Biologia (2026) 81:192
https://doi.org/10.1007/s11756-026-02260-y

RESEARCH

Syntaxonomy and functional diversity of *Buddleja davidii*-(co) dominated plant communities in Europe

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Received: 14 December 2025 / Accepted: 1 July 2026

Abstract

Buddleja davidii Franch. is a Chinese ornamental plant that has become successfully naturalised and potentially invasive in most of Europe over the past century. Regarded as a species of unstable and disturbed sites, its ecological niche, invasiveness, and syntaxonomy have often been overlooked. In this study, we examined plant communities in which the species occurs in Slovenia and Europe using multivariate methods, focusing on differences in their ecology, taxonomical and functional diversity. To evaluate the invasiveness potential of *B. davidii* in communities it inhabits, we tested the extent to which its cover explains variation in Shannon–Wiener's diversity index, evenness, disturbance severity and frequency indices, proportions of life forms, Grime's life strategies and neophytes' cover and number, using linear regression. Our results show that *B. davidii* has its ecological optimum in various types of shrub communities, primarily in riparian zones and abandoned quarries, which represent newly proposed subassociations of the typical *Buddlejetum* association. Communities with *B. davidii* can withstand varying levels of disturbance and generally consist of species with a competitive life strategy, while the most dominant life forms are hemicryptophytes and phanerophytes. Increasing cover of *B. davidii* accounted for little variation in taxonomical and functional diversity, and this effect was the most prominent in riparian shrub communities, followed by the *Buddlejetum* association and communities on wall crevices. Occurrences in different plant communities confirm the species' ecological plasticity, whereas its invasiveness is relative, due to its limited relationship with the diversity parameters.

Keywords Butterfly bush · Classification · Disturbance · Diversity · Invasive species · Life strategies · Vegetation

Introduction

Intensive globalisation and facilitated transfer of non-native species between biogeographic areas have significantly contributed to the issue of invasive species (Richardson et al. 2000; Hulme et al. 2008; Catford et al. 2009; van Kleunen et al. 2018). Non-native species can be introduced to new biogeographic areas intentionally through trade, or accidentally as *'stowaways'* during various commercial activities (Hulme et al. 2008). After their introduction and successful naturalization, non-native species may become invasive and cause negative changes, such as diversity deterioration and disruption of ecosystem services (Richardson et al. 2000). This ability of non-native species is generally defined as invasiveness potential (Colautti et al. 2014) and depends on numerous factors, including their abundance in the new area and their morphological, physiological, and ecological traits. Therefore, these traits need to be thoroughly studied in risk assessments and invasiveness potential quantifications upon

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Published online: 20 July 2026

their arrival in new biogeographic areas (Pyšek et al. 2012; Colautti et al. 2014).

Horticulture is a crucial global contributor to plant invasions due to the consistent transportation and introduction of novel ornamental plants to new areas (van Kleunen et al. 2018). In Europe, escapes of ornamental and horticultural plants account for approximately 52% of all plant invasions, with main exporters being North and South America, and Asia (Lambdon et al. 2008). Among Asian countries, China is one of the main exporters of ornamental plants to Europe. Recent study revealed 449 ornamental woody plants, China-native plant species found in Europe, including *Buddleja davidii* (Feng et al. 2016). *B. davidii* was introduced to Europe from East Tibet in the nineteenth century (Nelson 1983), followed by multiple re-introductions in the following decades (Tallent-Halsell and Watt 2009). Its popularity in Europe peaked after the Industrial Revolution, when it was favoured by the middle class, who often grew it in enclosed gardens. The first records of its escape from gardens were reported in the 1930s in Great Britain (Miller 1984), followed by its rapid naturalization in quarries and on urban walls. Due to the increased disturbances during and after the Second World War, *B. davidii* continued to naturalise successfully throughout the urban centres of Western and Central Europe. Species' popularity did not fade in the post-war era, with over 90 cultivars currently available on the market (Tallent-Halsell and Watt 2009). According to the results of the DAISIE project, *B. davidii* is currently present in 28 European countries, 16 of which classify it as successfully naturalized (Lambdon et al. 2008). In a more recent study by Kalusová et al. (2024), its presence in 28 European countries was confirmed. It was classified as invasive species in 9 countries, as potentially invasive in 1, as successfully naturalized in 7, in process of naturalization in 2, and as casual in 5, whereas its status in 4 countries wasn't clarified. Additionally, it is classified as a widespread species with major potential impact on the European Union's biodiversity, proposed for prioritised risk re-assessment in 2025 (Carboneras et al. 2018), what could make *B. davidii* a potential candidate for future inclusion in the List of Invasive Species of Union Concern (EU 2014). Despite the general agreement on the species' invasiveness, studies of *B. davidii*'s invasiveness and its impact on the plant communities it occurs in are relatively rare, particularly in Europe. The available information offers dividing results and mostly focuses on its low impact on the riparian shrub communities in New Zealand (Smale 1990; Bellingham et al. 2005; Peltzer et al. 2009), whereas Gasperini et al. (2020) studied and confirmed its negative impact on riparian shrub habitats in Italy. Focus on studies of shrub communities is however not coincidental, since *B. davidii* has long been associated with the shrub vegetation, although with a somewhat unclear syntaxonomic position. The first formal description of a *Buddleja davidii*-dominated plant community was published by Schmitz (1991). *Buddlejetum* Schmitz 1991 is an urbanophilous, shrub-dominated plant association, commonly found in urban and industrial areas, or along traffic infrastructure. It was first classified in the alliance *Sambuco-Salicion* Tx. et Neumann ex Oberd. 1957 of the class *Epilobietea angustifolii* Tx. et Preising ex von Rochow 1951 (Schmitz 1991). Mucina (1993) assigned plant communities with *B. davidii* to the informal syntaxon *Buddleja davidii*-(*Lamio albi-Chenopodietalia*)-Gesellschaft and the class *Galio-Urticetea* Passarge ex Kopecký 1969. Mucina et al. (2016) defined *B. davidii* as a diagnostic species of the class *Robinietea* Jurko ex Hadač et Sofron 1980, vegetation of forest clearings and anthropogenic successional scrubs and thickets, found on nutrient-rich soils of temperate Europe. However, studies by several other authors (de Foucault and Wattez 2005; Fernez and Causse 2017; Giupponi et al. 2023) suggest assigning *B. davidii*-dominated communities to the vegetation class *Crataego-Prunetea*.

Considering the species' documented occurrences in a wide range of habitats in Europe, differing opinions on its ecological optimum and syntaxonomic framework, and insufficient information on its invasiveness, we conducted a comparative analysis of plant communities with *B. davidii* in Slovenia and Europe. Additionally, we assessed the taxonomic and functional diversity of these communities. Aims of our study were (i) to analyse vegetation diversity of *B. davidii*-communities in Europe, (ii) to study differences in taxonomical and functional diversity of *B. davidii*-communities, (iii) to assess the potential invasiveness of *B. davidii* by testing the extent to which of species' cover explains variation in diversity parameters using regression analysis.

Materials and methods

Studied species

Buddleja davidii Franch. (butterfly bush) is a semi-deciduous, 0.5–5 m tall, multi-stemmed shrub from family *Scrophulariaceae* (Ebeling et al. 2008a, b; Tallent-Halsell and Watt 2009). Individual shrubs live up to 40 years (Ebeling et al. 2008b) and grow most rapidly during the first 15 years (Ebeling et al. 2011). The species is native to China (Tallent-Halsell and Watt 2009), India, Japan and Pakistan, where it occurs from lowlands to mountain slopes at elevations from 360 to 3.800 m a.s.l. (Chen et al. 2011). It was introduced to Europe in 1869 by the French missionary Father David (Nelson 1983) and was repeatedly re-introduced from Asia in the last decade of the nineteenth century, as it quickly became a popular ornamental plant (Tallent-Halsell and Watt 2009). Apart from Europe, *B. davidii* is reported as at least naturalised or invasive in Europe, Australia, New Zealand, Africa,

South America, North America, and Canada, as well as in parts of Asia where it is not native (Tallent-Halsell and Watt 2009).

The species is an ecological opportunist, usually found at various disturbed, degraded, and ruderal sites such as quarries, traffic infrastructure, and forest clearings (Tallent-Halsell and Watt 2009), wall crevices (van Dort and van Landuyt 2004; Francis and Hoggart 2012), wastelands (Godefroid et al. 2007; Muratet et al. (2007), and urban ruderal ecosystems rich with other neophytes (Lososová et al. 2018; Kalusová et al. 2019). It is considered as thermophilous, mesohygrophilous, facultatively calciphilous, non-obligately heliophilous species (de Foucault and Wattez 2005) and a species typical of nutrient-poor or moderately nutrient-rich sites (Chytrý et al. 2018).

Materials, sampling and data compilation

In total, we compiled three datasets for our analyses. For the first – Slovenian data subset, we sampled vascular vegetation on all known *B. davidii* localities in Slovenia (Jogan 2018; Ogris 2025) where the species is present, using the Braun-Blanquet method (1964). Vegetation sampling was conducted from June to October during 2021–2023 and resulted in 59 original relevés. Plot sizes depended on the ecological conditions at the sites and ranged from 4 m^2 to 100 m^2 (35 m^2 on average). Sampled vegetation relevés were stored in the Vegetation of Slovenia database (Šilc 2012) using Turboveg software (Hennekens and Schaminée 2001). Additionally, we added 10 existing relevés with *B. davidii* from the Vegetation of Slovenia database (Šilc 2012) to the Slovenian *B. davidii* subset, which in total consisted of 69 relevés. The second dataset consisted of 276 relevés from Slovenian shrub communities, classified into the vegetation class *Crataego-Prunetea* Tx. 1962. This dataset was used to establish the syntaxonomical position of newly sampled *B. davidii* shrublands in Slovenia. Third – European dataset combines all available relevés with presence of *B. davidii* from Europe and was used to show overall diversity of vegetation with *B. davidii*. It was obtained from the European Vegetation Archive (EVA) (Chytrý et al. 2016). It comprised 296 relevés with *B. davidii* from 28 national databases, referenced in Online Resource 1. Additional 16 relevés were collected from the literature (Schmitz 1991; van Dort and van Landuyt 2004; de Foucault and Wattez 2005; Gasperini et al. 2020). Original 59 relevés from Slovenia were added to the European *B. davidii* dataset, resulting in a total of 371 relevés, which is why we refer to the Slovenian dataset of *B. davidii* communities as a subset. Due to data inconsistencies on vegetation layers in the European relevés, those were merged into one. Bryophytes were deleted because they were recorded only in a small proportion of relevés. The 276 relevés from the Slovenian shrub vegetation dataset were not included into the European dataset.

The nomenclature of vascular plant species follows Plants of the World Online (POWO 2025). The nomenclature of associations follows Šilc and Čarni (2012), of higher syntaxa follows Mucina et al. (2016).

Statistical analyses

Plant cover values of Braun-Blanquet scale were converted to mean values of percentage cover classes and transformed using the Hellinger transformation (Hellinger 1909). We used hierarchical classification (Relative Sørensen Index, Flexible beta (−0.25) method) to classify the collected relevé material. Classification was performed using PC-ORD software (McCune and Mefford 1999). Diagnostic species were determined in the JUICE programme (Tichý 2002), based on their fidelity values (phi values) (Chytrý et al. 2002). The threshold fidelity value for diagnostic species was set to 0.1, threshold frequency value for constant and dominant species was set to 25%.

The Slovenian data subset and the European dataset were analysed using NMDS (Non-metric Multidimensional Scaling). We calculated unweighted mean ecological indicator values (EIV) for each relevé. For the Slovenian data subset, we used EIVs according to Pignatti et al. (2005), and for the European data dataset, according to Tichý et al. (2023). Ecological indicator values were passively plotted onto the ordination diagrams to illustrate ecological relationships among vegetation types and their ecology. For EIV calculations, we used the JUICE programme (Tichý 2002), R software (R Core Team 2025) and the *vegan* package for ordinations (Oksanen et al. 2022), which were used for creation of classification and ordination figures. The distribution map was created using QGIS programme, version 3.40 Bratislava (QGIS Development Team 2025).

We analysed the taxonomic and functional diversity of relevés in the European dataset. Taxonomic diversity was assessed using the Shannon–Wiener diversity index and species evenness. Functional diversity was analysed using indices of disturbance severity and frequency (Midolo et al. 2023), percentages of Grime's CSR strategies (Grime 2006), neophytes cover and number, and plant life forms. Each of the diversity parameters was assessed for each relevé in each cluster of the European data dataset, as defined in the previous classification analysis. We calculated proportions of neophytes number and cover; each fundamental life strategy – competitors (C), ruderals (R), and stress-tolerators (S); life forms – therophytes, phanerophytes, hemicryptophytes, chamaephytes, geophytes and hydrophytes; and diversity indices in JUICE (Tichý 2002) and R (R Core Team 2025) programmes. Data on CSR strategies was obtained from the BiolFlor (Kühn et al. 2004) and Pladias (Chytrý et al. 2021)

databases, for plant life forms from the FloraVeg database according to Dřevojan et al. (2023). Neophytes were defined according to Plants of the World Online (POWO 2025), Euro+Med PlantBase (Euro+Med 2025), GloNAF (van Kleunen et al. 2019) and European Alien Species Information Network (EASIN 2025) databases.

Prior to the statistical analysis, assumption of normality was tested with the Shapiro–Wilk test, with statistical significance set at $p < 0.05$. Since our taxonomic and functional diversity dataset didn't meet normality assumption, we assessed differences between clusters using non-parametric tests. For analyses of Shannon–Wiener diversity index, evenness, disturbance indices and percentages of neophytes cover and number, we used Kruskal–Wallis test, followed by subsequent pairwise Mann–Whitney U test with Bonferroni correction ($p < 0.05$). We analysed differences in proportions of Grime's life strategies and life forms as independent variables between clusters with permutational ANOVA (PERMANOVA) with 9999 permutations ($p < 0.05$). Average values for the Shannon–Wiener diversity index, species evenness, disturbance indices and percentages of neophyte cover and number were presented as violin graphs with box plots with minor outliers (°): values 1.5–3 times the Interquartile Range away from the nearest quartile, and major outliers (*): values more than 3 times the Interquartile Range away from the nearest quartile. Proportions of life strategies were shown graphically in ternary plots for each cluster. We used R software (R Core Team 2025) for calculations and the PAST programme (Hammer et al. 2001) for graphical analysis.

To test to which extent cover of *B. davidii* explains variation in parameters of taxonomic and functional diversity at the cluster level, we used robust regression analysis in PAST programme (Hammer et al. 2001), due to the non-parametric distribution. Statistical significance of r^2 was set at $p < 0.05$, with 9999 permutation replicates applied. Cover of *B. davidii* was transformed to ordinal scale (Westhoff and Van Der Maarel 1978) and defined as the independent variable, while values of the Shannon–Wiener index, evenness, disturbance indices, percentages of neophytes cover and number, life strategies and life forms were defined as dependent variables.

Results

Plant communities with *Buddleja davidii* in Slovenia

We recorded the presence of 396 plant taxa from 72 families in the Slovenian subset. The most abundant plant taxa in the Slovenian subset are *Erigeron annuus* ($n = 43$), *Taraxacum* sect. *Taraxacum* ($n = 31$), *Artemisia vulgaris* ($n = 30$), *Salix eleagnos* ($n = 29$), and *Daucus carota* ($n = 24$); families with the most species (taxa) are *Asteraceae* ($n = 64$), *Poaceae* ($n = 46$), *Lamiaceae* ($n = 32$), *Fabaceae* ($n = 22$) and *Scrophulariaceae* ($n = 21$).

Hierarchical classification of Slovenian relevés revealed five well-defined clusters, shown in Fig. 1. The analytical table for the Slovenian data subset shows diagnostic, constant, and frequent species (Online Resource 2).

The first cluster (Fig. 1) comprises one relevé originally classified to the class *Adiantetea*, found on rock crevices in Posočje (NW Slovenia). It is the most sciophilous and xerophilous variety of *B. davidii* communities in Slovenia, developed under the most nutrient-poor conditions. Its diagnostic species include the ferns *Adiantum capillus-veneris* and *Asplenium ruta-muraria*, and the angiosperms *Parietaria judaica* and *Paederota lutea*. In this stand, *B. davidii* occurs only in the herb layer with low cover.

Clusters 2, 3 and 4 consist of true shrub communities, in which *B. davidii* co-dominates with high cover. We classified these communities in the association *Buddlejetum* Schmitz 1991. General diagnostic species of *Buddlejetum* association in Slovenia are *Salix eleagnos*, *Erigeron annuus*, *Lotus corniculatus*, and *Poa compressa*.

Cluster 2 includes relevés from gravel riparian sites along alpine rivers (Soča, Nadiža, and Tržiška Bistrica). Its diagnostic species are *Tussilago farfara*, *Medicago lupulina*, and

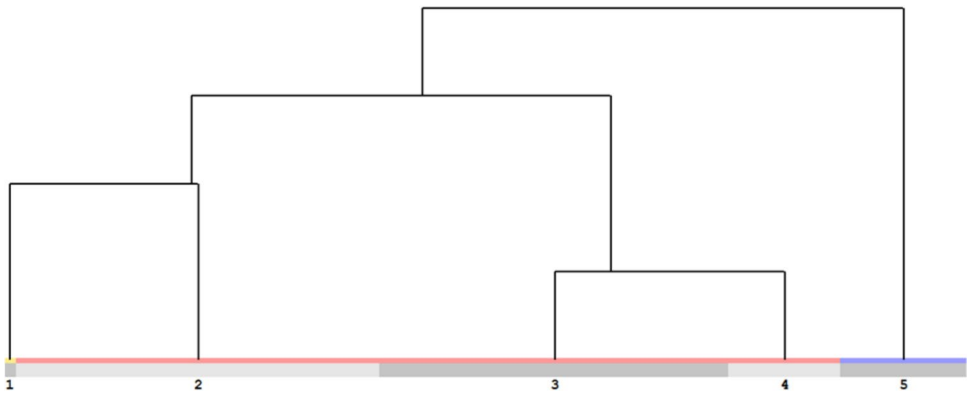

Fig. 1 Hierarchical classification of relevés with *Buddleja davidii* from Slovenia (Relative Sørensen and Flexible beta (−0.25) method). 1 – *Adiantetea*, 2 – *Buddlejetum tussilaginetosum* subass. nova, 3 – *Buddlejetum typicum*, 4 – *Buddlejetum buphthalmetosum* subass. nova, 5 – *Polygono lapathifoliae-Salicetum eleagni*

Populus tremula. We classified these communities into the *Buddlejetum davidii tussilaginetosum* subass. nova.

Cluster 3 represents the central part of the association *Buddlejetum*, lacking additional diagnostic species except *Clematis vitalba*. These communities are widely distributed, usually ruderalised, with a pronounced presence of other invasive species, such as *Erigeron annuus* and *Solidago canadensis*. We classified these communities as *Buddlejetum davidii typicum*.

Cluster 4 consists of communities from quarries in central Slovenia (Posavje and Zasavje), whose diagnostic species are *Buphthalmum salicifolium* and *Pinus sylvestris*. We classified these communities into the *Buddlejetum davidii buphthalmetosum* subass. nova.

Cluster 5 includes herbaceous communities developed on river gravel terraces in western Slovenia, classified in the association *Polygono lapathifoliae-Salicetum eleagni* (Dakskobler et al. 2019), rich in ruderal annuals. In these communities, *B. davidii* is present in juvenile form with low cover. Compared with clusters 2 and 3, cluster 5 generally consists of therophytes, diagnostic of various classes of synanthropic vegetation.

The results of the NMDS ordination (Fig. 2) further confirm floristic and ecological distinctions between individual clusters from the Slovenian subset. Clusters 1 and 5 show the greatest floristic and ecological dissimilarities compared to clusters 2–4, which are arranged along the first ordination axis and correlate with nutrients and moisture.

NMDS ordination of Slovenian shrub communities of *Crataego-Prunetea* (Fig. 3) shows an ecologically and syntaxonomically meaningful division into six groups (using the original classification by the authors). The most thermophilic and heliophytic communities are located on the far left of the ordination diagram and are classified in the alliance *Berberidion vulgaris* and the association *Irido illyricae-Cotinetosum coggygriae* (also *Berberidion*) (Accetto 2015) (clusters 1 and 3 in Fig. 3, respectively). Mesic shrub communities of the alliances *Astrantio-Corylion avellanae* and *Prunion spinosae* (clusters 4 and 5 in Fig. 3, respectively) are positioned on the central right of the ordination diagram. Clusters 2 (*Sambuco-Salicion*) and 6 (*Buddlejetum*) are separated from the other clusters along the second ordination axis, which corresponds to higher indicator values for nutrients and moisture.

Based on the results of multivariate analyses (Figs. 1, 2, and 3, Online Resource 2), we propose classifying relevés from Slovenia into three subassociations of the *Buddlejetum* association.

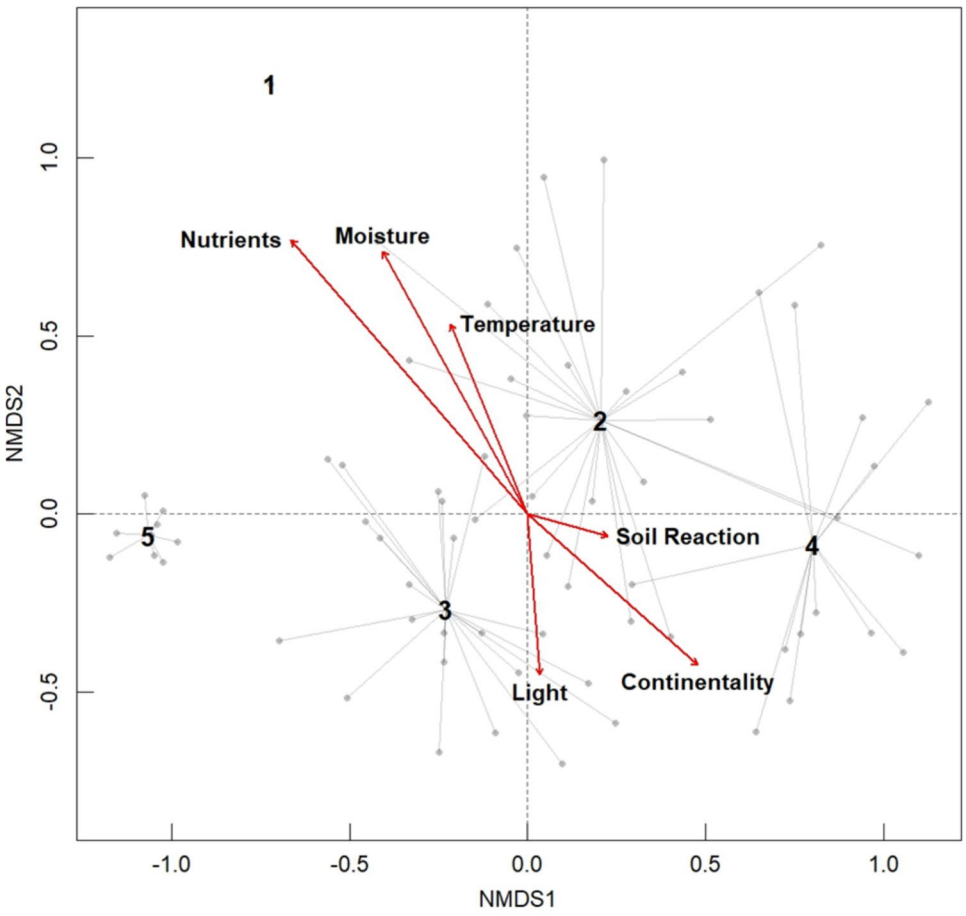

Fig. 2 NMDS ordination of relevés with present *Buddleja davidii* from Slovenia. Stress value 0.2368083. Clusters numbering and description corresponds to Fig. 1

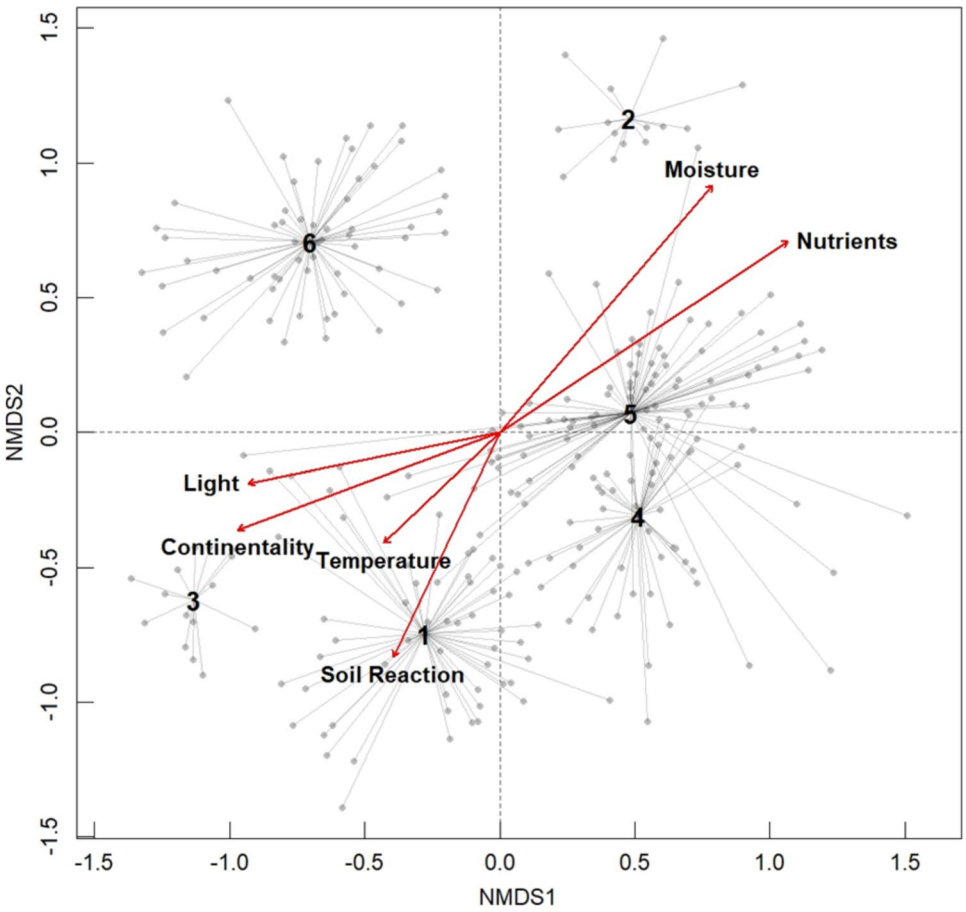

Fig. 3 NMDS ordination of the shrub communities from Slovenia: 1 – *Berberidion vulgaris*, 2 – *Sambuco-Salicion capreae*, 3 – *Irido illyricae-Cotinetosum coggygriae*, 4 – *Astrantio-Corylion avellanae*, 5 – *Prunion spinosae*, 6 – *Buddlejetum*. Stress value 0.2032278. Nomenclature and classification according to original authors of relevés

Robinietea Jurko ex Hadač et Sofron 1980

Chelidonio-Robinietalia pseudoacaciae Jurko ex Hadač et Sofron 1980

Aegopodio podagrariae-Sambucion nigrae Chytrý 2013

Buddlejetum davidii Schmitz 1991

tussilaginetosum subass. nova – cluster 2 on Figs. 1 and 2, with differential species *Tussilago farfara*, *Medicago lupulina* and *Populus tremula* (holotypus hoc loco relevé 11 in Online Resource 2)

Typus relevé (holotype) of the *Buddlejetum tussilaginetosum* subass. nova:

Slovenia, Tržiška Bistrica, 18. Oct. 2022, 40 m^2, 386 m asl, 0°, total cover: 85%, shrub layer: 85%, herb layer: 50%, moss layer: 10%, lat.: 46.280937, long.: 14.278441, authors: Azra Šabić, Jernej Jogan

E2: *Buddleja davidii* 5, *Alnus incana* 1, *Reynoutria japonica* 1, *Salix alba* 1, *Salix eleagnos* +, *Salix caprea* +, *Robinia pseudoacacia* +, *Populus nigra* +, *Rubus caesius* +, *Alnus glutinosa* +, *Physocarpus opulifolius* +

E1: *Tussilago farfara* 1, *Artemisia vulgaris* agg. 1, *Solidago canadensis* 1, *Buddleja davidii* +, *Salix eleagnos* +, *Erigeron annuus* +, *Galium mollugo* agg. +, *Agrostis stolonifera* agg. +, *Trifolium pratense* +, *Mentha longifolia* +, *Deschampsia cespitosa* +, *Vicia cracca* +, *Rubus caesius* +, *Daucus carota* +, *Achillea millefolium* agg. +, *Tanacetum vulgare* +, *Salvia glutinosa* +, *Angelica sylvestris* +, *Melilotus* sp. +, *Picea abies* +, *Equisetum telmateia* +, *Melampyrum nemorosum* +, *Mentha aquatica* +, *Ranunculus lanuginosus* +, *Symphytum officinale* +

typicum (*Buddlejetum* sensu stricto, in Schmitz, 1991).

buphthalmetosum subass. nova – cluster 4 on Figs. 1 and 2, with differential species *Buphthalmum salicifolium* and *Pinus sylvestris* (holotypus hoc loco relevé 58 in Online Resource 2)

Typus relevé (holotype) of the *Buddlejetum buphthalmetosum* subass. nova:

Slovenia, Log pri Sevnici, 20. Jun. 2023, 50 m^2, 203 asl, 40°, SW, total cover: 50%, shrub cover: 50%, herb cover: 10%, lat.: 46.998624, long.: 15.318829, authors: Azra Šabić, Jernej Jogan

E3: *Ostrya carpinifolia* +

E2: *Buddleja davidii* 3, *Pinus sylvestris* 2, *Salix eleagnos* 1, *Populus nigra* +

E1: *Salix eleagnos* +, *Lotus corniculatus* +, *Buphthalmum salicifolium* +, *Pinus sylvestris* +, *Hieracium porrifolium* +, *Genista tinctoria* +

Plant communities with *Buddleja davidii* in Europe

In total, 1083 plant taxa were included in the European dataset with communities with *B. davidii*. Classification analysis showed a distinction into seven clusters (Online Resource 3), presented in the NMDS analysis (Fig. 4). Clusters 1 and 3 (Fig. 4) are positioned in the central part of the ordination diagram and include communities of typical *Buddlejetum* community (cluster 1) and various types of shrub and forest communities with *B. davidii* (cluster 3). On the left side of the ordination diagram, along the moisture gradient, clusters 2 and 4 are separated along the moisture diagram and represent the most hygrophilous variations of *B. davidii* communities, which differ in their nutrient status. Clusters 5, 6 and 7 are positioned on the right part of the ordination diagram, where clusters 5 and 6 are positioned along the light and temperature diagram and represent the most heliophytic and thermophilic variations of *B. davidii*-dominated communities. Ecologically most distinct are communities from cluster 7. The synoptic table (Online Resource 4) presents the European dataset and shows data on species' percentage frequency and fidelity values.

Cluster 1 (Fig. 4) consists of 49 relevés, which resemble the typical *Buddlejetum* community (Schmitz 1991) and lack other diagnostic species with high fidelity values, apart from *Ostrya carpinifolia*.

Cluster 2 comprises 90 relevés of degraded hygrophilic communities, which can be classified into two vegetation classes. The first one is *Salicetea purpureae* (order *Salicetalia purpureae*), and the second one is *Alno glutinosae-Populetea albae* (order *Alno-Fraxinetalia excelsioris*). Diagnostic species are *Alnus incana*, *Salix eleagnos*, *Tussilago farfara*, *Galium album* and *Salix myrsinifolia*.

Cluster 3 comprises 120 relevés of mesophilic and hygrophilous shrub and forest communities (*Crataego-Prunetea*, *Carpino-Fagetea sylvaticae*, *Alnetea glutinosae*). Diagnostic species are *Alnus glutinosa*, *Hedera helix*, *Rubus caesius* and *Galium aparine*.

Clusters 4, 5, and 6 are positioned on the left side of the ordination diagram (Fig. 4) and include communities found on open, warm, and nutrient-rich sites.

Cluster 4 comprises 18 pioneer and highly anthropogenised relevés, floristically distinct from other clusters due to its high richness in annual therophytes and ruderals. These are species diagnostic of various syntaxa of anthropogenic vegetation, predominantly *Bidentetea* (*Persicaria lapathifolia*, *Solanum lycopersicum* and *Persicaria maculosa*) and *Artemisietea* (*Saponaria officinalis* and *Artemisia vulgaris*).

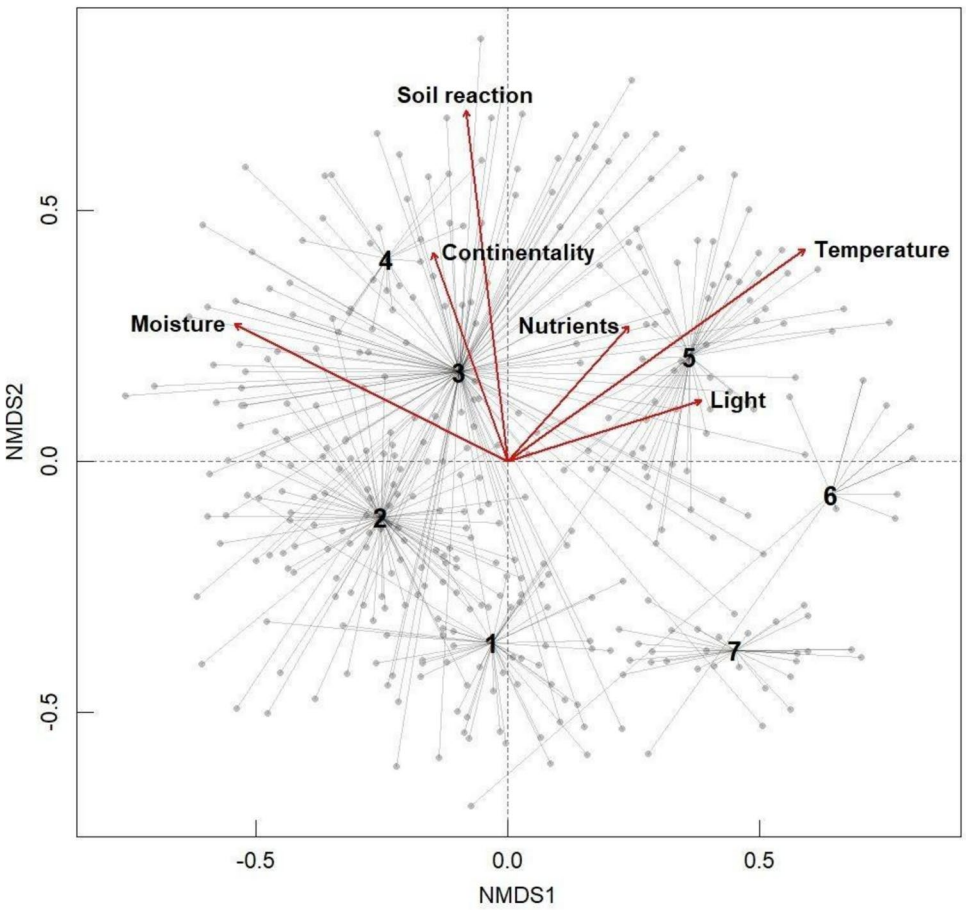

Fig. 4 NMDS ordination of relevés with *Buddleja davidii* from Europe. Eigenvalues of first two axes: 0.3824 and 0.3030. 1 – *Buddlejetum*, 2 – degraded riparian communities of classes *Salicetea purpureae* and *Alno glutinosae-Populetea albae*, 3 – shrub and forest communities of classes *Crataego-Prunetea*, *Carpino-Fagetea* and *Alnetea glutinosae*, 4 – ruderal communities rich in therophytes, 5 – Cantabrian ruderalized communities, 6 – communities on urban crevices and walls of class *Cymbalario-Parietarietea diffusae*, 7 – acidophilic Atlantic forests of alliance *Dicrano-Pinion sylvestris*

This cluster also includes relevés from Slovenian cluster 5 (Figs. 1 and 2).

European cluster 5 comprises 51 relevés from Southern Europe (Cantabrian coast) and represents the most thermophilic type of *B. davidii* communities in Europe. Diagnostic species are *Cortaderia selloana*, *Lotus rectus*, *Rubus ulmifolius*, *Salix cinerea* s.l. and *Dittrichia viscosa*.

Cluster 6 includes 14 relevés on urban wall crevices with elements of chasmophytic vegetation of the class *Cymbalario-Parietarietea diffusae*. Diagnostic species are herbaceous plants *Trachelium caeruleum, Parietaria judaica* and *Cymbalaria muralis* and fern *Adiantum capillus-veneris*.

Cluster 7 is segregated on the right side of the ordination diagram and is floristically and ecologically the most distinct from the other clusters. It comprises 29 relevés of acidophilic forest communities from the Atlantic biogeographical region (*Dicrano-Pinion sylvestris*), probably planted, with diagnostic species including *Agrostis capillaris*, *Betula pendula*, *Pinus sylvestris* and *Molinia caerulea*.

The geographical distribution of communities with *B. davidii* in Europe (Fig. 5) shows no clear pattern, except for communities from cluster 5, which are distributed in the Cantabrian Mixed Forests ecoregion, and communities from cluster 7, which are found in western Europe (Atlantic biogeographical region). The most common and widespread are communities from cluster 3, mesophilic shrub and forest communities with *B. davidii*, found across the continent.

Results show statistically significant differences in values of the Shannon–Wiener index ($df = 6$, $H = 157.5$, $p < 0.001$) and evenness ($df = 6$, $H = 113.7$, $p < 0.001$) between European clusters of communities with *B. davidii* (Fig. 6). Cluster 4 had the highest value of the Shannon–Wiener diversity index (3.75 ± 0.45), while cluster 6 had the lowest (1.38 ± 0.6). Values of Shannon–Wiener diversity index decreased significantly with the increasing cover of *B. davidii* in clusters 2 ($r = -0.23$, $r^2 = 0.05$, $p < 0.05$) and 6 ($r = -0.65$, $r^2 = 0.43$, $p < 0.05$). Similar trend was observed for evenness in clusters 1 ($r = -0.71$, $r^2 = 0.5$, $p < 0.001$), 2 ($r = -0.49$, $r^2 = 0.24$, $p < 0.001$) and 6 ($r = -0.73$, $r^2 = 0.53$, $p < 0.001$).

We confirmed differences among European clusters with *B. davidii* in their disturbance severity ($df = 6$, $H = 47.59$,

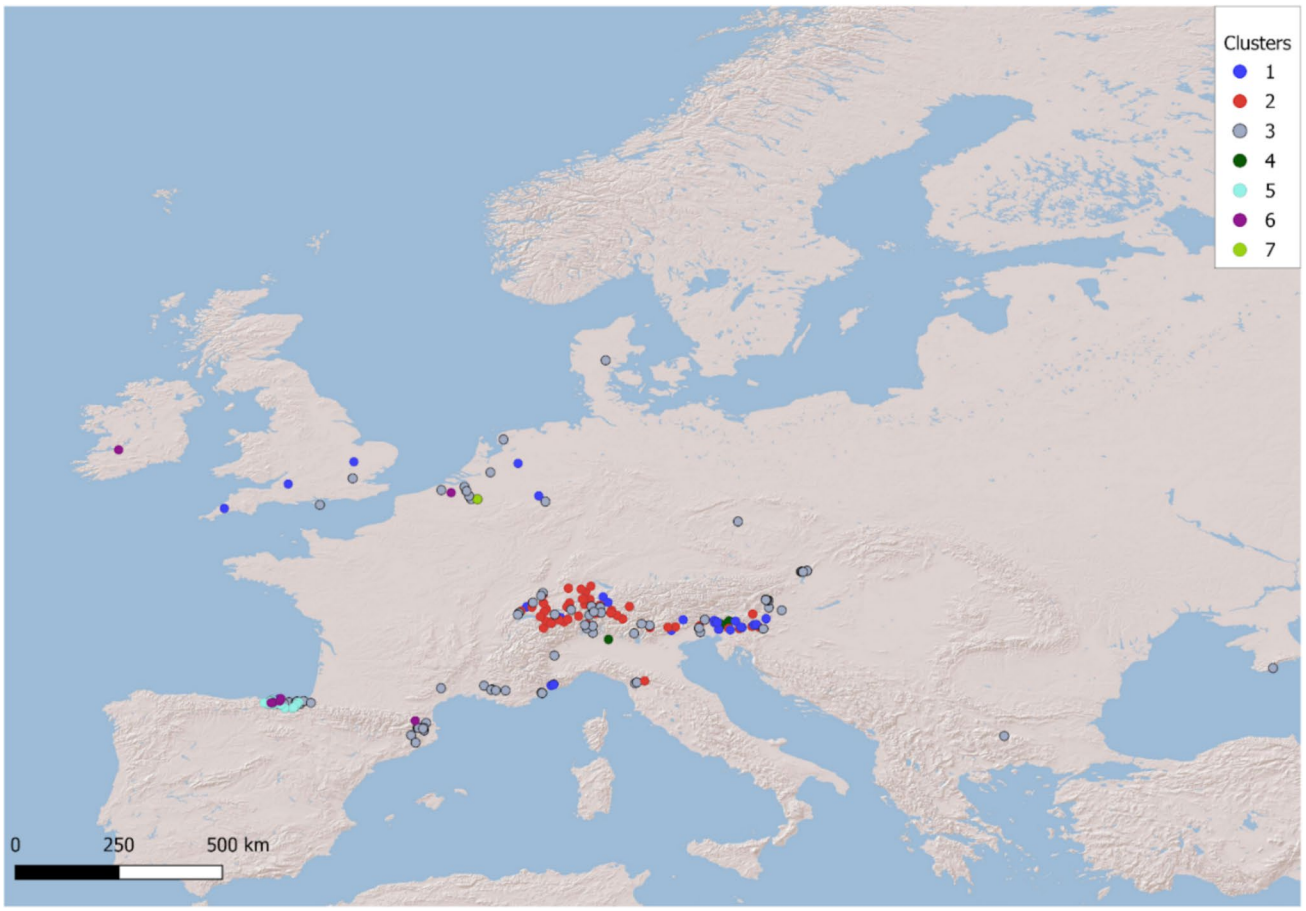

Fig. 5 Geographical distribution of European communities with *Buddleja davidii*. Map background: ESRI World Shaded Relief (2025). Clusters numbering and description corresponds to Fig. 4

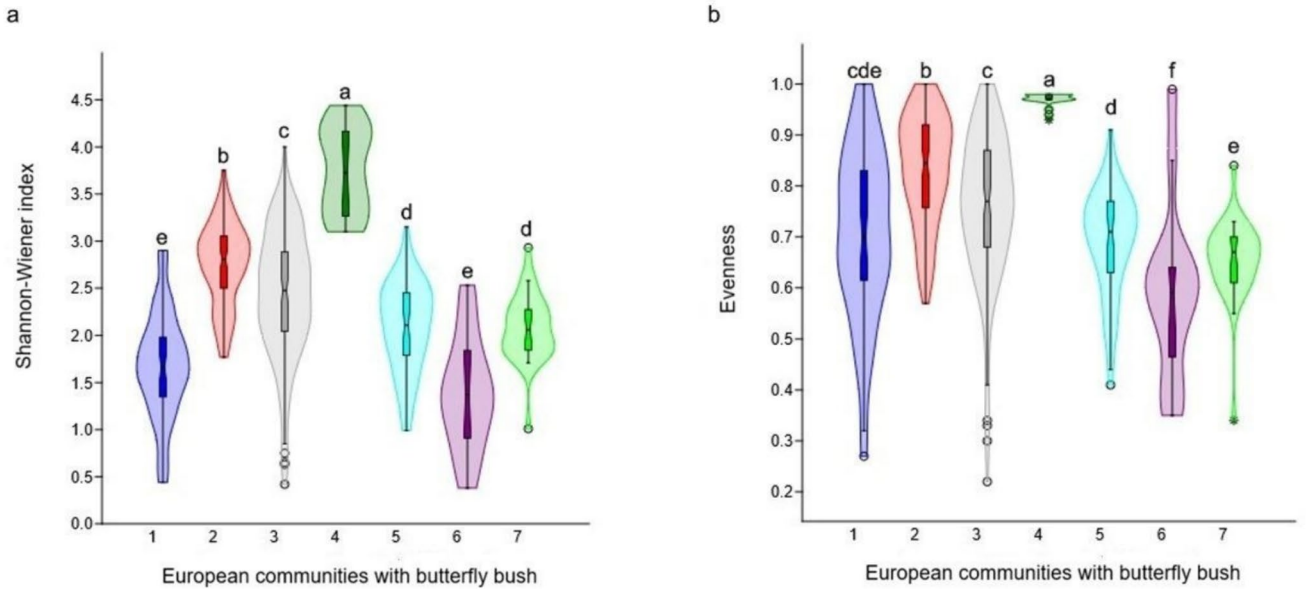

Fig. 6 Violin graphs with boxplots with values of Shannon–Wiener's diversity index (marked with letter **a** on the left) and evenness (marked with letter **b** on the right) in European communities with *Buddleja davidii*. Clusters numbering and description corresponds to Fig. 4. Different lowercase letters denote statistically significant differences between clusters ($p < 0.05$)

$p < 0.001$) and disturbance frequency (df = 6, H = 59.19, $p < 0.001$) (Fig. 7). The highest values for both disturbance parameters were observed in cluster 4 (0.65 ± 0.03 for disturbance severity and 1.03 ± 0.19 for disturbance frequency). The lowest value for disturbance severity was observed in cluster 7 (0.59 ± 0.02), and for disturbance frequency in cluster 1 (0.59 ± 0.25). Disturbance severity increased statistically significantly with the increasing cover of *B. davidii* in cluster 2 ($r = 0.37$, $r^2 = 0.13$, $p < 0.001$).

European communities with *B. davidii* differ significantly in their composition of life strategies (PERMANOVA, df = 6, $R^2 = 0.19512$, F = 14.707, $p < 0.001$). They primarily

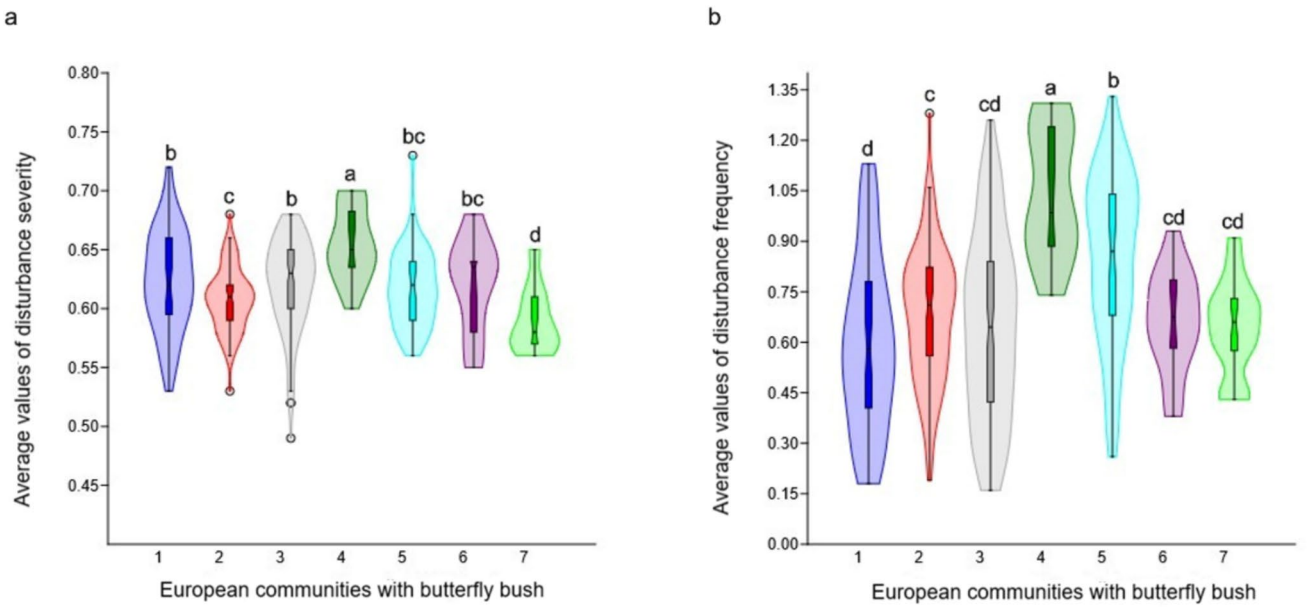

Fig. 7 Violin graphs with boxplots with values of disturbance severity (marked with letter **a** on the left) and frequency values (marked with letter **b** on the right) in European communities with *B. davidii*. Clusters numbering and description corresponds to Fig. 4. Different lowercase letters denote statistically significant differences between clusters ($p < 0.05$)

consist of species with competitive life strategies, which dominate in all clusters (average values 55–77%). The lowest percentage of competitors was observed in cluster 4, which has a higher average proportion of ruderals at 33% (Fig. 8). Stress tolerators are the least abundant life strategy, with average proportions of 9–16%. The proportion of competitors increased statistically significantly with the increasing cover of *B. davidii* in cluster 1 ($r = 0.05$, $r^2 = 0.09$, $p < 0.05$).

Additionally, European communities with *B. davidii* differ significantly in the proportions of life forms (PERMANOVA, df = 6, $R^2 = 0.14801$, F = 10.539, $p < 0.001$). All seven clusters are dominated by hemicryptophytes (46–62%), followed by phanerophytes (9–39%), whereas cluster 4 also has a considerable proportion of therophytes (31.74%). Hydrophytes were the least common life form, occurring only in clusters 3 and 4. The proportion of phanerophytes increased statistically significantly with the increasing cover of *B. davidii* s in cluster 3 ($r = 0.19$, $r^2 = 0.03$, $p < 0.05$).

European communities with *B. davidii* differ significantly in the proportions of percentages of neophytes' cover (df = 6, H = 84.56, $p < 0.001$) and number (df = 6, H = 77.76, $p < 0.001$; Fig. 9). Highest values of both parameters were observed in Cluster 6 – on average, neophytes made up 26.36% of species in those sites (± 14.79), with average cover 31.10% (± 27.48). Lowest proportion and cover of neophytes were observed in Cluster 2, where neophytes made 5.36% of all species (± 5.19), with average cover 4.64% (± 8.26). Increasing cover of *B. davidii* is significantly negatively correlated to percentage cover of other neophytes in clusters 5 ($r = –0,44$, $r^2 = 0,20$, $p < 0.001$) and 7 ($r = –0,39$, $r^2 = 0,15$, $p < 0.05$) whereas there was no correlation with percentage number of neophytes.

Discussion

Our results show that European communities with *B. davidii* generally differ greatly in their ecology, taxonomic and functional diversity. This is particularly evident in communities of the *Buddlejetum* association, which corresponds to its primary description as a plant community with very

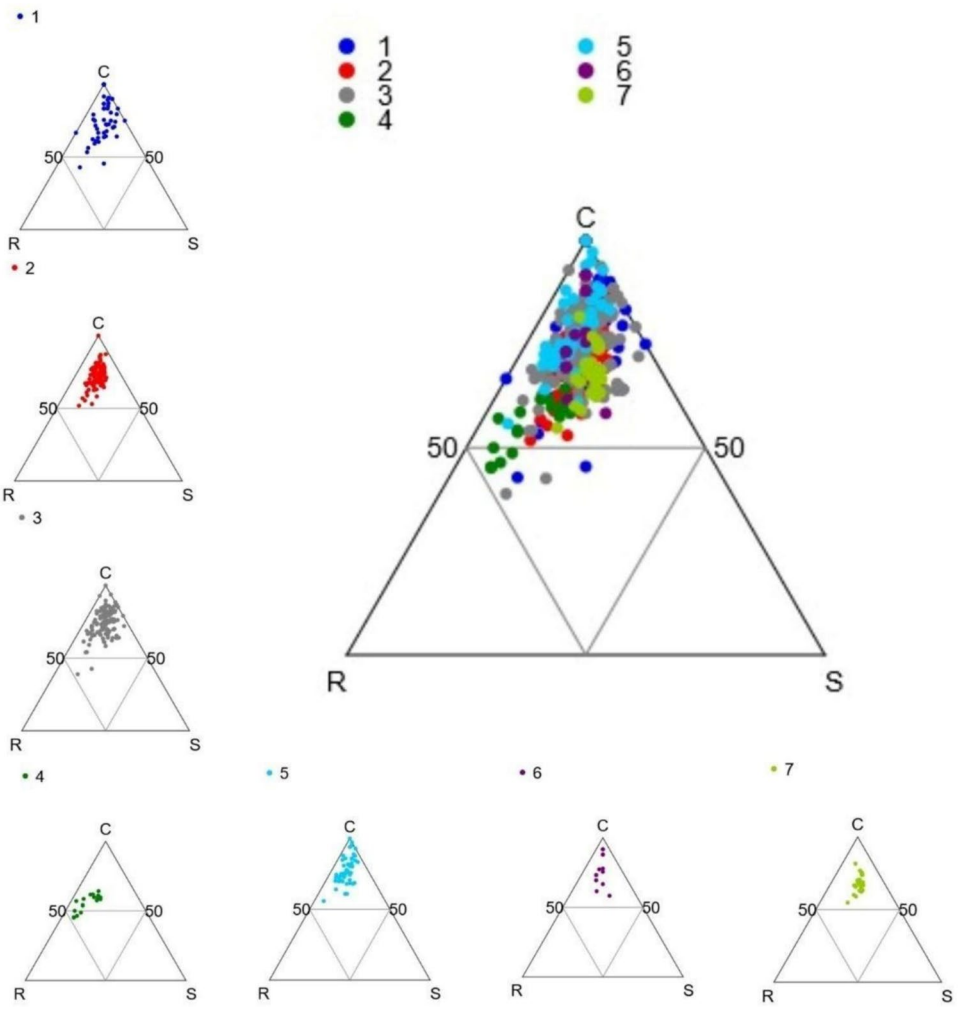

Fig. 8 Ternary plots of CSR strategies in European communities with *B. davidii*. C – competitors, S – stress tolerators, R – ruderals. Clusters numbering and description corresponds to Fig. 4

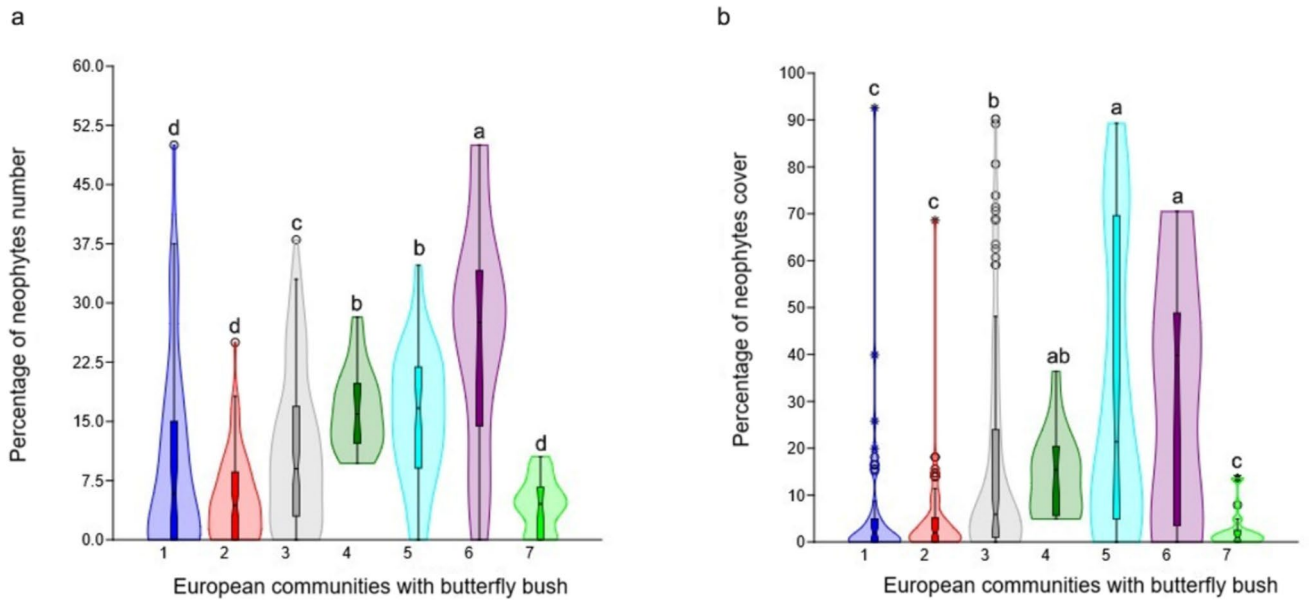

Fig. 9 Violin graphs with boxplots of neophytes' proportion number (**a**) and cover (**b**) in European communities with *B. davidii*. Clusters numbering and description corresponds to Fig. 4. Different lowercase letters denote statistically significant differences between clusters ($p < 0.05$)

few diagnostic species (Schmitz 1991). Classification and ordination analyses of the Slovenian subset (clusters 2–4 in Figs. 1 and 2) and the European dataset (cluster 1 in Fig. 4) confirm the primary ecological and phytosociological affiliation of *Buddlejetum* communities to the vegetation class *Robinietea* (Mucina et al. 2016). Although several authors (de Foucault and Wattez 2005; Fernez and Causse 2017; Giupponi et al. 2023) have previously suggested assigning *B. davidii*-dominated communities to the vegetation class *Crataego-Prunetea*, we found a clear distinction between the *Buddlejetum* association and other shrub communities from the class *Crataego-Prunetea*, which are generally less hygrophilous and nitrophilous than *Buddlejetum*. This is particularly evident in the results of the Slovenian shrub vegetation analysis (Fig. 3). *Buddlejetum* communities overall share the most similarities with communities from the alliance *Aegopodio-Sambucion nigrae* of the class *Robinietea*, which comprises shrub communities on nutrient-rich soils (Sádlo et al. 2013). *Buddlejetum* was originally classified into the *Sambuco-Salicion*, but it ecologically fits better into the *Aegopodio-Sambucion nigrae,* an alliance of mesophilous and xerophilous shrub vegetation with significant participation of nutrient-demanding and alien species, although diagnostic species proposed by Sádlo et al. (2013) are rare in our relevés.

Additionally, we found significant ecological variation within the *Buddlejetum* association in the analysis of Slovenian communities (Fig. 1). These are primarily reflected in occurrences in riparian communities and pioneer gravel communities in quarries, alongside the typical form; the latter is usually associated with heavily disturbed anthropogenic ecosystems. Consequently, we have proposed three subassociations of the *Buddlejetum* in Slovenia, reflecting these ecological differences: the hygrophilous subass. *tussilaginetosum* found in riparian sites, the subass. *typicum*, and the xerophilous subass. *buphthalmetosum* found in quarries. Apart from Slovenia (Jogan 2018), the establishment of *B. davidii* communities in quarries has previously been reported in Austria (Forstner 1984), Croatia (Boršić 2018), Italy (Gentili et al. 2011; Fanfarillo et al. 2024) and Belgium (Monty et al. 2019; Pitz et al. 2019), but no formal classification was carried out in these studies. In the European dataset, various subassociations of *Buddlejetum* were generally merged into cluster 1 (Fig. 4), which represented the *Buddlejetum* community sensu lato, the only syntaxon we defined at the association level.

On a larger scale, analysis of the European dataset has provided a more detailed insight into the ecological plasticity and adaptability of *B. davidii*. In addition to the *Buddlejetum* association (cluster 1 in Fig. 4), clusters 2 and 3 (Fig. 4) demonstrate the species' occurrence in other types of shrub communities (*Crataego-Prunetea*, *Salicetea purpureae*) and forest vegetation (*Alno glutinosae-Populetea albae*, *Carpino-Fagetea*). These communities usually represent various successional stages between shrub communities and pioneer forest communities, which complicates their definite syntaxonomic classification. This issue was first noted by Schmitz (1991) and Mucina (1993), who highlighted the species' occurrence in transitional communities of *Epilobietea* and pioneer forests with *Robinia*

pseudoacacia. The existence of similar transitional communities of mesophilic shrubs and forests (*Crataego-Prunetea*, *Carpino-Fagetea*) was later confirmed in France by de Foucault and Wattez (2005), Cavaillé et al (2013), Fernez and Causse (2017), in Italy by Giupponi et al. (2023) and Switzerland by Aranda et al. (2024), whereas species' occurrences in riparian communities (*Salicetea purpureae*, *Alno glutinosae-Populetea albae*) were studied in Italy by Picco et al. (2016), Fogliata et al. (2021) and Gasperini et al. (2020).

Despite the focus on occurrences of *B. davidii* in shrub or ruderal vegetation, the European dataset also shows that the species is not limited to a particular vegetation type, as it also occurs in other, more ecologically specialised habitats, such as wall crevices, and acidic forests of the alliance *Dicrano-Pinion* in the Atlantic region (clusters 6, and 7 in Fig. 4, respectively). While findings of *B. davidii* on wall crevices in Western Europe were previously reported by Roy et al. (1999), van Dort and van Landuyt (2004), and Francis and Hoggart (2012), we did not find scientific reports on occurrences in Atlantic acidic forest ecosystems, which confirms the underestimation and inadequate knowledge of the ecological niche of *B. davidii*. Interestingly, these ecologically specific occurrences of *B. davidii* are also the only ones that are biogeographically limited. In contrast, *Buddlejetum* communities, shrub, and forest vegetation co-dominated by *B. davidii* occur across the continent (Fig. 5), indicating that its ecological optimum is not geographically limited.

Ecological heterogeneity of *B. davidii* communities is also reflected in analyses of various parameters of their taxonomic and functional diversity. Overall, we found that most of the shrub and forest communities (*Buddlejetum*, *Alno glutinosae-Populetalia albae*, *Carpino-Fagetea*, *Dicrano-Pinion*; clusters 1–3 and 7 respectively in Figs. 6, 7, 8, and 9) have moderate species diversity, are disturbed to some extent, and are dominated by species with a competitive life strategy, which have been shown to be more successful invaders among non-native species (Guo et al. 2022), although our results have shown low presence of other non-native species apart from *B. davidii* in these communities (Fig. 9). However, competitors are usually found in low-disturbance habitats (Liu et al. 2025), which is not consistent with this study and probably indicates some degradation of these communities. Among shrub and forest communities, the lowest values of the Shannon–Wiener diversity index and evenness were observed in the typical *Buddlejetum* community (cluster 1 in Fig. 6). While this finding is consistent with the initial description, there was a notably lower proportion of species with a ruderal life strategy, even though the ruderality of *Buddlejetum* communities is emphasised (Schmitz 1991). Ruderality was pronounced in clusters 4 and 5 (ruderal communities rich in therophytes and Cantabrian ruderalised communities), which were also more diverse and disturbed, as previously noted in the literature (Liu et al. 2025).

When analysing the extent to which increasing cover of *B. davidii* explains variation in taxonomic and functional diversity parameters, we found that statistical relationships were generally inconsistent and relatively weak. The most significant negative relationship between the increasing cover of *B. davidii* and diversity parameters was found in European riparian shrub communities (cluster 2 in Fig. 4), where the increasing cover was negatively correlated with the Shannon–Wiener diversity index and species evenness, and positively correlated with disturbance severity. Additionally, cover of *B. davidii* is negatively correlated with the species diversity in *Buddlejetum* and communities on wall crevices (clusters 1 and 6 in Fig. 4, respectively). Overall, studies on the direct impact of *B. davidii* as an invasive species in ecosystems are scarce and generally do not confirm its competitiveness. According to Bellingham et al. (2005) and Peltzer et al. (2009), its competitiveness is generally limited to the early stages of succession on open riparian sites. Smale (1990) argues that the relatively short life cycle of *B. davidii* compared to trees limits its competitiveness in forest ecosystems. However, Gasperini et al. (2020) confirmed a negative impact of *B. davidii* on shrub and tree species abundance in communities of the alliances *Alnion incanae* and *Salicion eleagni*, while no negative impact was observed on graminoids. Our findings partially support these claims, as we statistically confirmed the negative relationship between species' increasing cover with the diversity parameters in open riparian communities. According to our results, the communities most resilient to *B. davidii* invasiveness are ruderal and herbaceous communities, including Cantabrian communities (clusters 4 and 5 in Fig. 4, respectively), where we did not confirm any relationship between cover of *B. davidii* and the observed diversity parameters. Both clusters are rich in ruderal therophytes and graminoid species, but *B. davidii* here generally occurs only transiently. Conversely, competitiveness is highly pronounced in communities where the species has a diagnostic role and fulfils its ecological optimum. However, most of these communities are already degraded and ruderalised, so accurately assessing the impact of *B. davidii* occurrence and cover in them would require more thorough observation studies, considering multiple aspects of ecosystem ecology.

Conclusions

Our results confirmed the ecological plasticity and adaptability of *B. davidii*, which occurs in various ecologically distinct plant communities and co-exists with species of different functional ecologies. The ecological optimum of *B. davidii* is found in ruderalised communities and shrubs

of the alliance *Aegopodio-Sambucion nigrae*, followed by riparian communities with regular disturbances. Although often characterised as an urbanophilous and hemerobic species, we found that it also occurs successfully in non-urban and non-hemerobic communities, such as acidic forests, although rarely. Despite occurrences in various plant communities, species' invasiveness is relatively low and limited to mesic and riparian shrub communities, *Buddlejetum* communities and wall crevices, in which *B. davidii* shows the highest competitiveness. However, since shrub communities represent the most common form of the *B. davidii* community in Europe, despite ecological limitations, species' invasiveness is therefore not local.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11756-026-02260-y.

Acknowledgements We are grateful to all data contributors. A.Š. acknowledges the Crop Science Department at the Agricultural Institute of Slovenia for the general support during the doctoral studies. We are thankful to the editor and the reviewer for their constructive feedback and commentary.

Author contributions A.Š., J.J. and U.Š. conceptualized the study and performed the field work for original studies. A.Š. and U.Š. carried out the statistical analysis, J.A.C. and W.W. contributed significantly to the European dataset. A.Š. and U.Š. wrote the first draft, which was substantially improved by J.J., J.A.C. and W.W. All authors agreed on the submitted version.

Funding The doctoral study by A.Š. was co-financed by the Ministry of Higher Education, Science and Innovation of Slovenia. A.Š. was also supported by the Agricultural Institute of Slovenia. J.J. was supported by the Slovenian Research and Innovation Agency (ARIS) through grant P1-0212, whereas U.Š. was supported by the Slovenian Research and Innovation Agency grant P1-0236. J.A.C. was supported by the Basque Government through grant IT1487-22.

Data availability Analytical table of Slovenian communities, classification of European communities and synoptic table of European communities with *Buddleja davidii* are available as Supplementary Information on journal's website, as **Online Resources 2, 3** and **4** respectively. List of national bases, used for creation of European dataset is available as **Online Resource 1**.

Declarations

Competing interests The authors declare no competing interests.

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