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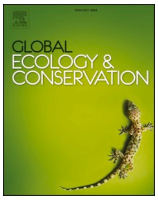

Original research article

Successional stages in Mediterranean grasslands differ in the quality of ecosystem services in urban greenspaces

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ABSTRACT

Urban habitats represent new opportunities to study natural processes such as ecological succession. Our work focused for the first time on the changes in ecosystem services occurring in the ecological succession from annual to perennial grasslands in Mediterranean peri-urban greenspaces. Student's t test was used to analyse the influence of the grassland type on plant and soil features, and showed that soil under perennial grassland had a significantly higher C content and arylamidase and arylsulfatase activity than annual grasslands. In contrast, annual grasslands showed a significantly higher plant-species richness, and their soils had higher bulk density and phenoloxidase and arylamidase activity compared to perennial grasslands. Neither the labile nor recalcitrant fractions of the organic matter showed any significant difference between communities. When all the soil factors were included together, Redundancy Analysis revealed a significant gradient in soil phenoloxidase activity and organic matter distinguishing perennial from annual grasslands. We conclude that when annual grasslands give way to perennial grasslands through natural succession in Mediterranean greenspaces, certain ecosystem services such as soil carbon storage and water regulation improve, while biodiversity maintenance declines. Thus, Mediterranean urban greenspaces where natural succession occurs should be handled in such a way as to preserve both type of habitats in order to improve a wider range of ecosystem services.

1. Introduction

The growing global trend towards urbanization in the coming decades, when a large majority of the world's population will be concentrated in cities (United Nations, 2019), increases the importance of having knowledge of urban ecosystem services (Cárdenas-Mamani and Perrotti, 2022) in order to explore the potential resilience and quality of life in cities (Gómez-Baggethun et al., 2013) and contribute to a more resource-efficient city structure and design (Bolund and Hunhammar, 1999). Urban ecosystems are considered in a good condition if they offer good living conditions for humans and urban biodiversity in terms of good air and water quality, a sustainable supply of ecosystem services and a high level of urban species diversity, among others (Maes et al., 2016, 2018). Within cities, urban greenspaces (UGs) are critical ecosystems for enhancing the quality of life in an urban environment by supporting

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biodiversity and supplying ecosystem services such as water and climate regulation (Carpenter et al., 2009; Vargas-Hernández et al., 2023; Valença Pinto et al., 2022). However, what primarily characterizes urban environments, including UGs, is their spatial heterogeneity in both biotic and abiotic components (Cadenasso et al., 2007; Cervelli et al., 2013; Greinert, 2015). The heterogeneity of habitats in UG spaces also implies spatial heterogeneity in their ecosystem services (Molina et al., 2023a, 2024; Paudel and States, 2023). Knowledge of this topic is a promising growth area, and is important for managing UGs towards greater sustainability.

UGs can contain remnants of forest and natural vegetation that provide important ecosystem services such as maintaining diversity (Yang et al., 2021) and carbon storage (Yesilonis and Pouyat, 2012). UGs also host ruderal habitats formed by spontaneous vegetation (Molina et al., 2023a) containing pioneer or opportunistic species that are closely related with frequent disturbance (Loidi, 2017). Additionally, ruderal vegetation is dynamic in that it constitutes a rapid and local response to disturbances but also follows natural ecological succession (Rivas-Martínez, 1978), a process which is important in urban landscapes in contrast to the adjacent rural landscapes (Zipperer, 2011). Little is known about this type of process in urban habitats, but their understanding will shed light on the measures to be applied in managing the transition to green cities.

Mediterranean urban ruderal vegetation (UV) includes a plethora of plant communities that are spatially distributed along soil disturbance gradients due to anthropogenic pressures, and whose ecosystem benefits are only beginning to be known. Ruderal vegetation in Mediterranean cities comprises mainly herbaceous annual or perennial vegetation (Dana et al., 2002; Molina, 2022) in which graminoid communities are an important component (Rivas-Martínez, 1978). Our work focused on two types of ruderal grasslands that are common in Mediterranean urban greenspaces, namely annual Mediterranean grasslands of *Hordeum murinum* and *Bromus* sp. pl., hereafter annual grasslands, and perennial grasslands with *Dactylis glomerata*, hereafter perennial grasslands. Based on field observations, perennial grasslands replace annual grasslands in the natural ecological succession (Fig. 1), although it is not yet known how this process changes the ecosystem services of urban grasses. We hypothesize that ecological services such as the maintenance of plant biodiversity, soil water regulation and soil C storage will increase as the succession proceeds from annual to perennial grasslands. Our specific objective was to compare plant diversity, soil physical-chemical features and soil enzyme activities between these two types of habitats. Determining the ecosystem conditions and their associated ecosystem services at different successional stages will make it possible to distinguish which stage has a better quality and should be promoted in urban greenspace management.

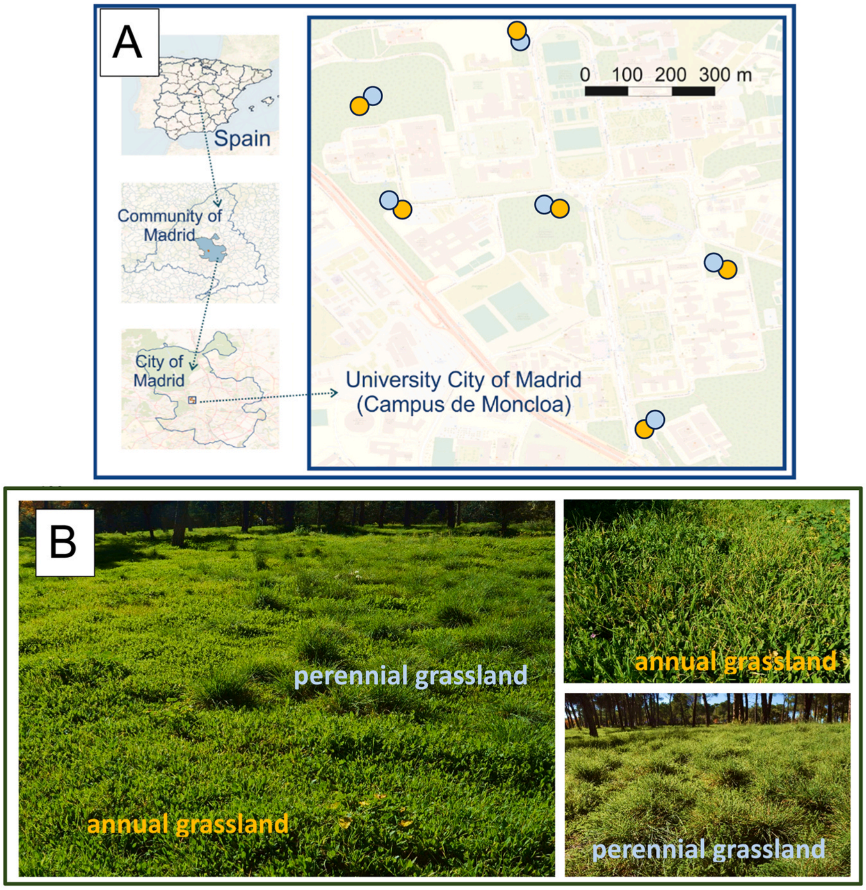

Fig. 1. (A) Study area with sample plot locations. Blue circles represent perennial grasslands, orange circles annual grasslands. (B) Plant communities in the study: general view and detailed view of perennial grassland dominated by *Dactylis glomerata* and annual grassland characterized by *Hordeum murinum* subsp. *leporinum* and *Bromus* sp.pl., among others.

2. Material and methods

2.1. Study area

We focused our study on the Ciudad Universitaria campus which is shared by different universities. It is located in a peri-urban area in the NW of Madrid City, Spain (Fig. 2). This campus includes extensive greenspaces of open to semi-forested areas in which formerly trees (mostly pines) have been planted since the 1940s after the Civil War, but whose main vegetation matrix is formed by herbaceous ruderal vegetation (Molina, 2022). They are mostly managed by annual clearing and biennial ploughing. In previous studies on the vegetation of the campus, both spontaneous annual and perennial grasslands were identified as extensive vegetation (Molina, 2022). Due to the significant anthropogenic pressure suffered by the Ciudad Universitaria, the most common soil type in the study area corresponds to Anthrosols, with the frequent appearance of artifacts at all depths of the profile (Quintana et al., 2022). The climate is typically Mediterranean with a warm dry summer and a mild to cold and humid period from autumn to winter and spring.

2.2. Field procedure and sample collection

We compared the role of annual versus perennial grasslands in terms of the efficiency of their ecosystem services, assuming that both types of grasslands indicate a different successional step from more pioneering (annual grasses) to more developed (perennial grasses) stages. We selected six of these areas and floristically surveyed two paired plots of 1 m^2 each. One of the paired plots corresponded to annual grasslands and the other to perennial grasslands; hence, six plots of each vegetation type were studied. Field sampling was carried out in May 2021. Spring is the period of maximum development of the two grass communities in the study. In each plot, the cover of the plant species present was estimated as a percentage. Soil sampling was performed in the centre of each plot after vegetation sampling. An unaltered soil sample was collected at each sampling point with a cylinder 5 cm in diameter and 5 cm high, and the physical properties of the soils, namely bulk density (BD) and soil water holding capacity (WHC), were determined. Soil samples from 0 to 10 cm deep were collected and divided into two subsamples. One subsample of each soil was refrigerated in the field and kept at 4 ºC until the analysis of the biological properties in the laboratory, and the other was air dried and used for the characterization of the organic fraction.

2.3. Laboratory soil analysis

The total organic carbon (TOC) content was determined by wet oxidation following the method proposed by Walkley and Black (1934). The soil organic matter was fractionated by acid hydrolysis with sulphuric acid in two successive steps (Rovira and Vallejo, 2000). This fractionation produced three organic matter fractions: labile pool I (LPI), consisting of polysaccharides of both plant and microbial origin; labile pool II (LPII), cellulose; and recalcitrant pool (R), mainly lignin, but also suberins, resins, fats and waxes (Oades et al., 1970; Rovira and Vallejo, 2007).

The biological activity of the soil was assessed by determining the activity of ten key enzymes involved in the functioning of the main macronutrient cycles (C, N, P and S). Four enzymatic activities were used for the C cycle, three of them related to the metabolism of labile C compounds (a-glucosidase – a-GLU –, b-glucosidase – b-GLU – and b-galactosidase – b-GAL –) and phenoloxidase – PHE – activity related to the metabolism of recalcitrant C compounds. The functioning of the N cycle was characterized by the activities of urease – URE –, N-acetylglucosaminidase – NAG – and N-arylamidase – AYRL-N –. Phosphatase – PHOS – and aryl-sulphatase – ARYL-S

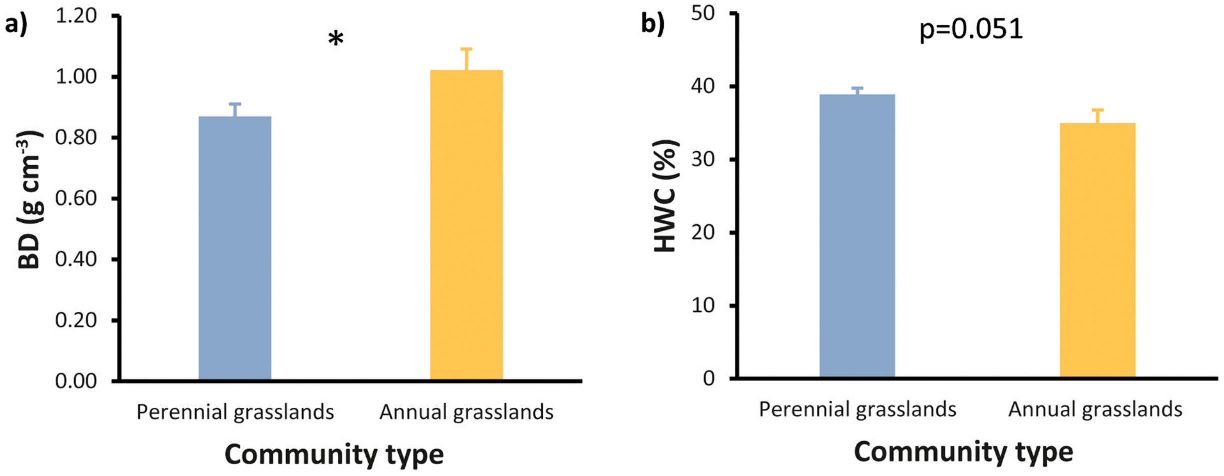

Fig. 2. Bulk density (BD) and soil water holding capacity (WHC) in perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The asterisk marks a significant difference at the level of $p \le 0.05$. The p-value is shown when it is close to a significance level of ≤ 0.05. Error bars represent standard error ($n = 6$).

– activities were analysed in relation to the P and S cycles respectively. Dehydrogenase activity – DH – was also determined to obtain information about the activity of the soil microbiota. Enzymatic activities were determined following the ISO 20130 method (ISO, 2018), except for phenoloxidase activity, which followed the method of DeForest (2009), and dehydrogenase activity, which was determined by the method of Schaefer (1963). All activities were measured on a TECAN NANOQUANT INFINITE M200 PRO

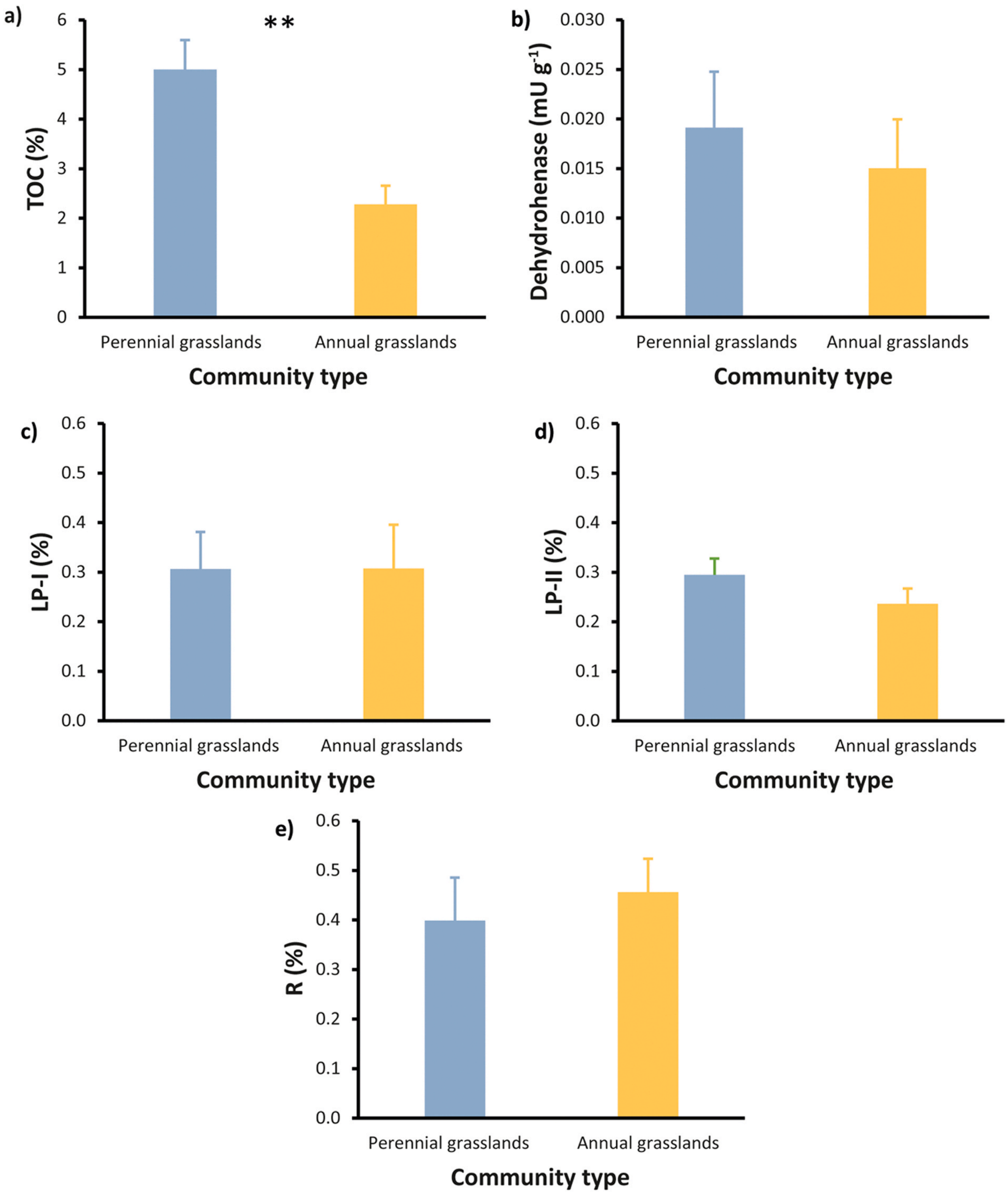

Fig. 3. Total organic carbon (TOC); fractions of organic matter: labile pool I (LP-I), labile pool II (LP-II), and recalcitrant pool (R) and dehydrogenase activity in perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The two asterisks mark a significant difference at the level of $p \leq 0.01$. Error bars represent standard error ($n = 6$).

UV–visible spectrophotometer with a multi-well plate reader. The incubation of the samples was enhanced in a MEMMERT IN 55 incubator. The unaltered sample was used to determine the soil WHC and BD following the methodology proposed by the Soil Survey Staff (2014) procedure.

2.4. Statistical analysis

Perennial and annual grasslands were floristically characterized by means of an agglomerative hierarchical classification performed on the floristic dataset using the program JUICE 7.0 (Tichý, 2002). The b-flexible linkage method (b = 0.25) with Sørensen distance was chosen as algorithms for vegetation grouping. Percentage plant cover values were square-root transformed to reduce the importance of dominant species. The main difference in the physiognomy of the communities was the high frequency and abundance of the hemicryptophyte *Dactylis glomerata* in the perennial grasslands, and the high frequency and abundance of therophytes such as *Hordeum murinum* subsp. *leporinum*, *Plantago lagopus* and *Bromus rubens* in the annual grasslands (Fig. 1; Table S1). We also performed a Detrended Correspondence Analysis (DCA) to seek the length of gradient and thus the response of the plant species model. As the DCA showed that the plant species cover had a linear response to the soil gradients, we performed a Redundance Analysis (RDA) to determine the relationships between plant community composition and the characteristics of the soil on which they grow. We selected the soil variables which showed significant differences between communities. These analyses were done in CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA).

A Student's t-test was performed to determine the differences in soil and vegetation variables between perennial and annual urban grasslands. Prior to calculate Student's t-test, the outlier values of each variable were detected and then discarded. Soil variables were logarithmized, except in the case of the percentages of organic matter fractions, which were transformed to arcsine. Vegetation

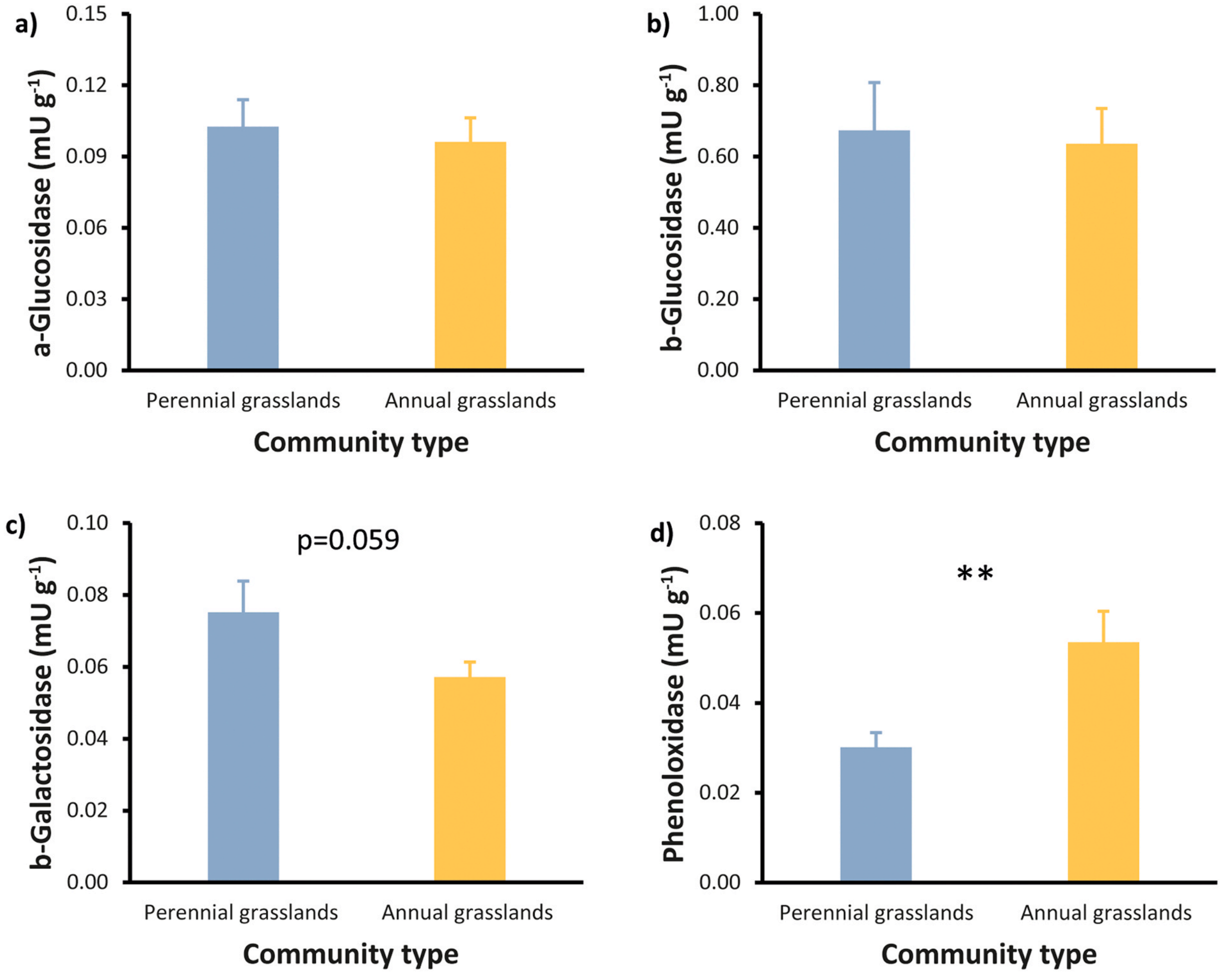

Fig. 4. Enzyme activities related to the C cycle. Alpha-glucosidase, beta-glucosidase, beta-galactosidase and phenoloxidase activity in perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The two asterisks mark a significant difference at the level of $p \leq 0.01$. The p-value is shown when it is close to a significance level of ≤ 0.05. Error bars represent standard error (n = 6).

variables were also transformed to arcsine since their raw values corresponded to percentages of coverage. Normality and homogeneity of variances were met. Statistical analyses were done using SPSS v.28 software.

3. Results

3.1. Soil physical properties and organic fractions

Student's t test calculated for the soil physical properties showed that BD was significantly lower in soils under perennial (Fig. 2a) than under annual grasslands. As can be expected the pattern was inverted for WHC, although in this case the differences, while not significant, were very close to significance ($p=0.051$) (Fig. 2b).

Regarding soil C content, a significant difference between both communities was found (Fig. 3a). Soil TOC values under perennial grasslands more than doubled compared with annual grasslands. No significant differences were observed between the labile or recalcitrant fractions of the organic matter (Fig. 3b-d). However, the labile II fraction of the organic matter was slightly higher under perennial grasslands and the recalcitrant fraction under annual grasslands. Dehydrogenase activity showed higher values in perennial grasslands, although the fact that these differences were not significant is explained by the error between plots (Fig. 3e).

3.2. Soil enzyme activities related to C, N, P and S cycles

The key enzymes responsible for metabolizing labile C substrates, namely a-GLU, b-GLU and b-GAL, showed a tendency to increase in soils developed under permanent grasses, and were close to significance in the case of b-GAL (Fig. 4a-c). The most evident differences in the functioning of the C cycle were seen in PHE activity, an enzyme responsible for the degradation of recalcitrant C substrates, which had higher significant values under the influence of annual grasslands (Fig. 4d).

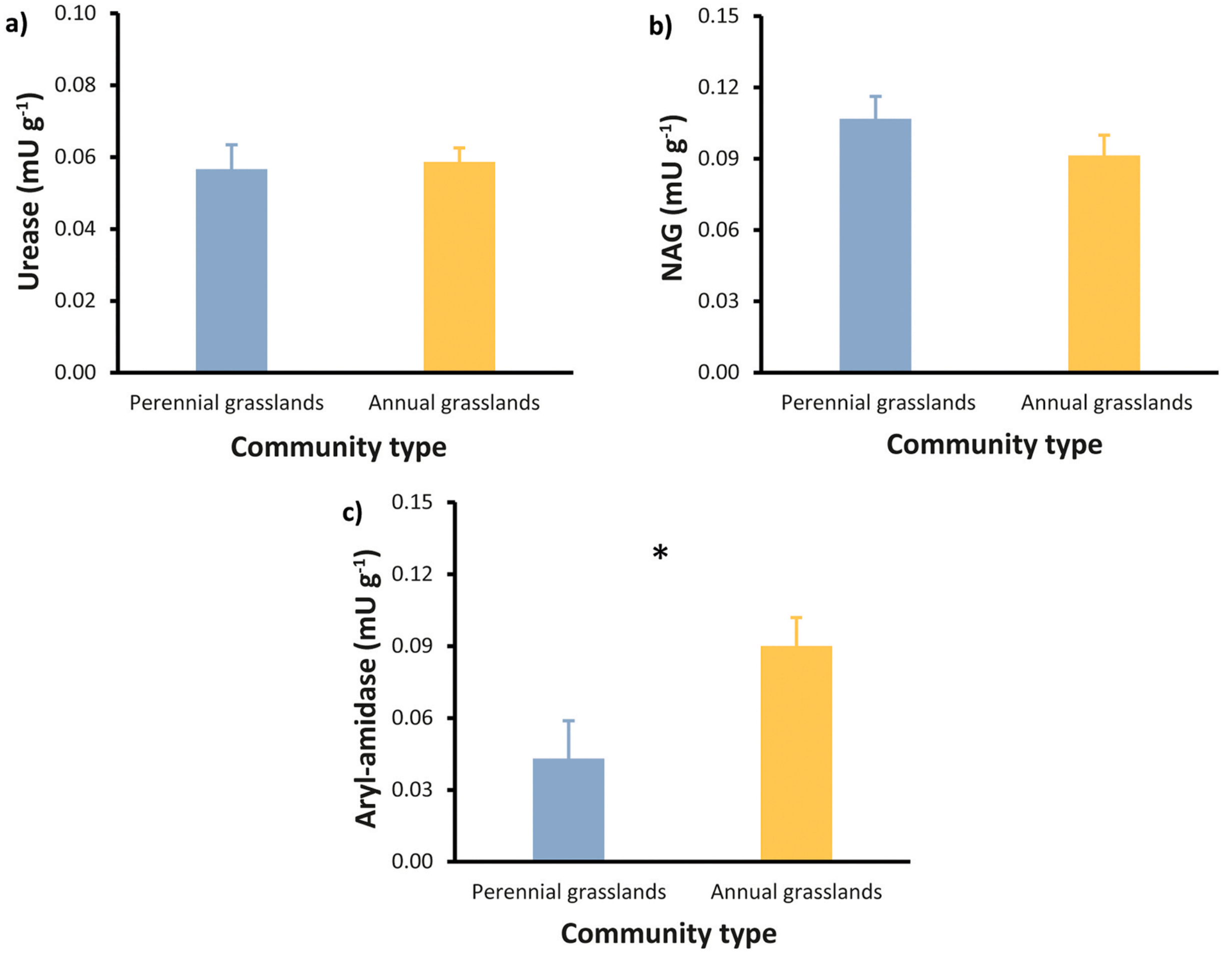

Fig. 5. Enzyme activities related to the N cycle. Urease, N-acetylglucosaminidase (NAG) and Aryl-amidase activity in perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The asterisk marks a significant difference at the level of $p \leq 0.05$. Error bars represent standard error ($n = 6$).

In relation to N cycling, ARYL-N, a key enzyme for the degradation of recalcitrant nitrogenous compounds, showed significantly higher activity in annual grasslands with a similar behaviour to PHE (Fig. 5a). Neither URE, related to labile N compounds, nor NAG, related to the degradation of chitin, which is part of soil entomofauna and the cell walls of fungi, showed significant differences between the types of grasslands, although NAG was somewhat higher in perennial grass communities (Fig. 5b-c). Regarding P cycling, no difference in PHOS activity between plant communities was found (Fig. 6a). In contrast, ARYL-S, a key enzyme in the degradation of organic compounds with sulphur in the S cycling, showed higher significant activity under perennial grasses (Fig. 6b).

3.3. *Plant diversity and ecological gradients*

Student's t test calculated for species richness showed that annual grasses had a significantly greater number of species compared to perennial grasses (Fig. 7). Both communities displayed quite similar qualitative beta biodiversity indexes (the Simpson and Jaccard index), although the scores were slightly higher in the case of perennial grasses (Table S1). The amount of variation in species composition among the sampling units was higher in annual grasslands, as can be seen in the DCA diagram (Fig. 8).

The representation of the first two axes of the RDA using the 12 floristic samplings (including 45 plant species) and the five soil variables which revealed significant differences between grassland types in the Student's t test (BD, TOC, PHE, ARYL-N, ARYL-S) showed a main and significant gradient related with higher PHE activity under the soil of annual grasslands characterized by *Hordeum murinum* subsp. *leporinum*, *Plantago lagopus* and *Bromus rubens*, among others (Fig. 9). In contrast, soils under perennial grasslands, characterized by an abundance of *Dactylis glomerata*, had a greater amount of organic matter.

4. Discussion

4.1. *Ecosystem condition changes throughout the ecological succession*

Ecosystem condition refers to the physical, chemical and biological condition or quality of an ecosystem (Maes et al., 2018). Since ecosystem function is the capacity of natural processes to provide goods and services (de Groot et al., 2002), a better ecosystem conditions a greater and better provision of ecosystem services, that is, the benefits that people obtain from ecosystems (TEEB, 2010; SEEA-EEA, 2012). Urban environments create unique conditions in which the vegetation dynamics and ecosystem function must be determined (Zipperer, 2011). Our work revealed significant changes in ecosystem functions on the ecological succession from annual to perennial Mediterranean ruderal grasslands. In Mediterranean urban habitats, a higher soil BD has been related to soil compaction and loss of soil organic matter (Molina et al., 2024). Since soil carbon sequestration impacts global climate change (Lal, 2004), UGs management should be directed to supporting habitats and ecological processes that offer a substantial mitigation of climate change. We found that permanent grasslands accumulated a greater amount of TOC in the soils, which would help mitigate the effects of climate change to a greater extent than annual grasslands. In addition, there is likely more surface runoff and less infiltration as the BD increases (Schueler, 2000). The increase in soil organic carbon storage also enhances soil porosity (Zhao et al., 2022). Thus, the differences in the physical properties of the soil (WHC and BD) that we found between grassland types are probably linked to the higher soil TOC content in perennial compared to annual grassland, and inversely correlated to soil BD, as occurs in Mediterranean grasslands succession in natural ecosystems (Valverde-Asenjo et al., 2020; Molina et al., 2023b). This suggests that perennial grasslands also improve the water regulation of urban green areas. These findings may be particularly interesting in Mediterranean areas where climate change is expected to have an even a greater impact and precipitation is projected to decrease (Ali et al., 2022).

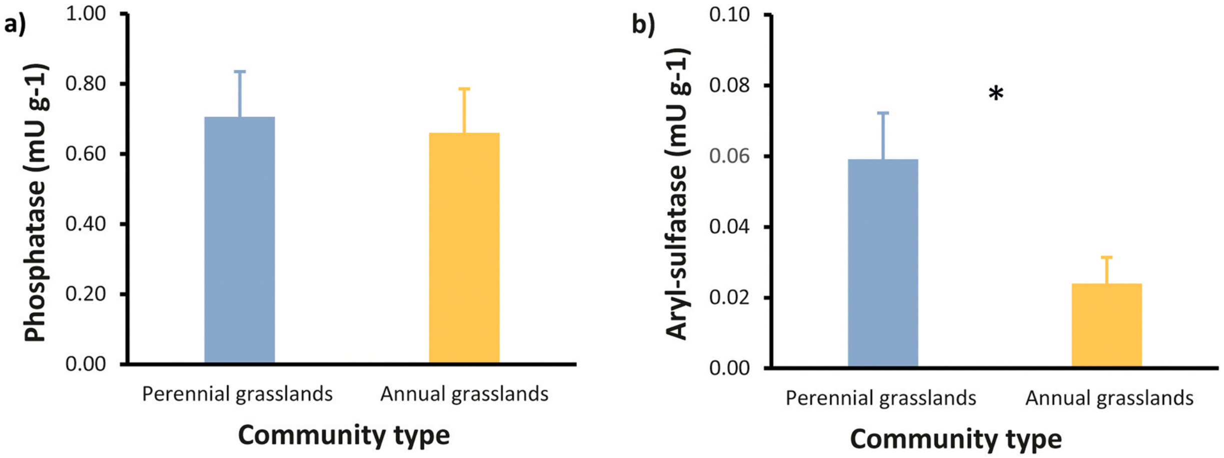

Fig. 6. Enzyme activities related to the P and S cycles. Urease, phosphatase and arylsulfatase activity (mean ± standard error) of perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The asterisk marks a significant difference at the level of $p \leq 0.05$. Error bars represent standard error ($n = 6$).

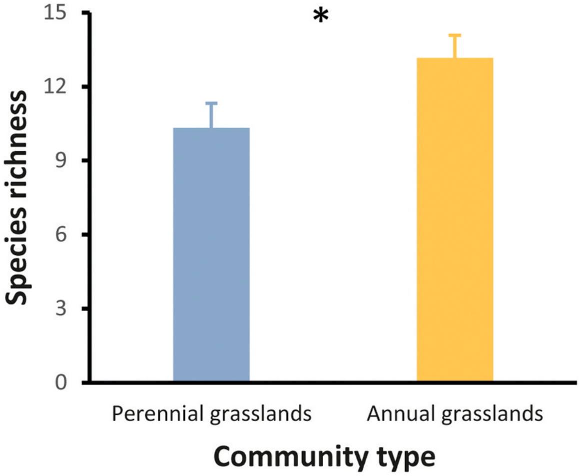

Fig. 7. Species richness in perennial and annual grasslands. The significance in the difference between the two community types was tested by Student's t test. The asterisk marks a significant difference at the level of $p \leq 0.05$. Error bars represent standard error (n = 6).

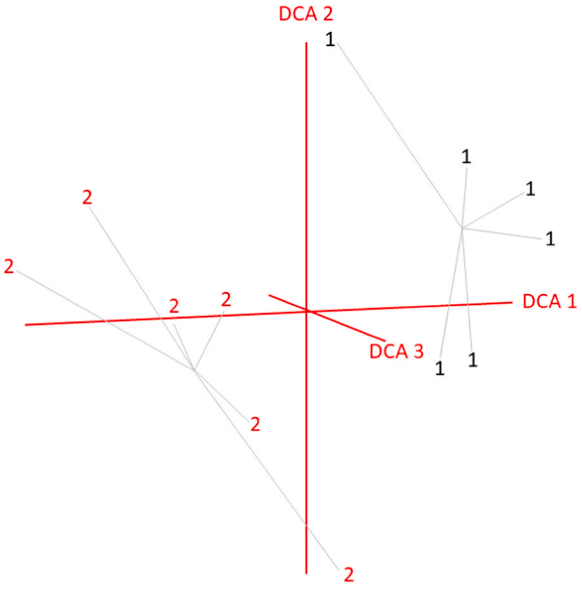

Fig. 8. Detrended Correspondence Analysis (DCA) ordination diagram of the entire data set. Eigenvalues and axis length for the four first axes (DCA1, DCA2, DCA3, DCA4). Eigenvalues: 0.3980 (DCA1), 0.2529 (DCA2); 0.1032 (DCA3); 0.1319 (DCA4). Axis length: 2.4286 (DCA1), 1.5859 (DCA2); 1.3430 (DCA3); 1.0803 (DCA4). 1: perennial grasslands; 2: annual grasslands.

The soil microbiome in UGs shows a higher proportion of genes associated with faster nutrient cycling, and more intense abiotic stress than natural environments (Delgado-Baquerizo et al., 2021). The significantly greater soil enzyme activity we found under annual grasslands related to the metabolism of recalcitrant C and N compounds indicates that these soils had a lower content of labile substrates —as our results also suggested—, and their microbiota needs to degrade recalcitrant substrates to maintain their activity. The slight increase in NAG activity in perennial grasslands could be due to the greater presence of fungi in the rhizosphere of this type of grasses. They also had greater – although not significant – DH activity, an indicator of soil microbiome activity. Soil chemical properties such as soil organic carbon and certain enzyme activities such as ARYL-S are important indicators of soil quality and are positively correlated (Teimouri et al., 2018). Our results supported this relationship and showed that ARYL-S activity was significantly higher in soils under perennial grasslands, which also seems to indicate that soils under perennial grasslands have a greater availability of sulphur as a macronutrient.

Mediterranean peri-urban grasslands have a higher species richness and diversity than other UGs (Güler, 2020). Our results show that annual grasslands maintained a greater species richness than perennial grasslands, and also had the highest plant diversity compared to other ruderal Mediterranean plant communities including herbaceous annual and perennial vegetation (Molina et al.,

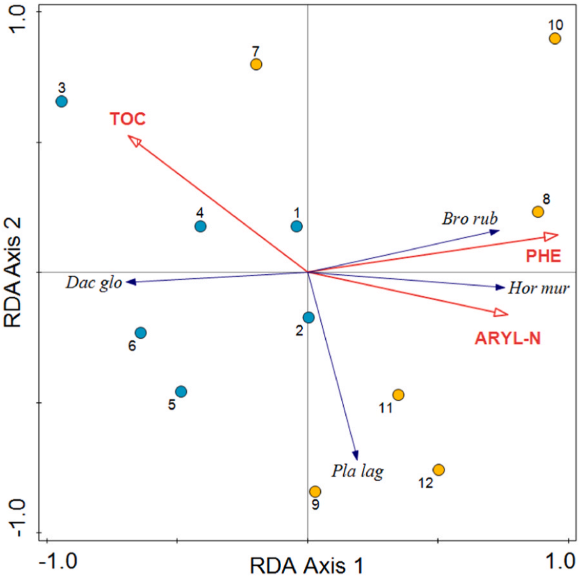

Fig. 9. Redundancy analysis triplot (RDA) showing the relationships between grassland types as circles. Grassland types are depicted as the classification groups described in Table S1; blue circles represent perennial grasslands, orange circles annual grasslands. Soil properties selected by the forward selection procedure are shown as red arrows (significant factors displayed as dashed arrows). TOC = total organic carbon, PHE = soil phenoloxidase activity, ARYL-N = soil arylamidase activity). Plant species are shown as blue arrows *(Bro rub* = *Bromus rubens*; *Dac glo* = *Dactylis glomerata*; *Pla lag* = *Plantago lagopus*).

2023a). The improved ecosystem condition in terms of biodiversity maintenance in the habitat characterized by annual grasslands is contrasted with the improved ecosystem condition in soil carbon storage, water regulation and nutrient cycling in the habitat characterized by perennial grasslands.

4.2. Ecological succession as a tool of greenspace management

The condition indicators for ecosystem attributes are based on spatial coverage and the configuration and state of the urban greenspace and urban vegetation (Maes et al., 2018). Therophytes (annual plants) correspond to the dominant growth form in Mediterranean flora (Mulroy and Rundel, 1977), including ruderal urban areas (Gavilán et al., 1993). The Mediterranean region is typically subjected to prolonged drought (Mulroy and Rundel, 1977) and prone to extreme heat, so the flora has acquired an ability to escape heat stress as seeds (Boyko et al., 2023). This inherent characteristic of Mediterranean grasslands makes them unappreciated to residents and decision-makers who rate the appearance of Mediterranean grasslands as very low, although Mediterranean urban grasslands can have high species richness, a very small percentage of alien species and a marked biogeographic linkage with the natural vegetation of the wider landscape (Filibeck et al., 2016). A reduction in mowing has been considered a simple and effective tool for increasing biodiversity in urban grasslands (Sehrt et al., 2020). However, under a Mediterranean climate a reduction in mowing, and especially ploughing activity, probably activates the natural succession towards perennial grasslands and decreases biodiversity, according to our results.

Urbanization reduces the regeneration potential of vegetation communities (Zhao et al., 2023). Passive restoration through natural succession is a site-adapted and sustainable method for the greening of raw urban soils (Rebele and Lehmann, 2016). In our study we found that natural succession from annual to perennial grasslands increased most of the ecological functions, namely soil carbon storage, soil water regulation and nutrient cycling. Only biodiversity maintenance decreased. Since Mediterranean grasslands harbour significant levels of plant biodiversity (Alrababah et al., 2007), leaving some areas under the current management would help to preserve biodiversity in urban greenspaces under a Mediterranean climate.

5. Conclusions

A higher state or level of ecosystem condition caused by natural regeneration or restoration leads to significant improvement thanks to decreasing pressure or increasing condition indicators (European Commission, 2014). In the Mediterranean urban greenspaces, the ecosystem services provided by the soils developed under perennial grasslands were of better quality than those under annual grasslands, since they had lower bulk density, improved water regulation and accumulated a greater amount of C – mitigating the consequences of climate change – and a higher soil enzyme activity, degrading labile macronutrients such as arylsulfatase. In contrast, annual grasslands supported a higher number of plant species than perennial grasslands. In addition, the activity of phenoloxidase and arylamidase enzymes were higher in soils under annual grasslands, indicating a greater need to degrade recalcitrant C and N compounds to maintain their biological activity. We conclude that natural succession should be left to act in urban greenspaces since it improves ecosystem services such as carbon storage and water regulation. Management in certain areas, preferably through ploughing every few years, will preserve the occurrence of annual grasslands and hence contribute to maintaining a higher biodiversity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03118.

References

Ali, E., Cramer, W., Carnicer, J., Georgopoulou, E., Hilmi, N.J.M., Le Cozannet, G., Lionello, P., 2022. Cross-Chapter. Paper 4: Mediterranean Region, in: Pörtner, H.-O. Roberts, D.C. Tignor, M. Poloczanska, E.S. Mintenbeck, K. Alegría, A. Craig, M. Langsdorf, S. Löschke, S. Möller, V. Okem, A. Rama, B. (Eds.), Climate change 2022: impacts, adaptation and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 2233–2272, 〈doi:10.1017/9781009325844.021〉.

Alrababah, M.A., Alhamad, M.A., Suwaileh, A., Al-Gharaibeh, M., 2007. Biodiversity of semi-arid Mediterranean grasslands: Impact of grazing and afforestation. Appl. Veg. Sci. 10, 257–264. https://doi.org/10.1111/j.1654-109X.2007.tb00524.x.

Bolund, P., Hunhammar, S., 1999. Ecosystem services in urban areas. Ecol. Econ. 29, 293–301. https://doi.org/10.1016/S0921-8009(99)00013-0.

Boyko, J.D., Hagen, E.R., Beaulieu, J.M., Vasconcelos, T., 2023. The evolutionary responses of life-history strategies to climatic variability in flowering plants. N. Phytol. 240, 1587–1600. https://doi.org/10.1111/nph.18971.

Cadenasso, M.L., Pickett, S.T.A., Schwarz, K., 2007. Spatial heterogeneity in urban ecosystems: Reconceptualizing land cover and a framework for classification. Front. Ecol. Environ. 5 (2), 80–88. 〈http://www.jstor.org/stable/20440583〉.

Cárdenas-Mamani, U., Perrotti, D., 2022. Understanding the contribution of ecosystem services to urban metabolism assessments: an integrated framework. Ecol. Indic. 136 https://doi.org/10.1016/j.ecolind.2022.108593.

Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., Defries, R.S., Díaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J., Whyte, A., 2009. Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. PNAS 106 (5), 1305–1312. https://doi.org/10.1073/pnas.0808772106.

Cervelli, E.W., Lundholm, J.T., Du, X., 2013. Spontaneous urban vegetation and habitat heterogeneity in Xi'an, China. ISSN 0169-2046 Landsc. Urban Plan. 120, 25–33. https://doi.org/10.1016/j.landurbplan.2013.08.001.

Dana, E.D., Vivas, S., Mota, J.F., 2002. Urban vegetation of Almería city –a contribution to urban ecology in Spain. Landsc. Urban Plan. 59, 203–216. https://doi.org/10.1016/S0169-2046(02)00039-7.

de Groot, R.S., Wilson, M.A., Boumans, R.M.J., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecol. Econ. 41 (3), 393–408. https://doi.org/10.1016/S0921-8009(02)00089-7.

DeForest, J.L., 2009. The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using MUB-l inked substrates and l- DOPA. Soil Biol. Biochem. 41, 1180–1186. https://doi.org/10.1016/j.soilbio.2009.02.029.

Delgado-Baquerizo, M., Eldridge, D.J., Liu, Y.-R., Sokoya, B., Wang, J.-T., Hu, H.-W., et al., 2021. 2021. Global homogenization of the structure and function in the soil microbe of urban greenspaces. Sci. Adv. 7, eabg5809 https://doi.org/10.1126/sciadv.abg5809.

European Commission, 2014. Mapping and assessment of ecosystems and their services - Indicators for ecosystem assessments under action 5 of the EU biodiversity strategy to 2020, 2nd report, Directorate-General for Environment, Publications Office. 〈https://data.europa.eu/doi/10.2779/75203〉.

Filibeck, G., Petrella, P., Cornelini, P., 2016. All ecosystems look messy, but some more so than others: a case-study on the management and acceptance of Mediterranean urban grasslands. Urban . Urban Green. 15, 32–39. https://doi.org/10.1016/j.ufug.2015.11.005.

Gavilán, R., Echevarría, J.E., Casas, I., 1993. Catálogo de la flora vascular de la Ciudad Universitaria de Madrid. Bot. Complutensis 18, 175–202. ISSN 0214-4565.

Gómez-Baggethun, E., Gren, Å., Barton, D.N., Langemeyer, J., McPhearson, T., O'Farrell, P., 2013. Urban Ecosystem Services. In: Elmqvist, T., et al. (Eds.), Urbanization, biodiversity and ecosystem services: challenges and opportunities. Springer, Dordrecht, pp. 175–251. https://doi.org/10.1007/978-94-007-7088-1_11.

Greinert, A., 2015. The heterogeneity of urban soils in the light of their properties. J. Soils Sediment. 15, 1725–1737. https://doi.org/10.1007/s11368-014-1054-6.

Güler, B., 2020. Plant species diversity and vegetation in urban grasslands depending on disturbance levels. Biologia 75, 1231–1240. https://doi.org/10.2478/s11756-020-00484-0.

ISO, 2018. ISO 20130: Soil quality-measurement of enzyme activity patterns in soil samples using colorimetric substrates in micro-wells plates. International Organization for Standardization, Geneva, Switzerland.

Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. Science (1979). https://doi.org/10.1126/science.1097396.

Loidi, J., 2017. Dynamism in vegetation. Vegetation changes on a short time scale. In: Loidi, J. (Ed.), The vegetation of the Iberian Peninsula. Plant and vegetation, 12. Springer, Cham, pp. 81–99. https://doi.org/10.1007/978-3-319-54784-8_3.

Maes, J., Zulian, G., Thijssen, M., Castell, C., Baro, F., Ferreira, A., Melo, J., Garret, C., David, N., Alzetta, C., Geneletti, D., Cortinovis, C., Zwierzchowska, I., Louro Alves, F., Souto Cruz, C., Blasi, C., Alós Ortí, M., Attore, F., Azella, M., Capotorti, G., Copiz, R., Fusaro, L., Manes, F., Marando, F., Marchetti, M., Mollo, B., Salvatori, E., Zavattero, L., Zingari, P., Giarratano, M., Bianchi, E., Duprè, E., Barton, D., Stange, E., Perez-Soba, M., Van Eupen, M., Verweij, P., De Vries, A., Kruse, H., Polce, C., Cugny-Seguin, M., Erhard, M., Nicolau, R., Fonseca, A., Fritz, M., Teller, A., 2016. Mapping and assessment of ecosystems and their services: urban ecosystems 4th Report. Publication Office of the European Union. JRC101639.

Maes, J., Teller, A., Erhard, M., Grizzetti, B., Barredo, J.I., Paracchini, M.L., Condé, S., Somma, F., Orgiazzi, A., Jones, A., Zulian, A., Petersen, J.E., Marquardt, D., Kovacevic, V., Abdul Malak, D., Marin, A.I., Czúcz, B., Mauri, A., Loffler, P., Bastrup-Birk, A., Biala, K., Christiansen, T., Werner, B., 2018. Mapping and assessment of ecosystems and their services: an analytical framework for ecosystem condition. Publications office of the European Union, Luxembourg.

Molina, J.A., 2022. Biodiversidad de los Campus UCM: vegetación y flora. In: Rescia Perazzo, A., Lucas Olegario, M., Gutiérrez Sáenz, M. (Eds.), Trabajos en sostenibilidad y resiliencia socio-ecológica en la Universidad Complutense de Madrid. Ediciones Complutense, Madrid, pp. 99–121.

Molina, J.A., Martín-Sanz, J.P., Casermeiro, M.A., Quintana, J.R., 2023a. Spontaneous urban vegetation as an indicator of soil functionality and ecosystem services. Appl. Veg. Sci. 26, e12728 https://doi.org/10.1111/avsc.12728.

Molina, J.A., Martín-Sanz, J.P., Valverde-Asenjo, I., Sánchez-Jiménez, A., Quintana, J.R., 2023b. Mediterranean grassland succession as an indicator of changes in ecosystem biodiversity and functionality. Biodivers. Conserv. 32, 95–118. https://doi.org/10.1007/s10531-022-02481-y.

Molina, J.A., Martín-Sanz, J.P., Casermeiro, M.A., Quintana, J.R., 2024. Soil depth and vegetation type influence ecosystem function in urban greenspaces., 105209 Appl. Soil Ecol. 194, 2024. https://doi.org/10.1016/j.apsoil.2023.105209.

Mulroy, T.W., Rundel, P.W., 1977. Annual plants: adaptations to desert environments. Bioscience 27, 109–114. https://doi.org/10.2307/1297607.

Oades, J.M., Kirkman, M.A., Wagner, G.H., 1970. The use of gas–liquid chromatography for the determination of sugars extracted from soils by sulfuric acid. Soil Sci. Soc. Am. J. 34, 230–235.

Paudel, S., States, S.L., 2023. Urban green spaces and sustainability: exploring the ecosystem services and disservices of grassy lawns versus floral meadows, 2023 Urban . Urban Green. 84, 127932. https://doi.org/10.1016/j.ufug.2023.127932.

Quintana, J.R., de la Cruz Caravaca, M.T., Casermeiro, M.A., 2022. Suelos de la Ciudad Universitaria. In: Rescia Perazzo, A., Lucas Olegario, M., Gutiérrez Sáenz, M. (Eds.), Trabajos en sostenibilidad y resiliencia socio-ecológica en la Universidad Complutense de Madrid. Ediciones Complutense, Madrid, pp. 91–97.

Rebele, F., Lehmann, C., 2016. Twenty years of woodland establishment through natural succession on a sandy landfill site in Berlin, Germany. Urban . Urban Green. 18, 182–189. https://doi.org/10.1016/j.ufug.2016.06.006.

Rivas-Martínez, S., 1978. La vegetación de Hordeion leporini en España. Doc. Phytosociol. 9, 377–392.

Rovira, P., Vallejo, V.R., 2000. Evaluating thermal and acid hydrolysis methods as indicators of soil organic matter quality. Commun. Soil Sci. Plant Anal. 31, 81–100. https://doi.org/10.1080/00103620009370422.

Rovira, P., Vallejo, V.R., 2007. Labile, recalcitrant, and inert organic matter in Mediterranean forest soils. Soil Biol. Biochem. 39, 202–213. https://doi.org/10.1016/j.soilbio.2006.07.021.

Schaefer, R., 1963. Dehydrogenase activity as a measurement of the global biological activity of soil. Ann. Inst. Pasteur 105, 326–331.

Schueler, T., 2000. The compaction of urban soil: the practice of watershed protection. Center for watershed protection, Ellicott City, MD, pp. 210–214.

SEEA-EEA, 2012. System of Environmental-Economic Accounting 2012: Experimental Ecosystem Accounting. ⟨http://unstats.un.org/unsd/envaccounting/eea_white_cover.pdf⟩.

Sehrt, M., Bossdorf, O., Freitag, M., Bucharova, A., 2020. Less is more! Rapid increase in plant species richness after reduced mowing in urban grasslands. Basic Appl. Ecol. 42, 47–53. https://doi.org/10.1016/j.baae.2019.10.008.

Soil Survey Staff, 2014. Kellogg soil survey laboratory methods manual, in: Burt, R. (Ed.) Soil survey investigations report no. 42, version 5.0. Lincoln, Nebraska: USDA- NRCS.

TEEB, 2010. The economics of ecosystems and biodiversity: ecological and economic foundation. Earthscan, Cambridge.

Teimouri, M., Mohamadi, P., Jalili, A., Dick, W.A., 2018. Assessing soil quality through soil chemical properties and enzyme activities in semiarid area, Iran. Appl. Ecol. Environ. Res. 16, 2113–2127. https://doi.org/10.15666/aeer/1603_21132127.

Tichý, L., 2002. JUICE, software for vegetation classification. J. Veg. Sci. 13, 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x.

United Nations, 2019. The world population prospects 2019: highlights. United Nations, New York.

Valença Pinto, L., Inácio, M., Santos Ferreira, C.S., Dinis Ferreira, A., Pereira, P., 2022. Ecosystem services and well-being dimensions related to urban green spaces – A systematic review. Sustain. Cities Soc. 85, 104072 https://doi.org/10.1016/j.scs.2022.104072.

Valverde-Asenjo, I., Diéguez-Antón, A., Martín-Sanz, J.P., Molina, J.A., Quintana, J.R., 2020. Soil and vegetation dynamics in a chronosequence of abandoned vineyards, 2020 Agric. Ecosyst. Environ. 301, 107049. https://doi.org/10.1016/j.agee.2020.107049.

Vargas-Hernández, J.G., Pallagst, K., Zdunek-Wielgołaska, J., 2023. Urban Green Spaces as a Component of an Ecosystem. In: Dhiman, S. (Ed.), Sustainable Development and Environmental Stewardship. Springer, Cham, pp. 165–198. https://doi.org/10.1007/978-3-031-28885-2_8.

Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. Soil Sci. 37, 29–38.

Yang, J., Yang, J., Xing, D., Luo, X., Lu, S., Huang, C., Hahs, A.K., 2021. Impacts of the remnant sizes, forest types, and landscape patterns of surrounding areas on woody plant diversity of urban remnant forest patches. Urban Ecosyst. 24, 345–354. https://doi.org/10.1007/s11252-020-01040-z.

Yesilonis, I.D., Pouyat, R.V., 2012. Carbon stocks in urban forest remnants: Atlanta and Baltimore as case studies. In: Lal, R., Augustin, B. (Eds.), Carbon sequestration in urban ecosystems. Springer, Dordrecht, pp. 103–120. https://doi.org/10.1007/978-94-007-2366-5_5.

Zhao, D., Sun, M., Xue, Y., Yang, Q., Liu, B., Jia, B., Song, C., Zhang, S., Zhang, Z., 2023. Spatial variations of plant species diversity in urban soil seed banks in Beijing, China: implications for plant regeneration and succession, 2023 Urban . Urban Green. 86, 128012. https://doi.org/10.1016/j.ufug.2023.128012.

Zhao, X., Zhang, W., Feng, Y., Mo, Q., Su, Y., Njoroge, B., Qu, C., Gan, X., Liu, X., 2022. Soil organic carbon primarily control the soil moisture characteristic during forest restoration in subtropical China. Front. Ecol. Evol. 10 https://doi.org/10.3389/fevo.2022.1003532.

Zipperer, W.C., 2011. The process of natural succession in urban areas. In: Douglas, I.;, Goode, D., Houck, M.;, Wang, R. (Eds.), The Routledge handbook of urban ecology. Routledge Press, London, pp. 187–197. https://doi.org/10.4324/9780203839263.ch16.