RESEARCH ARTICLE

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Spontaneous urban vegetation as an indicator of soil functionality and ecosystem services

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Abstract

Questions: Our study focused on spontaneous vegetation in urban greenspaces in a Mediterranean city with the aim of relating plant community properties with ecological services along soil disturbance gradients. We asked which plant communities have the greatest plant biodiversity and soil carbon storage and the best-performing nutrient cycles and water regulation.

Location: Madrid City (Central Spain).

Methods: We studied four types of plant communities following soil disturbance gradients: vegetation on trampled soils, roadside vegetation, annual grasslands and perennial forbs. Regarding vegetation, we studied plant composition and productivity, plant diversity, plant growth forms and functional groups. Regarding soils, we determined soil organic carbon (TOC), available nutrients, the activity of seven enzymes relating to the main macronutrient cycles, and physical properties such as bulk density (BD) and soil water-holding capacity (WHC). We used one-way ANOVA to determine the influence of the plant community type on both soil and vegetation variables. Canonical correspondence analysis was performed to interpret the relationships between plant species assemblages with environmental gradients.

Results: Perennial forbs showed greater biomass and developed on soils with the greatest TOC and available phosphorus. Annual grasslands displayed the highest plant diversity. Roadside vegetation developed on soils with higher phenoloxidase activity when compared to vegetation on trampled soils and annual grasslands. Vegetation on trampled soils developed on soils with lower WHC, lower beta-glucosidase, arylamidase and phosphatase activities and higher BD when compared to perennial forbs. Plant community distribution followed gradients most significantly associated with soil organic matter content, soil compaction and nutrient cycling performance.

Conclusions: We conclude that plant communities are good indicators of ecosystem function and services which are unevenly distributed throughout urban habitats. The management in Mediterranean unmaintained urban greenspaces should be aimed at avoiding soil compaction to promote biodiversity, carbon storage and water regulation.

1 | INTRODUCTION

More than 50% of the world's population currently lives in urban areas, defined as areas with a population of 10,000 residents or more, and this is projected to reach almost 70% by 2050 (United Nations, 2019). Urban ecosystems include cities and the surrounding socio-ecological systems where most people reside (Maes, 2016). Specifically in Europe, urban ecosystems have experienced a 7.1% increase in extent between 2000 and 2018 (Petersen et al., 2022).

Urban greenspaces including parks, gardens, vacant lots and wastelands are habitats for numerous wild species and thus a major source of biodiversity within cities (Dana et al., 2002; Meffert, 2017; Twerd & Banaszak-Cibicka, 2019; Zara et al., 2021), providing important social and ecological benefits (Kim, 2016). In addition to maintaining biodiversity, greenspaces deliver other important ecosystem services such as carbon sequestration, nutrient cycles, water regulation, pest control and pollination. However, our knowledge of ecosystem biodiversity and its benefits in terms of ecosystem services in urban environments is extremely poor for Mediterranean cities (Capotorti et al., 2013), where the impact of climate change is expected to be high (IPCC, 2014), and where their capacity to adapt may be crucial (Faeth, 2011; Solecki & Marcotullio, 2013).

Biodiversity and ecosystem functioning are linked (Gonzalez et al., 2020), as has been shown for natural and urban systems (Schittko et al., 2022). Thus, ecosystem service provisioning and the capacity to promote citizens' health and well-being depend on urban biodiversity. Given the strong human influence in urban greenspaces, understanding the natural and the human-controlled processes that alter urban biodiversity is essential for its conservation and associated service provisioning (Dearborn & Kark, 2010). One central element of urban greenspaces, their diversity and functioning, is the soil (Schittko et al., 2022), which, however, has only started to be the focus of research studies recently (Delgado-Baquerizo et al., 2021). Thus, beside drivers of urban plant biodiversity, we also need to understand more about the drivers of urban soil properties and functioning.

Urban soils comprise a set of different soil types where human influence is the keystone of their genesis (Leguédois et al., 2016). They show anthropogenic diagnostic horizons in addition to other artefacts, and most can be classified as Anthrosols or Technosols (FAO, 2015). It is worth noting that certain soil features such as soil organic carbon have been found in quantities comparable to those in soils in natural and agricultural areas (Vasenev et al., 2013), although the presence of severe disturbance and/or potential toxic elements clearly influences the biological activity in urban soils (Piotrowska-Długosz & Charzyński, 2015; Zamulina et al., 2021). These disturbances can cause a decoupling of biogeochemical cycles with important implications for the functionality of ecosystems, as has been observed for N deposition (Ochoa-Hueso, 2016) and for the increase in atmospheric CO_2 (Ochoa-Hueso et al., 2019). The interaction between soils and plants is relevant since plant communities influence the functioning of the soil, through the biogeochemical cycles (Freschet et al., 2018).

Urban soils and plants are a primary contributor to essential ecosystem services such as biodiversity maintenance, air quality, flood mitigation, climate regulation and food production (Blanchart et al., 2018). However, the functionality and ecosystem services of the soil–spontaneous vegetation tandem is largely unknown in Mediterranean cities where soil disturbance likely plays an important role. Our working hypothesis is that the composition and functionality of Mediterranean urban spontaneous habitats are closely related to soil disturbance, and in turn to the ecosystem services they provide. To test our hypothesis, we selected four urban habitats following soil disturbance gradients. The specific objectives of our study were to compare common urban plant communities, taken here as descriptors of urban habitats, along environmental gradients of soil compaction and nutrient availability to identify which habitats provide the best ecosystem functions in terms of greater plant biodiversity and productivity, soil carbon storage and water regulation, as well as better soil performance of nutrient cycles. The identification of the soil and vegetation dynamics should guide the management of unmaintained urban green areas. To the best of our knowledge, our work is the first study of the biodiversity and functionality of various plant communities in green urban areas in a Mediterranean city.

2 | METHODOLOGY

2.1 | Sampling design

Our project was conducted in the Ciudad Universitaria—Moncloa Campus (http://www.campusmoncloa.es/en/campus-moncloa/welcome.php) within the urban area of Madrid City (Central Spain). The climate in the area is Mediterranean. From 1988 to 2018, the local climate has had a mean precipitation of about 400 mm, and the annual mean temperature was about 13°C. Ciudad Universitaria is formed by a set of buildings with maintained and irrigated greenspaces, gardens, avenues, and somewhat managed or abandoned areas where spontaneous plant communities are widely developed. These latter, which are the focus of our study, consist of wooded areas which are mostly derived from pine plantations, although spontaneous ruderal vegetation is the main vegetation matrix in the cover. They undergo a moderate management consisting of periodic mowing of the wild herbaceous vegetation and subsequent plowing to avoid fire risk in the summer, but no irrigation is applied.

2.2 | Vegetation survey

Using a stratified sampling procedure (Kent, 2012), three squares (1 m^2) were randomly established within the area occupied by four selected plant communities as descriptor of habitats along soil disturbance gradients, which have been recognized as the most widespread urban plant communities in the study area (Figure 1, Molina, 2022). They are the following: (1) open annual dwarf herb vegetation on trampled soils; (2) medium-sized annual forbs rich in Brassicaceae on roadside slopes; (3) annual grasslands rich in Poaceae and Asteraceae dominated by low-growing plants in open fields; (4) forb vegetation characterized by medium-sized perennial and annual plants (Table 1). These plant communities are hereinafter referred to as follows: (1) trampled soils;

(2) roadsides; (3) annual grasslands; (4) perennial forbs. We performed three replicates for each habitat, thus a total of 12 sites—hereafter plots—were studied. Soil sampling was performed in April 2021, simultaneously with vegetation sampling when all the plant communities were developed. The plant species were identified in each plot and their cover in percentage was visually estimated (Table 1). Nomenclature of plants follows Castroviejo (1986–2021). The number of individuals in each plot was counted. Above-ground biomass was collected in each plot. Fresh plant biomass was dried in an oven (85°C) until its mass was stable before determining the biomass for each plant species. All the above-mentioned measurements allowed us to determine vegetation attributes such as floristic composition, abundance and dominance, species density and alpha diversity (Simpson and Shannon
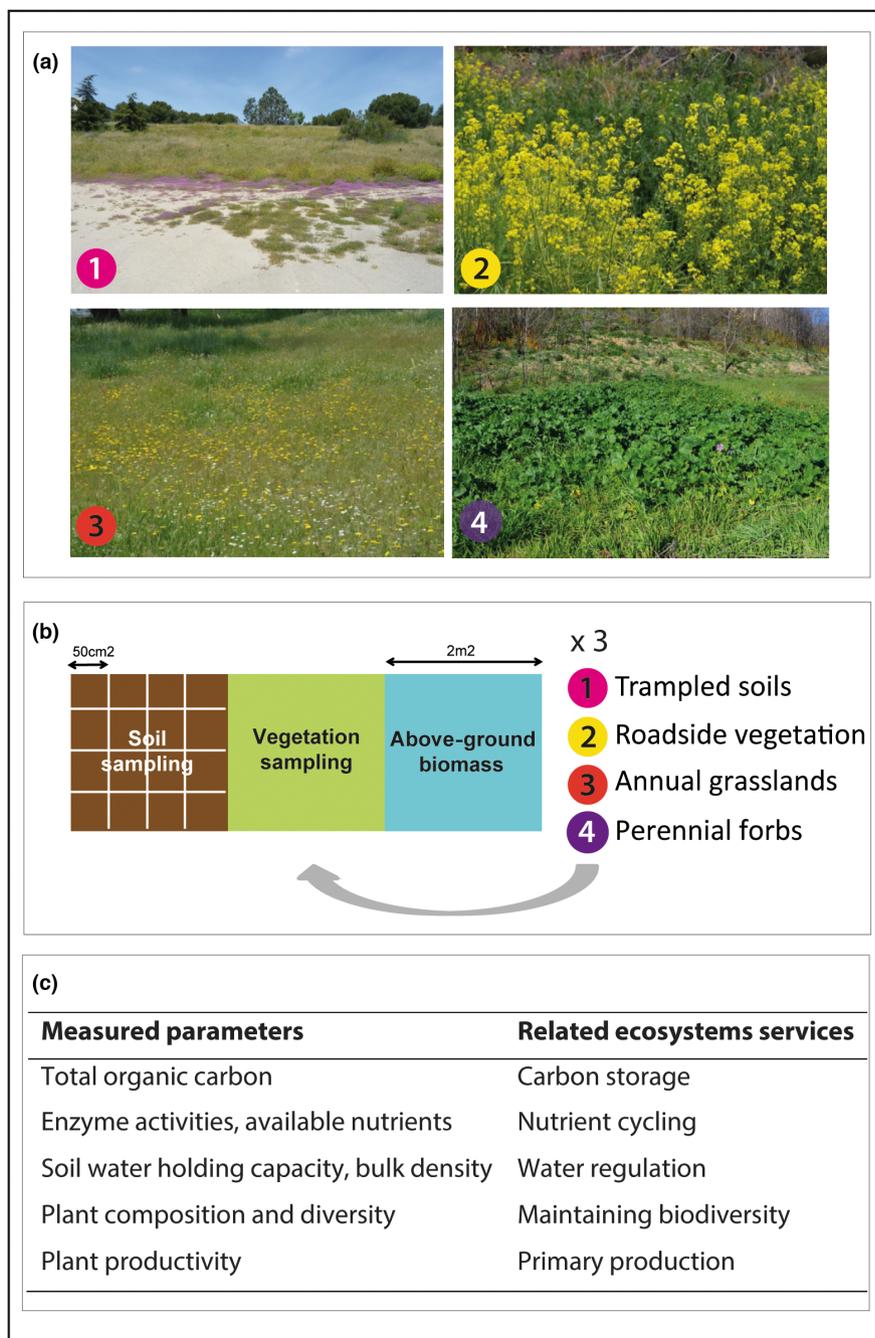
FIGURE 1 (a) Plant communities in the study; (b) experimental design; and (c) association between the measured parameters and their related ecosystem services.

TABLE 1 Synoptic table showing the average cover (%) and the frequency (superscript) of species in each of the four-study plant communities (columns).

	1	2	3	4
Plantago coronopus, T	22[3]			
Diplotaxis virgata, T	1[1]	20[2]		1[2]
Anthemis arvensis, T	2[1]		16[3]	1[1]
Malva sylvestris, H				48[3]
Crassula tillaea, T	1[2]			
Avena sterilis, T		6[3]		
Bromus scoparius, T			17[1]	
Erodium ciconium, T				20[1]
Piptatherum miliaceum, H				14[1]
Plantago lagopus, T	3[2]	14[1]	4[2]	2[1]
Thrincia hispida, T	2[3]	1[1]	20[2]	
Erodium cicutarium, T	2[1]	1[1]	2[1]	
Polycarpon tetraphyllum, T	1[1]	1[1]	1[1]	
Trisetaria panicea, T	1[1]		2[1]	1[1]
Bromus madritensis, T	1[1]		1[1]	1[1]
Hordeum murinum subsp. *leporinum*, T		4[2]	9[1]	17[3]
Bromus rubens, T		2[2]	14[2]	1[1]
Astragalus hamosus, T		8[2]	1[2]	1[1]
Anacyclus clavatus, T		4[2]	1[1]	1[2]
Calendula arvensis, T		1[1]	1[1]	1[1]
Trigonella monspeliaca, T	1[1]		2[1]	
Filago pyramidata, T	1[1]		1[2]	
Eryngium campestre, H	1[1]		1[1]	
Trifolium tomentosum, T	1[1]		1[1]	
Centaurea melitensis, T		11[2]	1[1]	
Medicago minima, T		1[1]	9[1]	
Avena barbata, T		1[1]	1[2]	
Echium plantagineum, T		1[1]	1[1]	
Hymenocarpos cornicina, T		1[1]	1[1]	
Medicago orbicularis, T		4[1]		1[1]
Sonchus tenerrimus, C		3[2]		2[3]
Geranium molle, T			3[2]	7[1]
Bromus hordeaceus, T			1[1]	1[1]
Taraxacum obovatum, H			1[1]	1[1]
Rostraria cristata, T	2[2]			
Spergularia purpurea, T	2[1]			
Capsella bursa-pastoris	1[1]			
Sedum caespitosum, T	1[1]			
Spergularia rubra, T	1[1]			
Herniaria cinerea, T	1[1]			
Poa annua, T	1[1]			
Medicago rigidula, T		4[2]		
Chondrilla juncea, H		2[1]		
Sedum album, C		2[1]		
Hedypnois cretica, T		2[1]		
Anthriscus caucalis, T		1[1]		
Asphodelus aestivus, T		1[1]		

TABLE 1 (Continued)

	1	2	3	4
Carduus pycnocephalus, T		1[1]		
Euphorbia peplus, T		1[1]		
Reseda phyteuma, T		1[1]		
Misopates orontium, T		1[1]		
Trifolium cherleri, T		1[1]		
Vulpia myuros, T			3[3]	
Hypochaeris glabra, T			2[2]	
Trifolium scabrum, T			2[1]	
Alyssum granatense, T			1[1]	
Astragalus pelecinus, T			1[1]	
Petrorhagia nanteuilii, T			1[1]	
Trifolium campestre, T			1[1]	
Valerianella locusta, T			1[1]	
Vulpia membranacea, T			1[1]	
Convolvulus arvensis, G				2[2]
Erodium moschatum, T				2[2]
Stellaria media, T				1[1]
Allium ampeloprasum, G				1[1]
Arenaria leptoclados, T				1[1]
Cichorium intybus, H				1[1]
Crepis capillaris, T				1[1]
Euphorbia helioscopia, T				1[1]
Cardaria draba, H				1[1]
Medicago sativa, H				1[1]

Notes: 1, Open annual dwarf herb vegetation on trampled soils; 2, annual forbs on roadsides; 3, annual grasslands; 4, perennial forbs. Abbreviations after the plant-species name as follows: C, chamaephytes; G, geophytes; H, hemicryptophytes; T, therophytes.

indexes). Each plant species was assigned to its corresponding growth form and its cover was determined. We identified the following four life-form categories according to Raunkier (1934): therophytes, hemicryptophytes, geophytes and chamaephytes. Based on plant physiological characteristics potentially linkable with biogeochemical cycles, we recognized the following six plant functional groups, and studied their abundance: sulfur accumulators, N-fixers, N-compounds-bearing plants, mucilage accumulators, terpenoid accumulators and silica accumulators. Similar plant functional groups have been successfully used to study Mediterranean grassland dynamics on abandoned lands (Quintana et al., 2021; Molina et al., 2023).

2.3 | Soil sampling and analysis

Soil samplings were taken using cores of 5 cm in diameter from the top 0–5 cm in each square to determine the soil water-holding capacity (WHC) and bulk density (BD). About 1000 g of soil samples were collected and stored in plastic bags to be taken to the laboratory to analyze the soil physical–chemical and biological variables. Fresh samples were sieved with a 2 mm sifter and subdivided into two subsamples, one of

which was air-dried for physical–chemical analyses, while the other was refrigerated at 4°C for later use, within one month, to determine enzyme activity and nutrient available content. The following soil chemical parameters were determined: total organic carbon (TOC) using the Walkley and Black (1934) wet oxidation procedure, available phosphorus (AP) using the Olsen and Sommers (1982) method, and available ammonium (NH4-N) obtained by extraction in 2 M KCl and later measured by UV–visible spectrophotometry following the Keeney and Nelson (1982) method. The biological characterization of soils was done by determining the enzyme activities related to the biogeochemical cycles of carbon, nitrogen, sulfur and phosphorus. They were the following: β-glucosidase (Beta-GLU), and phenoloxidase (PHE) for the C cycle; arylamidase (ARYL-N) and urease (URE) for the N cycle; phosphatase (PHO) for the P cycle; and arylsulfatase (ARYL-S) for the S cycle. Dehydrogenase (DH) activity was used as an index of microbial activity. All the activities were obtained following ISO 20130 methods (ISO, 2018), except PHE activity which was obtained following the DeForest (2009) method, and dehydrogenase (DH) which followed the Schaefer (1963) method. All activity measurements were determined in a UV–visible spectrophotometer with a TECAN NANOQUANT INFI-NITE M200 PRO multi-well plate reader. The samples for the enzyme activity were previously incubated in a MEMMERT IN 55 incubator. The physical properties for WHC and BD were determined using the Soil Survey Staff (2014) procedure.

2.4 | Statistical methods

A one-way ANOVA was carried out followed by a least significant difference (LSD) test to study the influence of the plant community type on soil variables and vegetation features. The soil variables were normalized by converting them to logarithms. All analyses were done using the SPSS-Statistical Package for the Social Sciences v.27 (SPSS, Inc.) software.

We used correspondence analysis to determine the relationships between plant community composition and their environment. As the detrended correspondence analysis showed that the plant species cover exhibited a unimodal response to the soil gradients, we performed canonical correspondence analysis (CCA) for the compositional analysis. We used a square-root transformation of the species cover and the downweighting of rare species. The variables with the most impact on communities were selected by means of permutation tests following a forward stepwise procedure. These analyses were done in CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA).

3 | RESULTS

3.1 | Primary production and maintaining biodiversity

The one-way ANOVA calculated for biomass showed that perennial forbs had a significantly higher productivity than the rest of the communities in the study, whereas the biomass of vegetation on trampled soils was significantly lower than that of roadsides and perennial forbs

(Figure 2a). Annual grasslands showed a significantly higher density than the rest of the communities (Figure 2b). Regarding functional traits, plants with mucilage (Malvaceae) had a significantly higher cover in perennial forbs (Figure 2c); and silica accumulator plants (Poaceae) had the highest cover in annual grasslands, with significant differences compared to their cover in vegetation on trampled soils (Figure 2d).

3.2 | Carbon storage, nutrient cycling and water regulation

Soils under perennial forbs had a significantly higher content of organic carbon (TOC) than in other plant communities (Figure 3a). The soil under perennial forbs had a significantly higher β-glucosidase (Beta-GLU) activity compared to trampled soils, with the other communities presenting intermediate values (Figure 3b). Phenoloxidase (PHE) activity, responsible for metabolizing recalcitrant organic matter, was significantly higher in roadsides than in trampled soils and annual grasslands, with perennial forbs showing intermediate values (Figure 3c).

Arylamidase (ARYL-N), a key enzyme in the N cycle, differentiated significantly perennial forbs with higher activity and trampled soils, with lower activity (Figure 3d). This pattern was very similar to that found for Beta-GLU activity. AP was significantly higher under perennial forbs than in other plant communities (Figure 3e). Phosphatase (PHO) showed a significantly higher activity under perennial forbs than in trampled soils and annual grasslands (Figure 3f).

Soil WHC had significant lower values in trampled soils when compared with roadsides and perennial forbs (Figure 3g). BD showed a significantly higher value on trampled soils than on roadsides and perennial forbs (Figure 3h). In addition, soils under annual grassland had significantly higher BD than under perennial forbs.

3.3 | Plant species assemblages and soil gradients

The representation of the first two axes of the CCA using floristic and soil variables showed two main gradients, in soil organic matter content and soil compaction (Figure 4). Perennial forbs, characterized by an abundance of *Malva sylvestris*, were related to soils with a higher amount of organic matter. Vegetation on trampled soils, characterized by higher abundances of *Plantago coronopus*, was related to more compacted soils. Annual grasslands, characterized by the abundance of *Anthemis arvensis*, *Trincia hispida* and *Bromus* species, were also related to compacted soils but to a lesser extent. Roadside vegetation was mainly characterized by *Diplotaxis virgata*, and mostly linked to soils with higher activity in ARYL-S.

4 | DISCUSSION

The distribution of biodiversity, species assemblages and amount of C storage in cities is highly dependent on the local spatial variation in
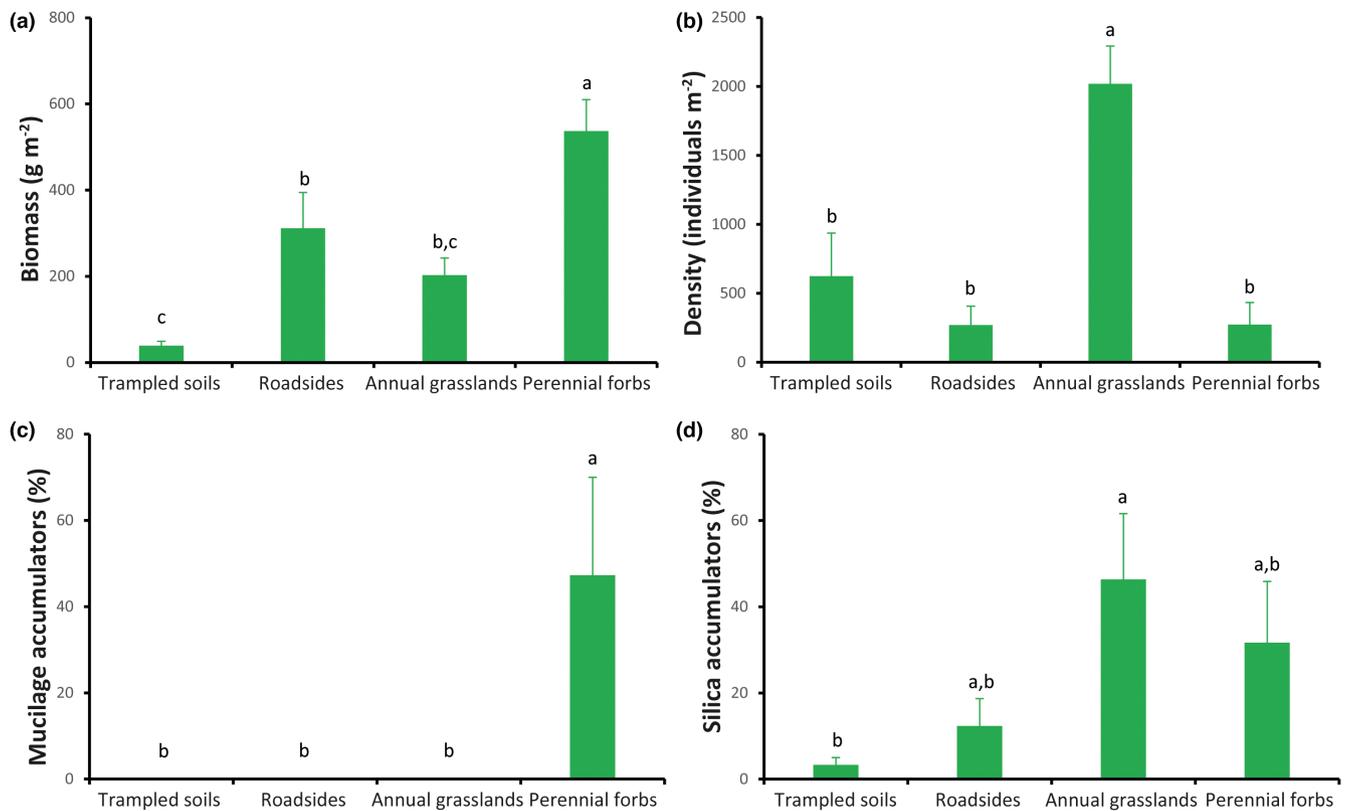
FIGURE 2 (a) Biomass; (b) density; (c) cover of mucilage accumulators; and (d) cover of silica accumulators in four habitats (trampled soils, roadsides, annual grasslands, perennial forbs). Letters indicate significant differences between habitats (one-way ANOVA with least significant difference [LSD] test, $p < 0.05$). Error bars represent standard error ($n = 3$).

factors such as soil parent material, land use and land cover (Lorenz & Lal, 2009; Norton et al., 2016). Our results highlighted that plant community distribution follows gradients of soil anthropogenic pressure, which can be most significantly associated with organic matter content, soil compaction and nutrient cycling performance.

Vegetation on trampled soils has been included in the *Polyono-Poetea* phytosociological class, characterized by therophytic communities of subcosmopolitan dwarf herbs (Rivas-Martínez, 1975). Recreational human trampling causes soil compaction, which decreases total porosity and vegetation cover and height (Sun & Liddle, 1993). In a comparison with the rest of the study habitats, our results showed that trampled soils provided reduced ecosystem services in water regulation, nutrient cycling, and carbon storage. It has been observed that vegetation dominated by hemicryptophytes and geophytes recovers from trampling more successfully than vegetation dominated by other life forms (Pescott & Stewart, 2014). However, in our study, vegetation on trampled soils was dominated by therophytes, and the closeness of the floristic and ecological relationships we found between annual grasslands and trampled soils (CCA) likely points to the possibility of one community transforming into another by promoting or preventing soil compaction.

Mediterranean ruderal annual grasslands are the most widespread vegetation in abandoned and moderately managed lands in the study area (Molina, 2022). This type of vegetation has been included in the *Hordeion murini* phytosociological alliance (Mucina et al., 2016) and

has been considered as subnitrophilous (Rivas-Martínez & Izco, 1977; Rivas-Martínez, 1978). Our results support this adscription of nutrient status, since annual grasslands grow on soils with moderate AP. Annual grasslands are rich in silica accumulator plants, which effectively alleviated both biotic (pathogens and pests) and abiotic (e.g., drought, heavy metals, nutrient imbalance) stresses (Pavlovic et al., 2021). This functional group has a major influence on soil processes by increasing the macro- (N, P, K) and micronutrient (Fe, Mn, Cu, Zn) absorption in plants (Luyckx et al., 2017). Our results showed that Mediterranean subnitrophilous annual grasslands play a significant role in maintaining diversity. This type of vegetation could therefore be considered as valuable from the standpoint of biodiversity conservation in Mediterranean urban ecosystems.

Mediterranean roadside vegetation consists of plants with short life cycles developing in early spring (Rivas-Martínez et al., 2002). As in the case of the preceding vegetation it is ascribed to the *Hordeion* alliance (Rivas-Martínez et al., 2001). Roadsides are largely characterized by sulfur accumulator plants (crucifers) related to soils with higher aryl-S activity, an enzyme that promotes the breakdown of sulfate esters. The relationship between crucifer abundance and soil sulfur availability in recently abandoned fields has been mentioned (Valverde-Asenjo et al., 2020). We found that roadside vegetation was subjected to a high abiotic stress since they developed on soils with a clear imbalance between a low TOC content and high activity of soil microbiota. Roadsides were also related to barely compacted
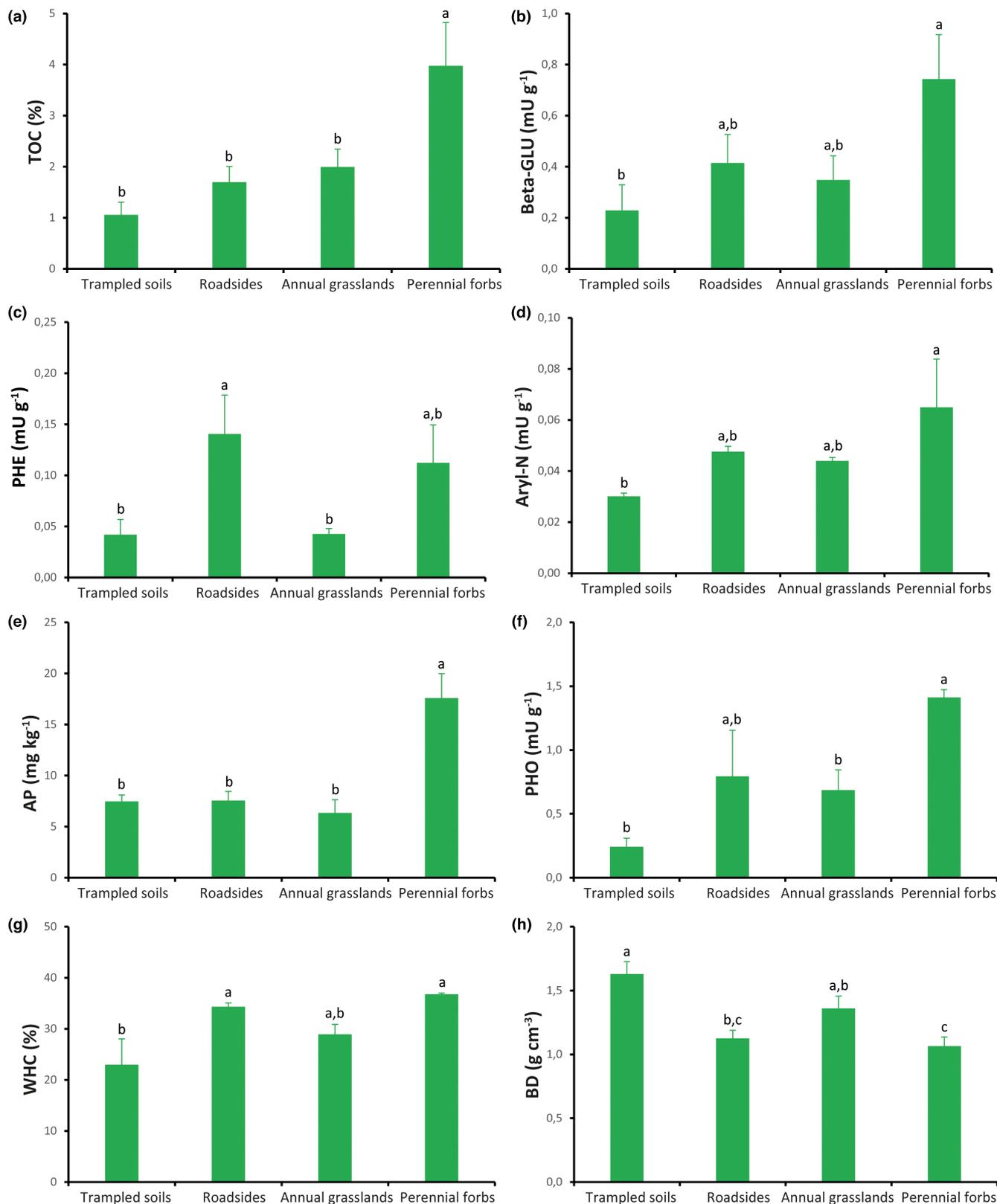
FIGURE 3 (a) Soil total organic carbon (TOC); (b) beta-glucosidase activity (Beta-GLU); (c) phenoloxidase activity (PHE); (d) arylamidase activity (Aryl-N); (e) available phosphorus (AP); (f) phosphatase activity (PHO); (g) soil water-holding capacity (WHC); and (h) bulk density (BD) in four habitats (trampled soils, roadsides, annual grasslands, perennial forbs). Latin letters indicate significant differences between habitats (one-way ANOVA with least significant difference [LSD] test, $p < 0.05$). Error bars represent standard error ($n = 3$).
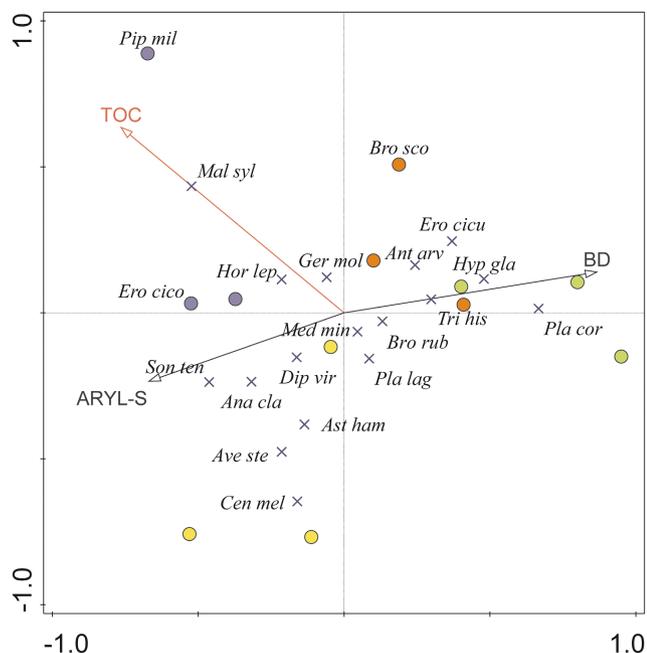
FIGURE 4 Canonical correspondence analysis ordination triplot for samples, response variables (species) and explanatory variables (soil features of the 0–5 cm horizon). The first two axes explain 13.86% and 24.83% of cumulative variance. Samples are indicated by colored dots as follows: green dots, vegetation on trampled soils; orange dots, roadside vegetation; yellow dots, annual grasses; purple dots, perennial forbs. Explanatory variables are abbreviated as follows: ARYL-S, arylsulfatase; BD, bulk density; TOC, total organic carbon. The soil variable in red is significant in the Monte Carlo test ($p < 0.05$). The diagram shows a maximum of 20 species with the largest weight response. Plant species are abbreviated as follows: Ana cla = *Anacyclus clavatus*; Ant arv = *Anthemis arvensis*; Ast ham = *Astragalus hamosus*; Ave ste = *Avena sterilis*; Bro rub = *Bromus rubens*; Bro sco = *Bromus scoparius*; Cen mel = *Centaurea melitensis*; Dip vir = *Diplotaxis virgata*; Ero cico = *Erodium ciconium*; Ero cicu = *Erodium cicutarium*; Hyp gla = *Hypochaeris glabra*; Ger mol = *Geranium molle*; Hor lep = *Hordeum murinum* subsp. *leporinum*; Mal syl = *Malva sylvestris*; Med min = *Medicago minima*; Pip mil = *Piptatherum miliaceum*; Pla cor = *Plantago coronopus*; Pla lag = *Plantago lagopus*; Son ten = *Sonchus tenerrimus*; Thr his = *Thrincia hispida*. Eigenvalues: axis 1 = 0.104, axis 2 = 0.046.

soils, which suggests that the main ecosystem function provided by this habitat may be therefore be related to water regulation.

Perennial forbs in our study corresponded to ruderal vegetation abundant in *Malva sylvestris*, a mucilage accumulator plant. Mucilage accumulation in plants increases their capacity to retain water in case of soil water deficits and aids the storage of food and water (Tosif et al., 2021). In soil, this functional group enhances soil microaggregate stabilization, water storage ability and the absorption of ions through root cells. Perennial forbs showed the highest primary production and developed on soils with a significantly higher TOC and AP, and a lower BD and a higher rate of most enzyme activities involved in macronutrient cycling. This vegetation is a priori valuable for its high functionality in terms of soil carbon storage, primary productivity, nutrient cycling

and water regulation. However, a nitrophilous vegetation dominated by perennial and herbaceous species is also related to highly disturbed habitats (Dana et al., 2002). According to our results, the high soil nutrient availability and enzyme activity under perennial forbs demonstrates that they are nutrient-demanding. The fast cycles of macronutrient functioning—likely due to the high demand for nutrients coupled with a low biodiversity—indicate an imbalance in the ecosystem services they provide, so this habitat should not be prioritized in the management of urban greenspaces. A study is currently under way to determine the dynamics of this vegetation when disturbance is avoided (https://tribuna.ucm.es/news/parcelas-permanentes-una-herramienta-idonea-para-la-gestion-de-la-biodiversidad).

5 | CONCLUSIONS

From the results of our study, we conclude that in Mediterranean cities, plant communities are good descriptors of urban habitats and indicators of ecosystem function and services. The degree of soil disturbance determines the plant communities and the ecosystem services they provide. The management of urban greenspaces maintaining the spontaneous vegetation should be based on avoiding soil compaction to obtain better ecological services such as conserving biodiversity, soil carbon storage, nutrient cycling and water regulation. In this regard, perennial forbs are related to higher soil carbon content but also to a fast and high demand for nutrients. In a vegetation type as dynamic as ruderal Mediterranean vegetation, the way in which these patterns change or are maintained over time remains to be studied.

AUTHOR CONTRIBUTIONS

José Antonio Molina and José Ramón Quintana conceived of the ideas, designed the analysis, collected and curated the data, performed the analysis, interpreted the results and led the writing of the manuscript. Juan Pedro Martín-Sanz performed the analysis of the networks. All authors contributed data and critically reviewed the manuscript drafts.

DATA AVAILABILITY STATEMENT

Data are available on request from the data custodians (jmabril@ucm.es; jrquinta@ucm.es).

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