competition for their uptake and translocation in plants (McLaughlin et al., 2021). Cadmium toxicity affects N metabolism; the activity of some enzymes of N metabolism decreases, while the content of nitrates in plants increases (Kastori and Petrović, 1995). Optimal N supply decreases the stress induced by Cd in young sunflower (Panković et al., 2000). The Si alleviates uptake and accumulation of Cd in peanut and pea (Shi et al., 2010, Rahman et al., 2017). Reduction in rhizotoxicity and absorption of Cd by soybean and wheat roots were seen upon the application of Ca and K (Yang and Juang, 2015). Individual plant species and genotypes can differ significantly in intensity of uptake and accumulation of Cd (Petrović et al., 2003; Ai et al., 2022). Cadmium is absorbed by plants in the form of Cd^{2+} ions or in the form of chelating compounds. In the soil solution, Cd^{2+} ions reach the root surface by mass flow or diffusion. On the root surface, Cd adsorption occurs from the surface of rhizodermal cells through exchange with H^{+} ions, after which Cd reaches the cortex through the apoplast (Sasaki et al., 2012). There is an opinion that the transport of Cd ions is carried out by the same transmembrane carriers that participate in the uptake of some other cations. After entering the root hairs, Cd is transported through symplast and apoplast pathways to the xylem (Shaari et al., 2024). In long-distance transport, xylem plays a key

role. The driving forces of xylem transport are transpiration and root pressure. Phloem transport plays an important role in the redistribution of Cd in aerial organs (Tanaka et al., 2007). In general, it can be said that Cd is well mobile in plants, where transporter proteins play an important role (Hao et al., 2022; Zhang et al., 2024). Cadmium can also enter cells through the plasma membrane via Ca channels (Perfus-Barbeoch et al., 2002). Most of the absorbed Cd is retained in the roots, which can be considered as one of the protective mechanisms of above-ground organs against the toxic effects of Cd. In the case of beans, from the total Cd taken up, only 2% is transported to the aerial part. In the root, it is predominantly found in the apoplast or vacuole (Ouariti et al., 1997). In some plants, the cell wall plays a pivotal role in the accumulation of Cd (Peng et al., 2017). The presence of Cd in human and animal food is unacceptable; therefore, special attention is paid to the distribution of Cd in consumable parts of plants. The intensity of Cd accumulation in plants primarily depends on its concentration in the nutrient medium and it rises with its presence. (Logan et al., 1997; Dias et al., 2012). Cadmium also affects the accumulation of some micro- and macronutrients in plants. According to Dias et al. (2012), in the roots of young *Lactuca sativa* plants, Mn uptake was significantly decreased at 10 and 50 μM Cd, while in the leaves, Fe uptake significantly decreased. Plant species differ significantly in Cd accumulation. In soil enriched with 10 ppm Cd by sewage sludge, the concentration of Cd in the above-ground part among the 19 examined species, primarily cultivated, was the lowest in rice and the highest in turnip, 162.0 μg/g of dry matter. Significant differences between wheat genotypes in their response to different Cd concentrations were found *in vitro* (Kondić-Špika et al., 2005). Wheat cultivars originating from different parts of the world and then grown in the same ecological conditions differed only slightly in the accumulation of Cd in the grain. The concentration of Cd in the grain in the eight tested wheat genotypes was much higher in humid years (0.0423 mg/kg of dry weight) and was significantly lower in dry years (0.020 mg/kg) from the allowed maximum concentration (0.5 mg/kg) (0.3 mg/kg) (Maksimović et al., 2016). The World Health Organization (WHO) does not provide one single maximum permissible concentration (MPC) for cadmium in all plants (Commission Regulation (EU) 2023/915 of 25 April 2023). Worls Health Organization (WHO) and Food and Agriculture Organization (FAO) guideline suggests a maximum level of 0.2 mg/kg for leafy vegetables. However, other sources indicate different maximums, and some national limits are even higher for specific vegetables. For root vegetables, other organizations have set a maximum level of 0.3 mg/kg; for medicinal plants WHO have set a limit of 10 ppm (10 mg/kg); for rice, the allowable limit is often set at 0.2 or 0.4 mg/kg. There are plant species that are characterized by higher accumulation of Cd, so-called hyperaccumulators, such as bermuda grass, vetiver grass, bulrush, and turnip. They are characterized by a higher bioconcentration and translocation factor for Cd (Shanying et al., 2017). Owing to that, some of them can be used for phytoremediation of Cd-contaminated soils.

Seed germination is one of the most important events in the life cycle of plants. It can be influenced by numerous exogenous and endogenous factors, including the presence of Cd (Carvalho et al., 2023; Jabri et al., 2024; Chanpiwat and Numprasanthal, 2024). The first step towards germination is absorption of water, since it is essential for activation of hydrolytic enzymes and for hydrolysis of organic compounds stored in the endosperm. This initiates metabolic processes, including respiration and various anabolic pathways necessary for the growth and development of the embryo. Higher concentrations of Cd can weaken water absorption and thus limit the availability of water for the development of embryos and seedlings (Kuriakose and Prasad, 2008). The absorption of water depends on the structure of the seed coat as well as on the presence of osmotically active substances in the seed. Their presence, however, depends on the activity of hydrolytic enzymes, which is affected by Cd. Kalai et al. (2016) reported a reduction of alpha-amylase activity in germinating barley seed influenced by Cd stress, resulting in a decrease in starch release from cotyledons. A decrease in the activity of hydrolytic enzymes such as alpha-amylase, acid phosphatase and proteases in *Sorghum bicolor* led to a decrease in the mobilization of the seed nutrient reserves (Kuriakose and Prasad, 2008). Cadmium can affect the production of reactive oxygen species (ROS) and tangle the antioxidant system, which can affect numerous processes in plants, including seed germination (Senevirante et al., 2019). Elevated ROS (O_2^-, H_2O_2, HO•) causes lipid peroxidation (e.g., increased MDA), protein oxidation and DNA damage. Cadmium does not directly generate reactive oxygen species (ROS), but it interferes with electron transport chains in chloroplasts and mitochondria, leading to ROS overproduction. Reactive Oxygen Species (ROS) such as H_2O_2 and O_2 – cause lipid peroxidation, protein oxidation, and DNA damage. Plants respond with enzymatic antioxidants (SOD, CAT, APX, GR) and non-enzymatic antioxidants (ascorbate, glutathione, flavonoids). The balance between ROS production and scavenging capacity determines tolerance (Seregin & Kozhenkov, 2023).

According to Han et al. (2023), the antioxidant enzymes of wheat seeds and seedlings decreased under Cd pollution. Cadmium also affects phytohormones, which play a significant role in the processes of decomposition of organic matter accumulated in the endosperm during seed germination (Huybrechts et al., 2019). Seeds intensively absorb Cd dissolved in water, especially at higher concentrations. Higher concentrations of Cd adversely affect germination, seedling vigor and increase the percentage of atypical seedlings (Kastori et al., 2019). Based on a large number of literature data, Senevirante et al. (2019), and Carvalho et al. (2023) state that Cd does not always have a negative effect on germination and seedling vigor, but may have a neutral or even positive effect depending on the dose of Cd, properties of the medium, plant species and genotype, the state of plant and organ development.

Effect of cadmium on photosynthesis

Photosynthesis is of vital importance for higher plants, since in this process, organic matter is synthesized from CO_2 and water, using solar energy. Therefore, numerous researchers have recently studied the influence of Cd on photosynthesis (Chu et al., 2018; Song et al., 2019; Chen et al., 2022; Zhou et al., 2024). According to Chen et al. (2022), application of 20 μmol/L $CdCl_2$ to lettuce significantly reduced the chlorophyll (Chl) content in lettuce leaves. It was observed that important enzymes in the synthesis of chlorophyll, such as POR, DVR and HemB are less active under Cd-induced stress, which leads to a decrease in the content of Chl a, b and their total amount. At the same time, the degradation of carotenoids was stimulated and thus their content decreased. The ratio of Chl and carotenoids decreased, while the ratio of Chl a to Chl b increased. In *Oenanthe javanica*, 100 mg Cd/L reduced the content of Chl a and b, while the proportion of carotenoids was very little affected. Chlorophyll b showed greater sensitivity to Cd than Chl a. (Zhou et al., 2024). A significant decrease in Chl a and b content was also found in purslane plants when 100 mg Cd/L was applied (Takabayashi et al., 2011). Cadmium is thought to inhibit the phototransformation of protochlorophyllide to chlorophyll, as well as to promote the enzymatic degradation of chlorophyll by activating chlorophyllase. The possibility of replacing Mg in the chlorophyll molecule with ions of divalent metals Cd, Hg, Zn, Ni, Pb was published by Küpper et al. (1996). Heavy metal porphyrins have been known *in vitro* for a long time. The test results showed that Mg in the chlorophyll molecule was replaced by heavy metals in *in vivo* conditions, which made it impossible for photosynthesis to take place. It has been shown that there is an almost regular relationship between the toxicity of heavy metals and the tendency of their ions to bind in the center of the chlorophyll molecule. The replacement of Mg with heavy metals makes it impossible for the changed chlorophyll molecules to absorb light energy and thus the transfer of electrons is disabled, resulting in the interruption of photosynthesis. Light intensity has a great influence on Mg substitution reactions. In addition to the mentioned elements, Mg in the chlorophyll molecule can also be replaced by some rare earth elements, like La or Ce.

Higher concentrations of Cd affect not only the amount of chlorophyll but also the overall activity of the photosynthetic apparatus and hence, the decrease in the amount of chlorophyll under Cd stress results in a decrease in photosynthesis (Song et al., 2019). According to Dias et al. (2012), 10 and 50 μM Cd in lettuce leads to a significant reduction in the photochemical efficiency of PSII and a reduction of the net CO_2 assimilation rate. Cadmium can reduce or interrupt the photosynthetic electron flow (Voigt and Nagel, 2002; Song et al., 2019). Zhou et al. (2024) also report the influence of Cd stress on photosynthetic electron transport by influencing the amount of active PSII and PSI. Panković et al. (2000) mention that Cd stress affected the ribulose-1,5-bisphosphate regeneration capacity of the Calvin cycle more than other processes. According to Chen et al. (2022), Cd stress inhibited the synthesis of photosynthesis-related proteins or subunits and directly affected the protective mechanism of the photosynthetic system.

Growth responses to cadmium toxicity

In conditions of Cd stress, the reduction of plant growth and mass is closely related to its negative impact on photosynthesis. Even low Cd concentration (1 μM) induced reduction of lettuce growth (Dias et al., 2012). Cadmium exposure leads to significant alterations in plant anatomy. Root cortical cells exhibit wall thickening and increased suberin deposition, limiting Cd transport. In leaves, chloroplasts become swollen with disrupted grana. Mitochondria display condensed matrices and broken cristae. Scanning electron microscopy shows alterations in stomatal density and aperture control. Such changes compromise overall metabolic efficiency (Mushtaq et al., 2025).

Cadmium affected cell division and differentiation. Higher Cd concentrations decreased root dry mass and length while increasing root diameter in tomato (Gratao et al., 2009). In Cd-treated maize seedlings, the fresh root biomass, total root length and primary seminal root length were significantly lower than in the control and had thicker cortex and thicker parenchyma cells (Maksimović et al., 2007; Rahman et al., 2017). Cadmium changes leaf structure in young wheat plants and reduces leaf dry mass, mesophyll thickness, the number and size of vascular bundles and vessel diameter. Thinner chlorenchyma after Cd treatment is possibly due to its negative effect on cell division and elongation (Kovačević et al., 1999). The increases in Cd concentration from 0.5 to 5.0 μM $CdCl_2$ reduced plant height, leaf area, and fresh mass of leaves in young sunflower plants (Panković et al., 2000). In lettuce exposed to 1 and 20 μM Cd, there was a reduction of 16% and 46% of plant dry weight (Dias et al., 2012). Heavy metals and microplastics are almost always found in the soil. Han et al. (2023) have found that the co-existence of Cd and polypropylene-microplastics (PP-MPs) at 50 and 100 μm has a synergistic and antagonistic effect with Cd, depending on the size of PP-MPs. Cadmium accumulation in reproductive tissues leads to pollen sterility, reduced fertilization success, and impaired seed filling. In cereals such as rice and wheat, Cd disrupts assimilate partitioning, resulting in lower grain weight and nutritional quality. High Cd content in grains exceeds food safety thresholds (0.2 mg/kg in rice, WHO/FAO standard), making Cd contamination a global food security issue (Zhou et al., 2022).

According to Monteiro et al. (2012), Cd toxicity induced cyto- and genotoxicity and led to decreased antioxidant capacity in lettuce. The concentration of Cd >1 μM leads to an increase in the presence of hydrogen peroxide, the consequence of which is an increase in the oxidation of proteins and lipids. Silicon can reduce the impact of stress caused by some environmental factors (Lazić et al., 2020). Detoxification of Cd relies heavily on chelation and compartmentalization. Phytochelatins (PCs), short peptides derived from glutathione, bind Cd and facilitate transport into vacuoles. Metallothioneins (MTs) also contribute to binding. Ali et al. (2015) stated that application of salicylic acid can alleviate the toxicity of Cd in oilseed rape. Rahman et al. (2017) demonstrated that exogenous silica can compensate Cd toxicity in field peas. Boron can also alleviate its toxicity by promoting Cd chelation on cell wall components of root cells (Wu et al., 2020). Transport across the tonoplast is mediated

by HMA3, ABC-type transporters, and CAX transporters. Vacuolar sequestration prevents Cd from interfering with cytosolic processes and contributes to tolerance in hyperaccumulators such as Thlaspi caerulescens (Yu et al., 2024). According to Amirahmadi et al. (2020), biochar application reduces soil Cd bioavailability and encourages oak seedling growth. Cadmium hyperaccumulator plants have developed a complex mechanism to control the toxic effects of Cd. They form organic complexes with Cd and can thus protect key physiological processes from its harmful impact (He et al., 2017).

CONCLUSION

Soil pollution with heavy metals, including Cd, is a worldwide significant environmental problem. Plants primarily accumulate Cd from the soil, through which it enters the food chain and thus endangers the health of humans and animals. Higher plants can absorb Cd through roots and aerial organs. It is taken up in the form of ions or chelates, where it can interact with ions of other elements. Cadmium is highly mobile in plants in both xylem and phloem. Most of it accumulates in the roots and, to a much lesser extent, in the reproductive organs. Higher concentrations of Cd in plants cause visible, morphological (chlorosis, necrosis, etc.) and invisible physiological and biochemical changes. Phytotoxic concentrations of Cd can already affect the initial phases of plant life and seed germination by inhibiting water uptake and mobilization of seed reserves. The influence of Cd on photosynthesis was studied in the most detail. Cadmium reduces the activity of enzymes important for the synthesis of chlorophyll a and b and promotes their breakdown by activating chlorophyllase, as a result of which their content decreases. Cadmium can replace Mg in the chlorophyll molecule and thus enable photosynthesis to take place. Furthermore, Cd stress leads to a significant reduction in the photochemical efficiency of FSII and assimilation of CO_2 in the Calvin. Cadmium stress leads to a decreased antioxidant capacity in plants. Reduction of photosynthetic productivity and phytohormone activity results in reduction of growth of shoots and roots, reduction of leaf surface and numerous anatomical changes.

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УТИЦАЈ КАДМИЈУМА НА ВИШЕ БИЉКЕ

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РЕЗИМЕ: Кадмијум (Cd) се убраја у тешке метале. Загађење земљишта тешким металима, а тиме и кадмијумом, представља заначајан проблем широм света јер је при већим концентрацијама веома токсичан за живе организме. У ланац исхране кадмијум највећим делом доспева преко биљака. Више биљке могу да усвајају кадмијум преко корена и надземним органима. Највећим делом га усвајају преко корена, из земљишног раствора, због чега оптерећење земљишта кадмијумом преставља велик проблем. Код већине биљака кадмијум се накупља у корену, а у мањој мери у надземним, а посебно у репродуктивним органима. Кадмијум за биљке није токсичан при нижим концентрацијама. Међутим, више концентрације кадмијума код биљака изазивају анатомске, морфолошке, физиолошке и биохемијске промене. Фитотоксичне концентрације кадмијума могу да утичу већ у почетној фази живота биљака: на клијање семена инхибирајући усвајање воде и мобилизацију резервних материја семена, што се неповољно одражава на раст поника. Најдетаљније је проучаван утицај кадмијума на фотосинтезу, што је разумљиво ако се има у виду значај овог процеса у образовању органске материје виших биљака. Његов утицај на фотосинтезу веома је комплексан. Веће концентрације кадмијума смањују садржај хлорофила *а* и *б* и њихов однос, док су каротеноиди мање подложни дејству кадмијума. Кадмијум инхибира фототрансформацију протохлорофилида у хлорофил, а утиче и на његову разградњу активацијом хлорофилазе. Он може да замени магнезијум (Mg) у молекулу хлорофила и да и на тај начин онемогући одвијање фотосинтезе. Кадмијум изазива стрес који значајно смањује фотохемијске ефикасности FSII, утиче на фотосинтетички транспорт електрона, на активност ензима Калвиновог циклуса и тиме на уградњу CO_2 у органска једињења. Смањење фотосинтезе и активности фитохормона има за последицу смањени раст биљака, бројне анатомске и морфолошке промене, хлорозу, некрозу и др. Стога је веома важна заштита животне средине од штетног деловања кадмијума.

КЉУЧНЕ РЕЧИ: акумулација; тешки метал; кадмијум (Cd); дистрибуција; раст; биљке; фотосинтеза; клијање семена; токсичност

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REVIEW OF NATURE-INSPIRED POSITION-DEPENDENT MASS OSCILLATOR MODELS APPLIED IN QUANTUM SYSTEMS

ABSTRACT: This review explores position-dependent mass (PDM) oscillators, naturally occurring in biological systems and relevant to engineered quantum devices. In nature, PDM oscillations appear in the bending of plant stems, fish swimming, bird flight, and the motion of limbs, as well as in the oscillatory behavior of organs like the heart and vocal cords. These phenomena inspired models of oscillators whose effective mass varies with position, simulating elastic structures attached to bodies of variable mass. Mathematically, such systems are captured by Liénard equations with quadratic velocity terms. This review examines key features – motion type, period, and amplitude – of PDM oscillators, highlighting their versatility for describing spatially varying inertia and dynamic adaptation. Extending these concepts to quantum systems, spatial variations in carrier mass arise in semiconductor nanostructures like quantum wells, wires, and dots, due to compositional inhomogeneities and structural gradients. Position-dependent mass models refine quantum mechanics, enabling more accurate energy-level and carrier-dynamics predictions. Such models are central to the design of advanced electronic and photonic devices, including quantum cascade lasers, high electron mobility transistors, and scanning tunneling microscopy. Bridging biology and quantum engineering, PDM oscillators offer a robust framework for innovation in adaptive materials and biologically inspired technologies. Future research should address nonlinear effects, anisotropic materials, and leverage data-driven optimization to fully realize the technological potential of PDM oscillators.

KEYWORDS: Position-dependent mass, nature inspired models, nonlinear oscillators, quantum systems

INTRODUCTION

Recent advances in nanotechnology and semiconductor physics have increasingly highlighted the significance of position-dependent mass (PDM) in

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quantum systems. In particular, charge carriers in engineered nanostructures, such as quantum wells, wires, and dots, often experience spatially varying effective masses due to material heterogeneity, strain, and compositional gradients. Traditional quantum mechanical models must therefore be refined to account for these variations, leading to the development of PDM frameworks. Remarkably, the principles of PDM are not confined to the realm of quantum physics. A significant number of PDM oscillatory systems are evident in the natural world, from the bending of tree branches in the wind to the undulatory locomotion of fish and the dynamic shape changes in insect wings. These biological systems adapt their mass distribution to optimize movement and resilience, offering compelling analogies for both mechanical and quantum PDM oscillators.

This paper aims to bridge these natural inspirations and their theoretical interpretations in quantum systems. The authors first explore the occurrence of PDM oscillators in living systems, highlighting how nature leverages spatial mass variation for enhanced function. Afterwards, a comprehensive theoretical framework for PDM models is developed, inspired by these biological phenomena. Finally, the authors discuss the mechanical-quantum analogy and the applications of PDM models in advanced materials and devices.

The remainder of this paper is organized as follows: section 2 examines nature-inspired PDM oscillators across plant and animal systems, section 3 details the theoretical framework of PDM models, including their mathematical formulations and physical interpretations, section 4 focuses on the mechanical analogy and the cross-disciplinary relevance of PDM oscillators and quantum applications, section 5 concludes with key insights and future directions.

POSITION-DEPENDENT MASS OSCILLATORS IN NATURE AND APPLICATIOS

A significant number of position-dependent mass (PDM) oscillatory systems are evident in nature, both in the plant and animal world. During motion, there is a change in the distribution of mass and the moment of inertia within the body as a consequence of position changes. These changes may be of structural kind or arise from variations within the material itself. For instance, in botany, tree or plant oscillation in the wind is a classic example of such systems. Wind induces periodic bending of tree branches or stems. As water content and internal pressure vary along the length, the effective mass and inertia change with position (Niklas, 1992; Vogel, 2012). Large plant leaves and flower stalks, such as those in banana plants or sunflowers, exhibit PDM behavior under wind loading, where the structural response and effective mass vary with position (Spatz & Speck, 2002).

Locomotion in living beings is also frequently accompanied by changes in the effective mass of the body. In undulatory swimmers such as eels and lampreys, the body mass distribution changes dynamically along the spine due to fluid-structure interactions and muscle activation patterns (Tytell et al.,

2010). These organisms exhibit traveling wave oscillations with position-dependent inertia and damping, leading to highly efficient propulsion strategies in aquatic environments. Snakes also exhibit periodic body deformation during locomotion, changing their mass distribution and moment of inertia with each undulatory wave (Jayne, 1986).

Additional examples of PDM oscillators can be found in the flexible tail beats of swimming fish, such as tuna and sharks (Shadwick & Gemballa, 2005), and the morphing wings of birds like swifts, which dynamically adjust wing shape to control glide performance (Lentink et al., 2007).

Insects, including flies, bees, and moths, rely on wing flapping for flight. During flapping, the wings dynamically change their shape – an active deformation process – altering the mass distribution in each stroke (Combes & Daniel, 2003). The flexible wing structure modifies its effective mass and stiffness throughout the cycle, enabling agile and controlled flight maneuvers.

Furthermore, insect antennae, such as those of stick insects and moths, act as elastic oscillators with position-dependent effective mass due to hemolymph redistribution and dynamic shape changes (Dürr & Ebeling, 2005).

Propulsion mechanisms in aquatic organisms further exemplify PDM oscillators. Jellyfish contract and expand their bell to swim. Contraction expels water, reducing internal mass, and subsequent refilling restores it, resulting in a fluid-mass cycle that changes the inertia of the system (Gemmell et al., 2015). Similarly, octopuses and squids employ jet propulsion: they fill a cavity with water, increasing internal mass, and then eject it to generate thrust. Here, the system mass varies with internal volume, and the cavity shape directly affects the total system mass (Anderson & Grosenbaugh, 2005).

Particularly interesting is the occurrence of PDM oscillators within the human body. Heart valves and chambers act as oscillators with position-dependent mass during the cardiac cycle. Blood redistribution leads to changes in the effective mass of moving walls with each heartbeat (Chung & Im, 2012). As the heart fills and empties, its stiffness and effective mass vary, influencing overall hemodynamics. In voice production, the vocal folds oscillate dynamically. During phonation, their mass distribution changes with shape and tension, functioning as nonlinear oscillators with effective mass varying along the vocal fold length (Titze, 2008; Cvetićanin, 2012). This complexity contributes to the richness and variability of human voice production.

Finally, these principles are also evident in limb movements. During walking or running, human and animal limbs exhibit periodic motion, with changes in mass distribution and effective moment of inertia driven by muscle contraction, fluid shifts, and joint angles (Winter, 2009). These variations are essential for understanding the biomechanics of locomotion and for improving performance and rehabilitation strategies.

What is common to all these examples is that they represent oscillators in which mass and/or moment of inertia change depending on position. Consequently, to achieve the most accurate simulation of such systems, it is essential to develop precise models incorporating position-dependent mass (PDM). Such models should consider as many relevant factors as possible,

including material heterogeneity, structural geometry, and fluid interactions. Beyond mimicking natural systems, PDM models hold potential for diverse engineering and medical applications. They can support the development of medical devices for organ treatment, aid in the creation of artificial organs, and contribute to the production of artificial voices. Further research in this field can advance both our understanding of biological systems and the design of innovative bioinspired technologies.

MODEL OF POSITION-DEPENDENT MASS OSCILLATOR

Let us model the oscillator as a spring – particle system. The particle has the position dependent mass (PDM) $m(x)$, which depends on the displacement coordinate x. Including the specificity of structure and material properties of the system, the function $m(x)$ may describe any of aforementioned cases. For particle with PDM the kinetic energy is

$$E_k = \frac{1}{2} m(x)\dot{x}^2 \tag{1}$$

where $\dot{x}$. is the velocity. Thus, kinetic energy of PDM particle is not only the function of the velocity as is the case for particle with constant mass, but also of the displacement. Properties of the kinetic energy (1) are discussed in paper of Mustafa (2012) and Chargui (2019).

For the elastic spring with potential $V(x)$ the Lagrangian L of the oscillator is (Tkachuk & Voznyak, 2015; Mustafa & Algadhi, 2019; Mustafa, 2020; Biswas, 2020)

$$L = \frac{1}{2} m(x)\dot{x}^2 - V(x) \tag{2}$$

Using the Lagrange formalism $\frac{d}{dt}\frac{\partial L}{\partial x} - \frac{\partial L}{\partial x} = 0$ the equation of motion follows as

$$m(x)\frac{d^2x}{dt^2} + \frac{1}{2}\frac{dm(x)}{dx}\left(\frac{dx}{dt}\right)^2 + \frac{dV(x)}{dx} = 0 \tag{3}$$

Expression (3) is a special type of Liénard equation (Liénard, 1928; Jordan & Smith, 2007) with quadratic damping (Ruby et al., 2015; Rath et al., 2017). The effect of quadratic damping on the oscillatory motion was discussed for a long time (Tiwari et al., 2013). Verhulst (1996) gave the general treatment of quadratic damping and suggested the consideration of the Liénard equation within the framework of dynamical system. In the papers of Narayanan & Sekar (1996) and Bishop & Clifford (1996) not only the unforced but also the forced periodical oscillators are considered. The focus is on periodic response and stability of such systems. It is shown how quadratic damping alters response amplitudes and frequency behavior. Zhou & Zhang (2007) extended

the research considering chaos in the Liénard system. Bifurcation structures and the route to chaos in these systems is discussed.

For (1), significant number of analytic solving procedures are developed. Let us mention some of them: the multiple scale method (Nayfeh & Mook, 1979), perturbation techniques (Chatterjee & Mallik, 1994), harmonic balance method (Bishop & Clifford, 1996). Main disadvantage of the mentioned procedures is that they are based on the harmonic solution of the linear oscillator, in spite of the fact that the system is nonlinear. In Cvetićanin et al. (2025), modification of methods is done and the solution is assumed to be the perturbed version of the exact solution of the truly nonlinear oscillator. The procedure is suggested for various mass functions.

Harmonic like PDM oscillator

According to the formulation of the potential energy of the linear spring in the system with constant mass $V=k\frac{x^2}{2}$ where the stiffness coefficient k is defined as the product of the natural frequency ω^2 of the oscillatory system and mass, the potential energy of the PDM oscillator is (Rath et al., 2021)

$$V(x)=\frac{m(x)\omega^2x^2}{2} \tag{4}$$

Substituting (4) into (3) the equation of motion is

$$\ddot{x}+\omega^2x+\frac{dm(x)}{dx}\frac{1}{m(x)}\left(\frac{x^2}{2}+\frac{\omega^2x^2}{2}\right)=0 \tag{5}$$

As the first two terms in equation correspond to harmonic oscillator and the last two represent the perturbation of the oscillator with constant mass, the equation (5) is named '*harmonic like PDM oscillator*' (Carinena et al., 2004; Asad et al., 2020, Takou et al., 2025a). Various mass variations are considered (Dong et al., 2007; Costa-Filho, 2011; Dong et al., 2022) and their effect on motion is analyzed. Ghosh and Modak (2009) discussed the role of PDM-symmetry on trajectory of motion and Khlevniuk (2018) established a geometric interpretation of the motion of a classical particle with PDM in a harmonic potential. Rath et al. (2021) and Jafarov & Nagiyev (2023) extended the research by formulating oscillators with position-dependent finite symmetric decreasing and increasing mass. Classical phase portraits of the systems were analyzed using analytical approaches. Takou et al. (2025b) introduced a thermodynamic analysis of a harmonic oscillator with position-dependent mass and explored also the statistical properties and thermodynamic quantities of the system.

Mathews and Lakshmanan (1974) considered the so called '*Mathews-Lakshmann oscillator*' with PDM of Lorentzian profile type (Mathews & Lakshmanan, 1975). This equation has the exact analytic solution in the form of the

cosine trigonometric function (Lakshmanan & Chandrasekar, 2013; Karthiga et al., 2017; Santos & González-Borrero, 2023).

Truly nonlinear like PDM oscillator

In general, let us assume the spring to have nonlinear elastic property. The potential energy for the spring is (Cveticanin, 2018)

$$V(x)=\frac{m(x)\omega_\alpha^2|x|^{\alpha+1}}{\alpha+1} \tag{6}$$

where $\alpha \geq 1 \wedge \alpha \cup R$ (integer or noninteger) is the nonlinearity order of the oscillator and ω_α^2 is a constant. Substituting ( ) into ( ) – ne znam šta treba da bude u zagradama (Lj.Tubić) the equation of motion is

$$\ddot{x}+\omega_\alpha^2 x|x|^{\alpha-1}+\frac{dm(x)}{dx}\frac{1}{m(x)}\left(\frac{x^2}{2}+\omega_\alpha^2\frac{x|x|^\alpha}{\alpha+1}\right)=0 \tag{7}$$

Comparing (7) with the oscillator with constant mass

$$\ddot{x}+\omega_\alpha^2 x|x|^{\alpha-1}=0 \tag{8}$$

the difference is evident. The additional terms in (7) are the products of PDM function and its position derivative. As the equation (7) represents the perturbation of (8), i.e. of the truly nonlinear oscillator (Mickens, 2010), the equation (7) is usually called '*truly nonlinear like PDM oscillator*'.

Analyzing (7) it is obtained that it has the first integral

$$m(x)\left(\frac{x^2}{2}+\omega_\alpha^2\frac{x|x|^\alpha}{\alpha+1}\right)=K=const. \tag{9}$$

The first integral (9) is of energy type where both energies (kinetic and potential) are mass dependent. For initial conditions

$$x(0)=A,\quad \dot{x}(0)=0 \tag{10}$$

where A = const. the constant is $K=m(A)\frac{A^{\alpha+1}}{\alpha+1}$ and the energy integral is

$$m(x)\left(\frac{x^2}{2}+\omega_\alpha^2\frac{x|x|^\alpha}{\alpha+1}\right)=m(A)\frac{A^{\alpha+1}}{\alpha+1} \tag{11}$$

i.e.

$$\dot{x}=\pm\sqrt{2\left(\frac{m(A)}{m(x)}\frac{A^{\alpha+1}}{\alpha+1}-\omega_\alpha^2\frac{|x|^{\alpha+1}}{\alpha+1}\right)} \tag{12}$$

Expression (11) i.e. (12) describes the orbital periodic motion with amplitude A. Using (12) the period of vibration is

$$T=\sqrt{\frac{2(\alpha+1)}{m(A)A^{\alpha+1}}}\int_{-A}^{A}\frac{dx}{\sqrt{\frac{1}{m(x)}-\omega_{\alpha}^{2}\frac{|x|^{\alpha+1}}{\alpha+1}\frac{\alpha+1}{A^{\alpha+1}m(A)}}} \tag{13}$$

Unfortunately, the exact analytic solution of (13) is not evident. Because of that the method for calculation of the approximate period of vibration is introduced.

Modified He's formulation

He, in his paper (He, 2006), introduced the formula for computing of the approximate frequency of vibration of the perturbed linear oscillator

$$\omega^{2}=\frac{\omega_{1}^{2}R_{2}(0)-\omega_{2}^{2}R_{1}(0)}{R_{2}(0)-R_{1}(0)} \tag{14}$$

where ω_1 is the exact frequency of the nonperturbed linear oscillator, $\omega_2 = \omega$ is unknown frequency, and $R_1(0)$ and $R_2(0)$ are residuals obtained for the linear solution Acos(ωt) and corresponding frequencies.

For the truly nonlinear oscillator (8) and initial conditions (10) there is the exact solution $x = Aca(\alpha, 1, \omega t)$ in the form of the ca cosine Ateb function (Cveticanin, 2025) with exact frequency

$$\omega_{1}^{2}=\omega_{\alpha}^{2}A^{\alpha-1}\frac{\alpha+1}{2} \tag{15}$$

Substituting (15) into (14) and after some modification the approximate frequency of the ca Ateb function follows as

$$\omega=\sqrt{\omega_{\alpha}^{2}A^{\alpha-1}\frac{\alpha+1}{2}+\omega_{\alpha}^{2}\frac{A^{\alpha}}{2}\left(\frac{dm}{dx}\frac{1}{m}\right)_{0}} \tag{16}$$

Knowing that the Ateb function is periodic with period $B\left(\frac{1}{\alpha+1},\frac{1}{2}\right)$ where B is the complete beta function, the period of vibration is

$$T=\frac{2\mathrm{B}\left(\frac{1}{\alpha+1},\frac{1}{2}\right)}{\omega}=\frac{2\mathrm{B}\left(\frac{1}{\alpha+1},\frac{1}{2}\right)}{\sqrt{\omega_{\alpha}^{2}A^{\alpha-1}\frac{\alpha+1}{2}}}\frac{1}{\sqrt{1+\frac{A}{\alpha+1}\left(\frac{dm1}{dx\,\mathrm{m}}\right)_{0}}} \tag{17}$$

In (17) the first term corresponds to the period of the truly nonlinear oscillator with constant mass, and the second is the correction term which depends on the PDM function and its position derivative. Analyzing the relation (17) it

is obvious that the period is longer for decreasing PDM than for the oscillator with constant mass. In opposite, if mass is increasing the period is decreasing in comparison to the oscillator with constant mass. The higher is the mass increase, the period is shorter.

THEORETICAL FRAMEWORK AND APPLICATIONS OF PDM IN QUANTUM SYSTEMS

This section reviews the theoretical framework and practical implications of PDM models in quantum systems, particularly in the modeling of quantum oscillators. It highlights how the PDM formalism modifies standard quantum models, enabling more accurate descriptions of carrier behavior in heterostructures, quantum wells, and quantum wires. The theoretical foundations of PDM are examined, along with its significance in capturing the spatial variations of effective mass and its relevance in multiple application domains.

In engineered nanostructures such as heterostructures, quantum wells, and quantum wires, the spatial nonuniformity of material parameters necessitates refined theoretical models to enable accurate simulation and device optimization (Capasso et al., 1995; Zawadzki, 2005). The PDM approach thus represents an essential tool for describing quantum mechanical systems where the effective mass of charge carriers varies spatially (Roos, 1983; Bastard, 1988). Namely, recent advances in nanotechnology and semiconductor physics have increasingly emphasized the importance of spatially varying material parameters, especially the effective mass of charge carriers in semiconductor nanostructures. The PDM framework emerges as a crucial refinement to standard quantum models, accounting for the inhomogeneities encountered in real-world systems (Dekar et al., 1999; Plastino et al., 1999).

Furthermore, the analogy between mechanical and quantum PDM oscillators has been demonstrated (Carinena et al., 2007; Schulze-Halberg & Roy, 2016). The use of PDM models is widespread in quantum dynamics studies of low-dimensional systems (Costa Filho et al., 2011; El-Nabulsi, 2021a), particularly in the coherent state framework, where a specific quantum state closely approximates classical behavior. This is especially significant in the context of quantum dots, quantum wells, and other semiconductor nanostructures (Cruz & Ortiz, 2009; Costa et al., 2023).

PDM model and applications

In nanostructures such as quantum dots, quantum wells, and superlattices, the effective mass of carriers (electrons and holes) is not constant but varies with position. The PDM model captures this spatial variation, providing improved accuracy in describing energy states and carrier dynamics. Coherent states in these structures often serve to describe the quasi-classical behavior of confined carriers (e.g., in laser-based nanostructures and quantum emitters).

Key application areas include:

- *Semiconductor quantum dots*: Electrons are confined in all three spatial directions, with PDM models accurately describing energy levels and wave functions (Ghosh et al., 2016; El-Nabulsi, 2020a; 2020b; Sari et al., 2022).
- *Quantum wells*: Electrons can move freely in the plane of the well but are confined in one dimension, forming discrete, quantized energy levels (Harrison, 2005; Dekar et al., 1999).
- *Superlattices and nanoscale layers*: These structures exhibit engineered potential profiles relevant to nonlinear optics and coherent emission properties (Chen, 2008).

A heterostructure consists of multiple layers of dissimilar semiconductor materials, each with distinct electronic band structures (El-Nabulsi, 2021a; 2021b; Costa et al., 2021). These structures are typically fabricated using epitaxial growth techniques such as molecular beam epitaxy (MBE) or metal-organic chemical vapor deposition (MOCVD), allowing atomic-level control of layer thickness and composition (Chen, 2008).

Quantum wells arise when a thin semiconductor layer with a lower bandgap is confined between layers of higher bandgap material (Harrison, 2005). This structure creates a potential well that confines carriers in one spatial dimension, leading to discrete energy levels (Dekar et al., 1999). Quantum wires extend this confinement to two dimensions, allowing motion only along a single axis and are typically fabricated using electron-beam lithography and anisotropic etching (Chen, 2008). While idealized models assume a constant effective mass, real-world systems exhibit spatial variations due to changes in alloy composition, band structure, and quantum confinement effects (Roos, 1983; Bastard, 1988; Zawadzki, 2005). Accurate modelling thus requires incorporating PDM effects to account for variations in energy spectra, carrier mobility, and tunneling rates (Serra & Lipparini, 1997; Koç & Koca, 2003).

Quantum Oscillators with Position-Dependent Mass

The PDM oscillator approach is essential for simulating devices where material inhomogeneity strongly affects carrier motion (Serra & Lipparini, 1997; Mottaghizadeh & Sadeghi, 2020). These oscillators extend classical harmonic and inharmonic oscillator models by incorporating mass variation, leading to modified energy levels and wavefunction profiles (Dutra & Almeida, 2000; Bagchi et al., 2005; Bagchi et al., 2012; Costa et al., 2023; Takou et al., 2025b). These models are particularly relevant in:

- *Quantum wells and dots with smooth interfaces* (Harrison, 2005; Sayrac et al., 2025).
- *Semiconductor devices with spatially graded composition or doping* (Bastard, 1988).
- *Superlattices and nanostructures with engineered potential landscapes* (Christiansen & Lima, 2023; Lima & Christiansen, 2023).

For instance, high-electron-mobility transistors (HEMTs), utilized in high-frequency RF and satellite circuits, involve heterostructures such as GaAs/AlGaAs where PDM arises at interfaces between materials with different band-gaps (Roos 1983; Capasso et al., 1995; Peter, 2020). In scanning tunneling microscopy (STM) systems, the tip interacts with layered quantum materials where electronic properties–and effective mass–vary spatially, influencing tunneling probability and imaging resolution (Chen, 2008; Jaradat et al., 2024a; 2024b). Resonant tunneling diodes (RTDs) utilize double-barrier quantum wells, where varying effective mass influences tunneling rates and energy levels (Bagchi et al., 2005; Bagchi et al., 2012). Quantum cascade lasers (QCLs), employed in spectroscopy, gas sensing, and medical diagnostics, consist of repeated quantum wells with alternating materials, resulting in PDM across the layers (Capasso et al., 1995; Callebaut & Hu, 2005). Graded-index waveguides, quantum dot LEDs, and solar cells similarly exhibit PDM effects due to compositionally graded materials (Bastard, 1988; Mottaghizadeh & Sadeghi, 2020; Ullah & Ullah, 2020; Sayrac et al., 2025).

The PDM effects also manifest in strongly inhomogeneous plasmas, where spatially varying electric and magnetic fields modulate effective mass, impacting Langmuir wave propagation and particle trapping (Christiansen & Lima, 2023; El-Nabulsi & Anukool, 2022). These systems often display nonuniform energy spacing, asymmetric tunneling, and position-sensitive resonance phenomena, underscoring the importance of PDM oscillator models in understanding such effects (Quesne, 2023).

CONCLUSION

This review has provided a thorough overview of position-dependent mass (PDM) models and their theoretical frameworks, highlighting their essential role in understanding natural and engineered oscillatory systems. From undulatory swimmers and flexible plant structures to insect flight mechanisms, PDM models accurately capture dynamic mass variations crucial to locomotion, fluid–structure interactions, and adaptive responses in biological systems.

In engineering and quantum domains, PDM models have proven vital for the design and optimization of advanced electronic, photonic, and nano-scale devices–including quantum cascade lasers, high-electron-mobility transistors, and scanning tunneling microscopy. Their ability to integrate mass variation and motion dynamics makes them indispensable in both fundamental and applied research.

The broad relevance of PDM models in biology, engineering, and quantum systems underscores their versatility in capturing the complex dynamical behavior of oscillators with position-dependent inertia. This unified framework holds promise for guiding the development of biomimetic devices, soft robotics, and adaptive materials inspired by natural strategies for movement and stability.

Future research should aim to refine these models to incorporate nonlinear effects, anisotropic material behavior, and complex damping mechanisms while validating their predictions experimentally in both natural and engineered systems. Integrating PDM-based models into next-generation quantum devices, photonic systems, and plasma-based technologies offers substantial opportunities for innovation and performance enhancement. Ultimately, PDM-inspired oscillators bridge the gap between natural insights and engineering solutions, paving the way for transformative applications across diverse scientific and technological fields.

OUTLOOK AND FUTURE WORK

The advancement of accurate PDM models for living systems demands interdisciplinary collaboration among biomechanics, physiology, fluid dynamics, and computational modeling. Future research should prioritize the refinement of mathematical formulations for PDM systems–particularly in the context of complex biological tissues and fluid–structure interactions–supported by high-fidelity experimental data from time-resolved MRI, high-speed imaging, and other advanced techniques.

Furthermore, leveraging machine learning and optimization algorithms will be instrumental in identifying key parameters that govern PDM system behavior, facilitating more robust and precise control strategies in real-world applications. Integrating these data-driven approaches with theoretical models promises to accelerate the development of predictive and adaptive PDM frameworks.

Looking ahead, the combination of theory, experimentation, and computational simulation will be crucial to unlocking new insights into these complex yet elegant natural phenomena. Such efforts will not only enhance our understanding of biological and quantum systems but also inspire the next generation of bioinspired, energy-efficient, and adaptable engineered devices that fully exploit the rich dynamical properties of PDM-based oscillators.

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ПРЕГЛЕД ПРИРОДОМ ИНСПИРИСАНИХ МОДЕЛА ОСЦИЛАТОРА СА ПРОМЕНЉИВОМ МАСОМ ПРИМЕЊЕНИХ У КВАНТНИМ СИСТЕМИМА

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РЕЗИМЕ: Преглед истражује концепт осцилатора са масом зависном од положаја (МЗП) препознат код природних система а који је применљив код квантних уређаја. Биолошки осцилаторни системи показују динамичко прилагођавање расподеле масе кретању и положају. Промена ефективне масе и момента инерције дешава се код савијања стабљике биљке, код вијугања тела рибе при пливању, код крила при летењу птица али и инсеката, код удова човека и животиња при корачању и трчању. Рад низа унутрашњих органа у телу човека омогућен је и пропраћен осцилаторним кретањем уз промену масе (рад срчаног мишића, трепереље гласне жице). Инспирисани овим природним феноменима сачињени су модели осцилатора са ефективном масом која је променљива, и функција положаја. Физички модел осцилатора који симулира кретања састоји се од еластичног елемента за који је везано тело променљиве масе. У општем случају математички модел

система је Лиенардова једначина са квадратном функцијом брзине. У раду су приказане специфичности овог осцилатора које се односе на тип кретања, период и амплитуде осциловања. Ови модели нуде свестран теоријски оквир за разумевање осцилатора са просторно променљивом инерцијом, обухватајући сложене интеракције између структуре и кретања. У раду је, користећи карактеристике механичког модела, повучена паралела између природних система и инжењерских квантних уређаја. Преглед обухвата теоријски развој МЗП модела, њихове механичко-квантне аналогије и њене примене. У квантним системима, нарочито у полупроводничким наноструктурама као што су квантне јаме, жице и тачке, просторне варијације ефективне масе носилаца наелектрисања проистичу из композиционих нехомогености и структурних градијената. МЗП модели омогућују усавршавање традиционалног приступа квантне механике, побољшавајући тачност предвиђања нивоа енергије и динамике носилаца у овим системима. Такође, ови модели чине основу за пројектовање и рад напредних електронских и фотонских уређаја попут квантних каскадних ласера, транзистора са великом покретљивошћу електрона и скенирајуће тунелске микроскопије. Повезујући природне и инжењерске перспективе, овај рад указује на велики потенцијал МЗП осцилатора као оквира за вођење иновација у биолошки инспирисаним технологијама, адаптивним материјалима и квантним уређајима следеће генерације. Будућа истраживања треба да укључе нелинеарне ефекте, анизотропне материјале и стратегије оптимизације засноване на подацима, како би се додатно усавршили МЗП модели и искористио њихов пуни технолошки потенцијал.

КЉУЧНЕ РЕЧИ: маса зависна од положаја (МЗП); модели инспирисани природом; нелинеарни осцилатори; квантни системи

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