



The importance of university campuses for the avian diversity of cities

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ABSTRACT

In a world of increasing urban areas and their subsequent negative effect on biodiversity, university campuses arise as environmentally friendly designs that can help enhancing biodiversity. However, current information on the topic is mainly based on single-campus studies, taxonomic diversity variables (e.g., species richness), and specific geographic regions like Asia or North America. Multi-campus comparisons, studies on other components of biodiversity (e.g., functional or phylogenetic diversity) and biodiversity information from other regions of the world are needed to generalize the previous findings. In this study, we try to fill in these gaps by simultaneously investigating taxonomic, functional, and phylogenetic diversity of bird communities on 15 university campuses of Spain, which is located within the Mediterranean hotspot of biodiversity where no previous study on this topic have been conducted. We compared campus areas with other randomly selected urban areas to test whether university campuses hold higher levels of bird diversity than non-campus areas. We also analyzed other environmental variables (e.g., green and building cover in and around campuses) to identify whether their influence in university campuses varies from other urban areas. Our results show that taxonomic diversity was higher within university campuses compared to other areas, but this pattern was not confirmed for functional and phylogenetic diversity. We found that grass cover, buildings, and the green area around the study areas have different associations with taxonomic, functional, or phylogenetic diversity respectively in campuses or non-campus areas. Our findings highlight the importance of university campuses for the conservation of Mediterranean urban biodiversity and support their use as relevant resources for promoting nature conservation among citizens.

1. Introduction

Urbanization is one of the most transforming land use changes in our planet (Groom et al., 2006) and it is tightly linked to the growing human population (Annez and Buckley, 2009). In this sense, recent UN reports predict that human population will only increase in urban areas in the next 30 years (United Nations, 2019). This increase and associated urban landscape transformation is deeply connected with important environmental changes in habitat structure, ecosystem functioning, and biodiversity (Gaston, 2010). The negative effects of urbanization are particularly relevant for biodiversity at a global scale (McKinney, 2006; Aronson et al., 2014; Ibáñez-Álamo et al., 2017), with an expectation of getting more profound in the near future (Seto et al., 2012). Therefore,

this situation sets out the relevance of reconciling urban development with biodiversity conservation, and as such it has been included within the Sustainable Development Goals (goals 11 and 15; UN, 2022).

Despite their negative impact, cities can also host a range of habitats and structures suitable for life, with some cities showing high levels of biodiversity (Jokimäki & Suhonen, 1993; Hope et al., 2008). Some studies have even highlighted the role of cities as a refuge for some threatened species (Aronson et al., 2014; Ives et al., 2016) and suggested that urban ecosystems can serve as models to understand and mitigate possible effects of climate change in non-urban areas (Parris and Hazell, 2005). Therefore, one of the main current questions about urbanization is how urban areas can contribute to maintaining biodiversity (Heyman et al., 2017). Because not all species respond similarly to the process of

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urban development, it is important to know which species are more tolerant and, for those less tolerant, study how to minimize the negative impact of urban management in order to maintain or even enhance their presence (Jokimäki et al., 2018). From this perspective, a well-designed urban environment can be instrumental in our aim of balancing human population growth (and its associated urban expansion) with biodiversity conservation (Müller et al., 2010; Garrard et al., 2018).

In the context of biodiversity-friendly urban designs, university campuses can play a key role (Colding, 2007; Vallejo et al., 2009), as they can easily link nature preservation, scientific research and education (Moerman & Estabrook, 2006; Colding & Barthel, 2017). Indeed, university campuses have been previously described as important urban green spaces for biodiversity in several world regions (Liu et al., 2021). Many university campuses were initially built in rural areas near cities rather than within them, so they include big green patches of the original nature (Wheeler, 2008). Many universities also promoted the creation of botanical gardens or faunal refuges for research. As a result, university campuses today host high biodiversity levels (Pautasso & Parmentier, 2007; Liu et al., 2021) and even serve as places for the discovery of new species. For example, Mironov and Chandler (2017) described eight new mite species from samples obtained in university campuses of the US. However, this relative importance in biodiversity is usually obtained through the comparison with large scale information and regional inventories (e.g., Guénard et al., 2015; Zhang et al., 2018). To our knowledge, whether university campuses, a specific urban development type, hold higher biodiversity levels compared to other nearby urban areas with different urban landscape organization has not yet been tested. This prediction is justified given that many university campuses were originally built in more natural areas and contain introduced/exotic species (e.g., within botanical gardens; Pautasso & Parmentier, 2007; Wheeler, 2008). Furthermore, current biodiversity data from university campuses is geographically biased, as evidenced by the recent review published by Liu et al. (2021): most of these studies were performed in China, India, or the US. There is an apparent gap in the knowledge of other regions like the Southern Hemisphere or key biodiversity hotspot areas in the world, like the Mediterranean basin, that should be explored further.

In the present study, we first aim to investigate whether university campuses hold higher biodiversity levels than other nearby urban areas within the same cities. We investigated avian bird communities on 15 Spanish university campuses and in 15 same-sized nearby urban areas from each city. We explored this effect using complementary diversity components (taxonomic, functional, and phylogenetic variables) proven to be differently affected by the urban process (e.g., Morelli et al., 2016). Examining all these diversity components would therefore provide a more general overview of the potential effect of university campuses on biodiversity, which has seldomly been addressed (i.e., with functional or phylogenetic variables; e.g., Zhang et al., 2018). In addition, our multi-city approach would help us obtain more generalizable results and fill a gap in much needed knowledge for the Mediterranean region. Our second objective involves testing the key abiotic and biotic factors affecting avian diversity in university campuses, and whether they differ compared to other non-campus urban areas. Urban studies that have investigated the effect of local scale factors for the three major components of biodiversity simultaneously (taxonomic, functional, and phylogenetic) remain scarce (Ibáñez-Álamo et al., 2020; Morelli et al., 2021), making this a novel aspect of our study. We used birds as model organisms because they have been widely used to study how animals respond to urban-associated environmental changes (e.g., Gil & Brumm, 2014; Rega-Brodsky et al., 2022) and are good bioindicators for other taxa (Gregory et al., 2003). We consider that our study contributes to the better understanding of these relevant urban areas and could guide urban planners towards biodiversity-friendly decisions.

2. Material and methods

2.1. Sampling design and urban measurements

We studied bird communities in 12 cities of Spain (Fig. S1; Table S1) in Spring 2021. In total 15 localities (campuses) were analyzed together with their 15 paired nearby non-campus urban zones. Campus and non-campus pairs were at least 1 km apart to ensure the independence of the data (Morelli et al., 2018) and their areas were equivalent to control for confounding size-related effects. We took the campus perimeter as a reference for the university campus areas and used the same polygon to randomly select an equally-sized non-campus zone within the same city in a similar way as other previous urban research using paired study designs (e.g., Ibáñez-Álamo et al., 2020). We obtained the campus perimeters from the institutional webpage of each university.

Within each zone (campus and non-campus), we used 50 m radius point counts to quantify all birds seen or heard in 5 min as recommended by Bibby et al. (2000) and following the methodology of several other urban studies (e.g., Melles et al., 2003; Tzortzakaki et al., 2019; Ibáñez-Álamo et al., 2020). This method has proven sufficient to provide species presence, relative abundance, population tendency and use of habitat (Wunderle, 1994). Depending on the size of the zone (which is directly related with the boundaries of each university campus), the number of point counts ranged from seven to ten, randomly selected but with a minimum distance of 150 m among them to avoid double counting the same individuals. Sampling was performed within the first 4 h after sunrise, the time period of maximum bird activity (Bibby et al., 2000; González García, 2011). We carried out the point counts only under optimal weather conditions (e.g., no rain or strong wind) to collect reliable data on avian presence (Bibby et al., 2000; Morelli et al., 2018). Furthermore, we performed the sampling twice during the breeding season in order to collect data from early (April) as well as late breeding birds (May). We considered all species detected in both surveys for our analyses.

For each point count we quantified the percentage of land cover use such as the total vegetation cover (considering the following three categories: trees, bushes and grass) as well as water and building covers within a distance of 50 m of the point count (Paker et al., 2014; Morelli et al., 2016). Within this radius and at the same time of the point counts (four hours after sunrise) we also quantified the presence of pedestrians (number of citizens per 5 min) as a proxy for human disturbance following a previously published methodology (Ibáñez-Álamo et al., 2020; Morelli et al., 2021).

Finally, we identified land cover use variables at the zone level using the land use GIS database of the Spanish Government (SIOSE; Valcárcel et al., 2008). We calculated the percentage of the focus polygon covered by buildings (BuildingsPO) and green areas (GreenPO; Morelli et al., 2021). To do so, we reorganized the land use categories included in the SIOSE as they are much more detailed than these four categories. As part of this reorganization, we refined the polygons initially classified as 'Servicio Dotacional' (non-residential utilities) in the SIOSE given that they include a wide range of different land-use categories (e.g., administrative areas, cemeteries, educational areas -including universities-, or urban parks). We used recent Google Earth images for this purpose and manually created new polygons fitting into our previously described four categories. We followed a similar procedure to quantify the percentage of each land-cover type in a 500-m external buffer area around each campus/non-campus zone (i.e., BuildingsEX and GreenEX). This procedure and distance have been used before to account for potential effects of the surrounding habitat of the focus zone (external matrix) on the birds within the area (e.g., Huang et al., 2015).

2.2. Avian diversity and community metrics

For each point count ($n = 280$), we estimated taxonomic diversity as the total number of avian species recorded (bird species richness, BSR;

Magurran, 2004), functional diversity as the abundance-weighted variance of the dissimilarities between all species pairs (Rao's Q; Rao, 1982; Champely & Chessel, 2002), a measure of phylogenetic diversity richness (Faith's PD, phylogenetic diversity; Faith, 1992), and a metric of phylogenetic diversity divergence (phylogenetic species variability, PSV; Helmus et al., 2007). For PSV the number of point counts considered was 273 given that single-species point counts were excluded for this analysis. With this selection of community metrics, we followed the recommendation of Tucker et al. (2017) to explore more than one dimension of phylogenetic diversity as they can provide complementary information on the community assemblage.

Traits used to calculate the functional diversity were extracted from Pearman et al., (2014). These traits were: body mass, food type, acquisition behaviour, substrate from which food is acquired, activity period, foraging habitats and nesting habitats. For species not included in Pearman et al., (2014) (i.e., *Cairina moschata*, *Estrilda astrild*, *Myiopsitta monachus*, *Psittacula krameri*, *Saxicola rubicola*), data were obtained from Oliveira Hagen et al., 2017 and <https://birdsoftheworld.org>.

We obtained BSR and Rao's Q using the function 'dbFD' from the 'FD' R package (Laliberté et al., 2014). We calculated PD as the sum of accumulated differences among taxa and PSV (also known as phylogenetic relatedness) as the mean of the phylogenetic distances between species (Helmus et al., 2007). To estimate both PD and PSV, we used the average values of PD and PSV obtained using the function 'pd' and 'psv' from the 'picante' R package (Kembel et al., 2010), respectively, on 100 phylogenetic trees extracted from the avian genetic data available at www.birdtree.org. Using the Red Book of Birds in Spain (SEO/Birdlife, 2021), we extracted the IUCN conservation status and native or exotic/invasive category for each bird species.

2.3. Statistical analyses

We first performed spatial autocorrelation tests for each response variable. These analyses consisted of Mantel tests (Mantel, 1967; Legendre & Fortin, 2010) based on Monte Carlo permutations with 9999 randomizations and two matrices, one for the geographical distance among point counts (spatial distance matrix) and another for the differences in BSR, Rao's Q, Faith's PD, or PSV among point counts (response variable distance matrix; Oksanen, 2016). Our data showed no spatial autocorrelation issue for BSR ($N = 280$; $r = -0.016$, $p = 0.827$), Rao's Q ($N = 280$; $r = 0.029$, $p = 0.118$), or Faith's PD ($N = 280$; $r = -0.019$, $p = 0.855$) and therefore we used our point counts as statistically independent observations for these diversity metrics. However, our test for PSV showed evidence of spatial autocorrelation ($N = 273$; $r = 0.252$, $p = 0.0001$). We then proceeded to include the interaction term 'latitude x longitude' of each point count into the PSV model to resolve this potential problem (Legendre, 1993; Carsten F. et al., 2007).

We also checked for multicollinearity using the "vif.mer()" function and the R package performance (Lüdtke et al., 2021). We found medium collinearity issues between the total green area of the focus zone (GreenPO) and the total built area of the focus zone (BuildingsPO; VIF = 8.82 and 9.69 respectively) and high collinearity issues between the total green area of the surrounding matrix (GreenEX) and the total built area of the surrounding matrix (BuildingsEX; VIF = 11.87 and 12.39 respectively). Thus, we decided to only use the total green area variables for the focus zone (GreenPO) and surrounding matrix (GreenEX) in our analyses.

Before constructing the statistical models, we scaled and centered the continuous variables to allow easier comparisons of the estimates (Schielzeth, 2010). We then ran generalized linear mixed models (GLMMs) assuming Poisson distribution for BSR (using "glmer" function from the lme4 R package (Bates et al., 2015)) and Gaussian distribution for Rao's Q, Faith's PD, and PSV (using the "lmer" function included in the lme4 R package (Bates et al., 2015)). Fixed variables included the zone (campus vs non-campus), several predictors at the point count level (tree cover, shrub cover, grass cover, water cover, built cover, and

number of pedestrians), two predictors at the focus zone level (GreenPO and GreenEX) and the two-way interactions of all these predictors with zone (e.g., tree cover x zone interaction). Given that the species richness is usually strongly associated with Faith's PD (Tucker et al., 2017; Tucker and Cadotte, 2013), we included BSR as control covariable in the model for this phylogenetic diversity metric. To account for consistent differences among cities and the paired design of the study, locality ID (the general urban area including the paired campus and non-campus focus zones) nested within city ID was added as a random factor to all models. Using these models, we selected the predictors that best explain the variation in the response variables through the model selection and averaging approach (Zuur et al., 2009; Symonds & Moussalli, 2011; Barton 2022) implemented in the MuMIn R package (Barton 2022). The use of the model averaging approach allows to overcome the issue of model uncertainty. Our selection procedure used the criteria of $\Delta AIC < 2$ (see Table S2).

3. Results

We found a total of 69 bird species in the Spanish university campuses and 48 species in non-campus zones. Of these species, 12 found in university campuses were categorized as near threatened (6), vulnerable (3), or endangered (3; *Coturnix coturnix*, *Corvus monedula* and *Falco tinnunculus*) while 7 species from these three categories were found in non-campus urban areas (3 NT, 2 VU and 2 EN; *C. monedula* and *F. tinnunculus*). We also found 3 species classified as invasive in Spanish university campuses (*Estrilda astrild*, *Myiopsitta monachus*, and *Psittacula krameri*) but only one (*M. monachus*) in non-campus areas.

Overall, bird species richness showed a significantly higher value in university campuses than in their paired urban zones (Estimate \pm SE = -0.22 ± 0.06 , $Z = 3.43$, $p < 0.0001$; Fig. 1; Fig. 2A). In contrast, we found no significant association between campuses and non-campus urban areas for Rao's Q (Estimate \pm SE = -1.83 ± 2.34 , $Z = 0.78$, $p = 0.43$; Fig. 1; Fig. 2B). This effect was opposite regarding Faith's PD and PSV (though marginally significant for the latter), with non-campus areas showing higher levels of these two phylogenetic diversity variables than university areas (PD: Estimate \pm SE = 17.08 ± 7.90 , $Z = 2.16$, $p = 0.031$; PSV: Estimate \pm SE = 0.03 ± 0.02 , $Z = 1.81$, $p = 0.071$; Fig. 1 1; Fig. 2C-D). Interestingly and despite these general findings, not all campuses showed the same pattern compared to non-campus urban areas at the individual level with some campuses showing no biodiversity differences with their paired non-campus urban areas or even showing opposite results (Figs. S2-S5).

Bird species richness was significantly (positively) affected by tree cover (Estimate \pm SE = 0.12 ± 0.03 , $Z = 4.40$, $p < 0.0001$) and (negatively) by building cover at the point count level (50 m radius) but the latter only in the non-campus urban areas ($Z = 3.40$, $p = 0.0007$; Fig. 1; Fig. 3A). The number of pedestrians showed a marginally significant negative association with BSR (Estimate \pm SE = -0.08 ± 0.04 , $Z = 1.92$, $p = 0.056$; Fig. 1). Rao's Q decreased significantly with the presence of buildings but in this case independently on whether it is a university campus or not (Estimate \pm SE = -2.22 ± 1.05 , $Z = 2.10$, $p = 0.035$; Fig. 1). We also found a marginally significant effect for the interaction between grass cover and focus zone indicating that the percentage of grass at the point count has a greater impact on the Rao's Q of non-campus urban areas (Estimate \pm SE = 4.25 ± 2.24 , $Z = 1.89$, $p = 0.059$; Fig. 1; Fig. 3B). Regarding phylogenetic diversity metrics, Faith's phylogenetic diversity was significantly and negatively associated with grass cover at the point count level (Estimate \pm SE = -9.58 ± 3.85 , $Z = 2.49$, $p = 0.013$), but positively affected by the number of pedestrians (Estimate \pm SE = 6.83 ± 3.02 , $Z = 2.26$, $p = 0.024$) and water cover (Estimate \pm SE = 7.47 ± 2.84 , $Z = 2.63$, $p = 0.009$, Fig. 1). The percentage of green area of the external matrix (GreenEX) also had a significant association for this biodiversity component but mediated by the zone factor ($Z = 2.77$, $p = 0.006$; Fig. 1) showing a stronger positive association for university campuses than for their paired urban areas

	Taxonomic Diversity (BSR)	Functional Diversity (Rao's Q)	Phylogenetic richness (Faith's PD)	Phylogenetic divergence (PSV)
Zone (University Campuses)	(+)		(-)	(-)
Pedestrians	(-)		(+)	(+)
Grass cover			(-)	
Tree cover	(+)			
Bush cover				
Buildings		(-)		
Water cover			(+)	
GreenPO				
GreenEX			(+)	
Pedestrians x Zone (NC)				
Grass cover x Zone (NC)		(+)		
Tree cover x Zone (NC)				
Bush cover x Zone (NC)				
Buildings x Zone (NC)	(-)			
Water cover x Zone (NC)				
GreenPO x Zone (NC)				(+)
GreenEX x Zone (NC)			(-)	(-)

Fig. 1. Summary presentation of the averaged generalized linear mixed models (GLMM) for the three diversity components: taxonomic (bird species richness, BSR), functional (Rao's Q) and phylogenetic diversity (Faith's PD and phylogenetic species variance, PSV). Green cells indicate positive significant associations while red cells show significant but negative associations for the corresponding predictor. Lighter green and red correspond with marginally significant results. Grey cells indicate that the predictor was included in the averaged model for that response variable but was not significant while white cells show predictors that were not included in the averaged model for that diversity variable. GreenPO: Percentage of green area of the studied polygon. GreenEX: Percentage of green area of the external buffer zone (500 m width) of the studied polygon. NC: Non campus zone. The detailed results of the models can be found in [Table S2](#).

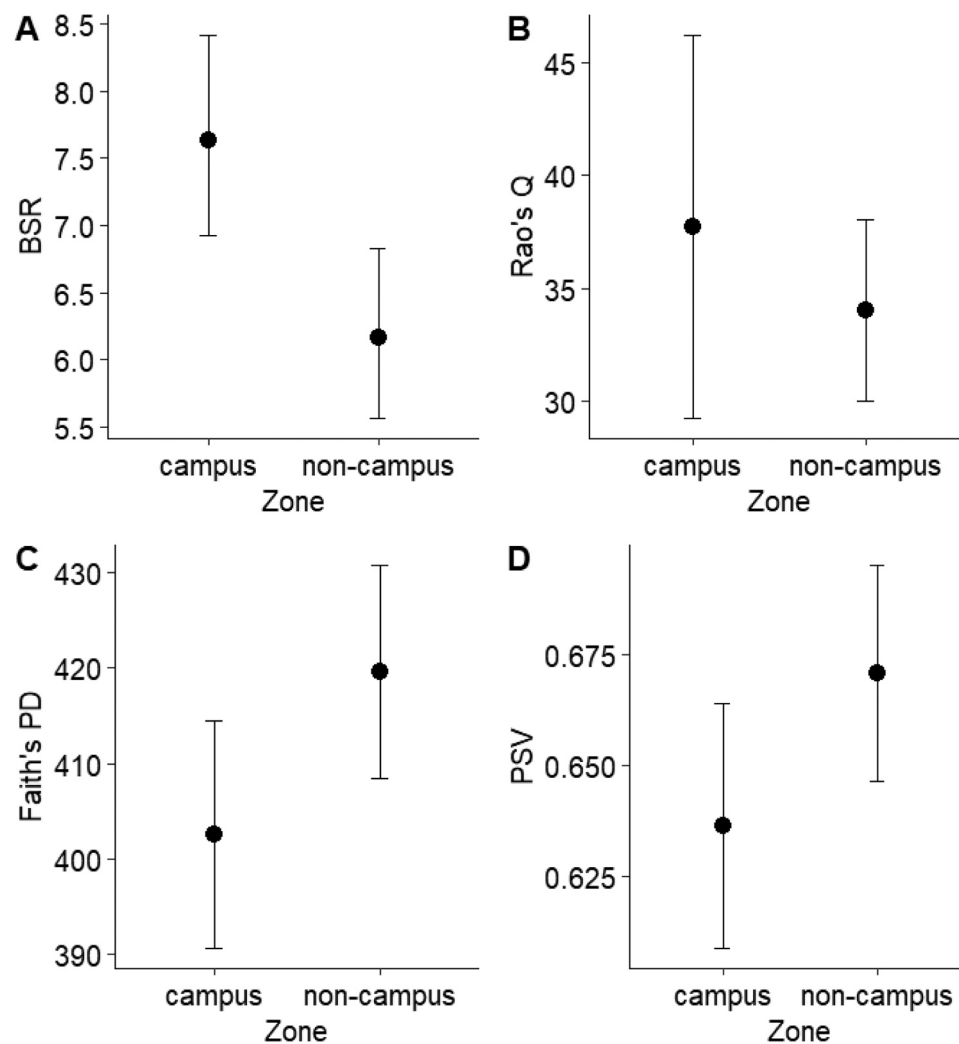


Fig. 2. Differences (mean \pm SE) between university campuses and their paired non-campus urban areas for four avian diversity components: (A) Taxonomic diversity (Bird Species Richness, BSR); (B) functional diversity (Rao's Q); (C) phylogenetic richness (Faith's PD); and (D) phylogenetic divergence (Phylogenetic Species Variance, PSV).

(Fig. 4B). This interaction (GreenEX \times Zone) was also significant for PSV ($Z = 2.11$, $p = 0.035$; Fig. 1) showing contrasting slopes for campus and non-campus areas (Fig. 4C). The data for phylogenetic relatedness (PSV) additionally showed a significant and positive association with the number of pedestrians (Estimate \pm SE = 0.03 ± 0.01 , $Z = 3.03$, $p = 0.002$; Fig. 1) and a marginally significant result for the percentage of green area of the studied polygon (GreenPO) depending on the focus zone ($Z = 1.88$, $p = 0.06$; Fig. 4 A). The complete results for all predictors can be found in Table S2.

4. Discussion

4.1. Biodiversity in university campuses

The results of our multi-city study show that Spanish university campuses hold a significantly higher number of bird species (almost 50% more) than other urban areas. This finding fits our initial prediction that university campuses are particularly species rich areas within cities and matches previous findings regarding species richness of birds and other taxa (e.g., Liu et al., 2021; Wang et al., 2021; see Fig. 2). However, our results suggest a different conclusion if we consider other components of avian diversity beyond taxonomic diversity. For functional diversity (Rao's Q), we found no differences between campus and non-campus urban areas. But our results even show the opposite

pattern when analyzing phylogenetic diversity (Faith's PD and PSV): lower levels of phylogenetic richness and divergence in university campuses compared with other randomly selected urban areas. These contrasting findings among different components of biodiversity are relatively common in urban settings (e.g., Ibáñez-Álamo et al., 2020; Morelli et al., 2021). In fact, the only previous study on university campuses exploring taxonomic, functional and phylogenetic variables also found that the different diversity components seem to be shaped by divergent predictors (Zhang et al., 2018). Our study thus leads to the same conclusion of these studies: biodiversity conservation in urban areas is complex and in need of multifactorial approaches.

Despite our contrasting findings, our investigation offers a valuable new piece of evidence in support for the importance of university campuses for urban biodiversity conservation in a relevant diversity hotspot. To our knowledge, it is the first time that several university campuses are compared with other urban areas rather than with regional species compilations or among them (e.g., Liu et al. 2021; Zhang et al. 2018). The relevance of enhancing the knowledge of university areas stems from its potential use for improving human well-being (Liu et al., 2018), educational policies (Struwe et al., 2014; Colding & Barthel, 2017) and biodiversity conservation (Liu et al. 2021; Susilowati et al., 2021). Our study supports the latter by highlighting the potential use of university campuses to retain a higher number of species in urban areas as well as species with special conservation concern.

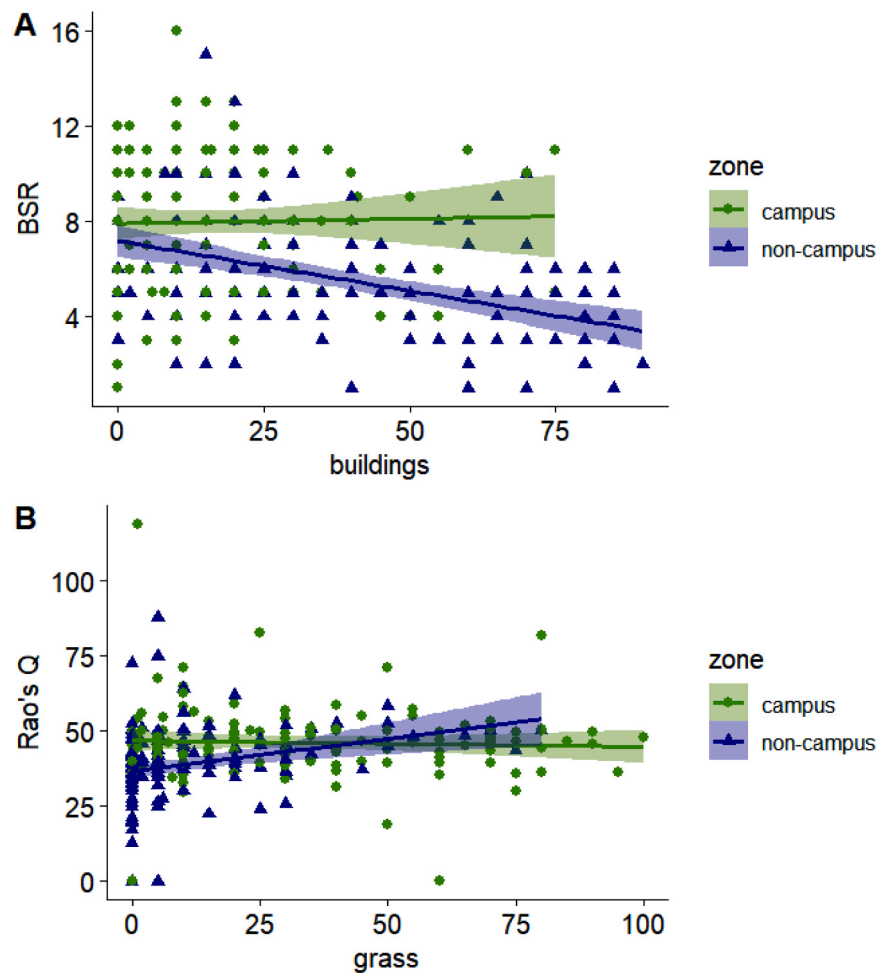


Fig. 3. A. Representation of the association between the percentage of buildings cover per zone and bird species richness (BSR) depending on the zone (campus vs non-campus). B. Representation of the association between the percentage of grass cover per zone and functional diversity (Rao's Q) depending on the zone (campus vs non-campus).

University campuses in Spain hold almost double the bird species of conservation concern than other urban areas (12 vs 7). Initially, our findings also suggest that university campuses could be areas of special interest in the management of invasive species in cities as they host more exotic bird species. However, we think this is not the case as the presence of the common waxbill (*Estrilda astrild*) and the Rose-ringed parakeet (*Psittacula krameri*) in Spanish university campuses corresponds only to a single campus each (Seville and Madrid, respectively) and we have records of these species in other non-campus urban areas in these or other cities of the country (Pârâu et al., 2016; Cardoso & Reino, 2018). Therefore, we cannot discard that this is a side effect of the random selection of non-campus urban areas.

The reasons explaining why university campuses hold higher bird species richness need further investigation, but it could be associated with the presence of certain landscape traits. Many studies have shown positive associations between vegetation cover and bird species richness in urban areas (e.g., Beninde et al., 2015; Morelli et al., 2021). As a matter of fact, we confirmed that our focal university campuses contain a significantly larger green area than their paired non-campus counterparts at the polygon level (GLMM: $F = 38.34$, $p < 0.001$; Fig. S6). Surprisingly, we found no significant association between the percentage of green cover within or surrounding our studied polygons and BSR. This could be explained if not all types of vegetation equally promoted BSR, which seems to be the case in our study system as only tree cover is positively associated with this biodiversity variable. Trees seem to offer a key resource for urban birds (White et al., 2005; Donnelly & Marzluff,

2006; Reis et al., 2012) as they provide a suitable habitat for many species, residents and migrants (Heyman et al., 2017). In contrast, other types of vegetation like bush or grass are not associated with BSR in our system while they are in others (e.g. Ibáñez-Álamo et al., 2020; Morelli et al., 2021), which could indicate that most urban bird species in Spain would correspond to woodland rather than open-country species (Table S3; see also Stagoll et al., 2010).

The findings obtained for phylogenetic richness (Faith's PD) and phylogenetic species variance (PSV), which showed the opposite pattern of that found for BSR, suggest that campuses are exerting a filtering effect for certain species (Cavender-Bares and Wilczek, 2003; Helmus et al., 2010). We do not think that these results could be explained due to specific landscape features (e.g., ponds or specific building structures) in non-campus urban areas in Spain that facilitate the presence of species with a different evolutionary background. In fact, the Muscovy duck (*Cairina moschata*) was the only species not present in campuses compared to non-campus areas in our analyses. This higher BSR (richer bird community) could hold more closely related species (e.g., higher number of warbler or parrot species) promoting a certain phylogenetic redundancy that would explain our results.

Finally, it should be noted that although there is a general pattern of bird diversity in university campuses compared to non-campus areas, we still detected considerable variation of this effect depending on the campus. These differences could be due to other factors we did not analyze such as age of the campus (influencing plant size and the establishment of ecological communities) or the percentage of native

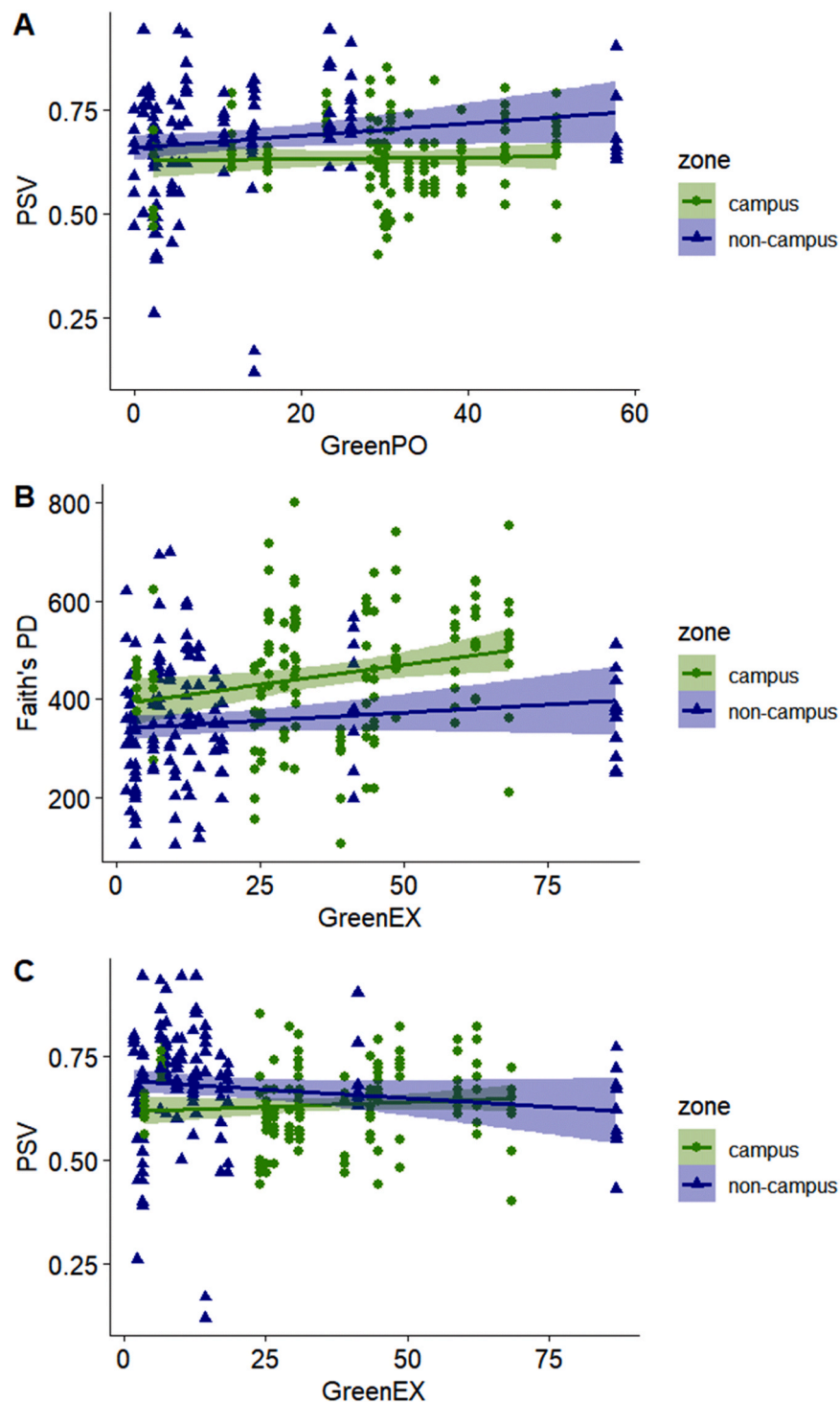


Fig. 4. (A) The effect of the percentage of green area of the polygon (GreenPO) per zone (campus vs non-campus) on phylogenetic divergence (PSV); (B) the percentage of green area of the external matrix (GreenEX) per zone (campus vs non-campus) on phylogenetic richness (Faith's PD) and on (C) phylogenetic divergence (PSV).

vegetation (Liu et al., 2017; Wang et al., 2021).

4.2. Factors that differ between university campuses and other urban areas

Our study also showed some novel findings regarding our second objective that aimed at identifying factors that could affect avian biodiversity differently in university and non-university urban areas. Bird species richness seems to be differently influenced by building

cover at the point count (small-scale) level as we found a significant interaction between this predictor and the campus (Fig. 3). In non-campus urban areas, building cover is negatively associated with BSR, as is the case in other urban ecology studies (e.g., Ibáñez-Álamo et al., 2020; Morelli et al., 2021). However, this effect is not negative in university campuses showing a striking contrast with our previous urban ecology knowledge. This contrasting effect of buildings according to zone (campus or non-campus) could also be a potential additional explanatory factor for our finding indicating a higher BSR in university

campuses. Additionally, this result suggests that university buildings could have a set of features that do not penalize (or favor) certain bird species. This is in agreement with the concept of biophilic universities proposed by Jones (2013). However, managers, city planners, and authorities should be careful when planning future university campuses as our result does not imply that intensification of campuses (increasing the built-up area of the campuses) is not negative for avian biodiversity and do not contradict previous findings in this sense (e.g., Subramanean & Davidar, 2004; Namba et al., 2010). In this sense, building cover has an important negative impact on functional diversity regardless of the zone.

Furthermore, avian functional diversity (Rao's Q) varied between campus and non-campus urban areas in its association with grass cover. When the grass cover is relatively low (<25%), functional diversity of the avian community is higher in point counts of university campuses than in those outside them. This difference disappears as the grass cover increases suggesting that non-campus urban areas would require a larger area of grass than those in university campuses to maintain a similar number of ecological functions. There are several potential explanations for this result. On the one hand, it could be that the type of grass in cities is different inside or outside university campuses. Botanists that work at the universities could be behind this potential difference as they have an active interest in plant diversity and could influence the decisions on which plant species to cultivate in their working campuses (Moerman and Estabrook, 2006). In fact, Liu et al. (2018) indicated that Chinese university campuses hold a wide diversity of plants, including herbs, and that these urban areas could play a similar role in the maintenance of plant diversity as botanical gardens. On the other hand, the difference in management practices on university campuses could be different than in other areas of the same city. Management practices are an important factor determining urban biodiversity (Beninde et al., 2015). Scientists from different universities have promoted the use of more biodiversity-friendly management practices in their campuses (Colding and Barthel, 2017). One example is the influence of scientists from the Complutense University of Madrid in the banning of glyphosate, a commonly used herbicide in many regions of the world (Grube et al., 2011) from the campuses of that university (Cabrero-Sañudo et al., 2022). According to this study, the insect species abundance in the campus doubled after the year this biocide product was not used anymore. The presence of more insects in these areas could also be reflected in bird species with additional functional traits (e.g., insectivorous) potentially explaining our results at this respect. In contrast to the association with avian functional diversity, grass cover is significantly but negatively associated with phylogenetic richness (Faith's PD) independently on whether it is a university campus or not. Our results contrast with those found in another study in which the authors found the opposite pattern for European urban areas (Morelli et al., 2021). It is possible that the differences are due to the different spatial scales (continental vs country-wide) or specific regional effects (Continental Europe vs Iberian Peninsula). According to our analyses, grass cover reduces the evolutionary history of bird assemblages which could happen if the presence of this land coverage mainly promotes the presence of bird species from certain families (e.g., finches or larks) by providing useful habitats for them. Or even if grass cover replaces other landscape traits such as water or tree cover that could filter out members of non-related birds such as ducks, shorebirds, woodpeckers or raptors.

Finally, the relative amount of green area at the landscape scale, particularly in the matrix surrounding our studied polygons, showed a contrasting association with some components of avian biodiversity. The percentage of green area at the polygon level seems to be more intensively and positively associated with phylogenetic divergence in non-campus areas than in university campuses (Fig. 4 A). This suggests that university urban areas in Spanish cities do not increase the presence of phylogenetically distant avian species as green cover area increases. This is an intriguing result that would need additional research. However, city planners could consider increasing the green area to promote this important biodiversity aspect in their urban areas. Interestingly, the

percentage of green area around the studied polygons seems to be an important factor for phylogenetic diversity (both richness and divergence). We found that this landscape predictor differs in its association with phylogenetic diversity (both Faith's PD and PSV) between campus and non-campus areas. The greener the area surrounding the studied campuses, the more phylogenetic diversity they hold, but the opposite trend is shown for non-campus urban areas (Fig. 5b and 5c). Previous studies also failed at finding a clear association between phylogenetic diversity and the urban green or built cover (Palacio et al., 2018; Leveau et al., 2020). A potential explanation for our result could be that university campuses are more permeable to phylogenetically different species (e.g., woodpeckers; see Table S3), therefore, if there are larger green areas surrounding them, unique species could be established. This increased permeability could be favored by a combination of factors that would include the increased green area (Fig. S6) or the positive influence of buildings in university campuses compared to other urban areas (Fig. 2), potentially due to their lower height (see Bhakti et al., 2021). In contrast, non-campus areas would filter out many more phylogenetically divergent species that cannot live in these more densely-built city areas. This is supported by our data showing, for example, the presence of certain phylogenetic groups such as the Picidae family in Spanish university campuses but not outside them (Table S2).

In addition to these contrasting factors, we found other predictors associated with different components of avian biodiversity regardless of the type of zone. For example, we detected that bird communities are also positively affected by the human presence for both phylogenetic components: richness (Faith's PD) and divergence (PSV), which means that bird assemblages of areas with more pedestrians have a richer evolutionary history and hold species that are less closely related. This is in agreement with other urban studies considering evolutionary history in diversity analyses (e.g., Morelli et al., 2021). In this case, our interpretation is similar to the one discussed previously regarding the campus/non-campus predictor. The density of pedestrians at the point count level is negatively associated with BSR indicating, like in other previous studies (e.g., Gagné et al., 2016; Ibáñez-Álamo et al., 2020), that human presence reduces the number of species in urban areas. This result in combination with those on phylogenetic diversity would suggest that there is a certain phylogenetic redundancy in urban areas with low human activity that is lost when human presence increases. This could be due to several species from different phylogenetic branches avoiding people, thus decreasing BSR while still keeping phylogenetic diversity high. This leads us to recommend caution when using this result to take management actions at this respect.

Water cover at the point count level is another relevant predictor for avian biodiversity, particularly for phylogenetic richness. Generally, the presence of water is associated with higher bird species richness (Beninde et al., 2015), mainly for waterbird species (Callaghan et al., 2018), which is worth mentioning provided the limitation of this resource in many Mediterranean areas, especially in summer (Burak and Margat, 2016). However, our data on BSR do not follow this pattern but match other European studies (e.g., Morelli et al., 2021) indicating that water cover is not significantly associated with a higher number of bird species. Our data from Spanish urban areas includes very few point counts ($n = 3$) with more than 10% of water cover, which could explain our results if the water cover in our study areas is not large enough to induce changes in species richness by promoting water-associated birds that would require larger water bodies (e.g., ducks, shorebirds). Nevertheless, the positive effect on phylogenetic richness suggests that even a small water body can attract water-associated birds. On the other hand, we could speculate that considering the key strategic importance of water in Mediterranean cities (Iglesias et al., 2011), alternative cover types that require fewer water (e.g., trees) are more commonly used in Spanish cities instead of water bodies to facilitate water saving. This practice would induce a higher BSR (see Fig. 1) by promoting additional species of similar evolutionary history compared to that of water bodies. Nevertheless, we consider that maintaining a minimum of small water

bodies would be crucial for the survival of many bird species due to the dry conditions of the Mediterranean region.

5. Conclusions

Our study is the first comparing campus and non-campus urban areas in the Western Mediterranean, a crucial hotspot of biodiversity worldwide (Myers et al., 2000; Pascual et al., 2011), using spatial replicates and multiple components of biodiversity (taxonomic, functional, and phylogenetic). The importance of studies similar to the presented here was stated by Uhl & Anderson (2001), so that those universities with campuses that maintain high biodiversity levels (and especially those with higher levels than other urban areas; Fig. S2-S5) should use their influence as strong institutions to improve local environmental policies of their communities, as they can serve as an urban model for hosting a wide array of biodiversity.

First, we found that not all biodiversity components are equally promoted in these specific urban areas in line with the only previous study analyzing taxonomic, functional and phylogenetic variables in this context (Zhang et al. 2018). Our data highlight that universities could play a key role in reducing the strong biodiversity loss associated with urbanization (e.g., Aronson et al., 2014; Ibáñez-Álamo et al., 2017), particularly regarding taxonomic diversity (bird species richness). However, our results suggest that university campuses could have a certain phylogenetic redundancy that provides an interesting additional evolutionary point of view useful in a conservation biology framework (Tucker et al. 2017).

Second, we identified that university campuses have several factors that are differently associated with urban avian biodiversity compared with other areas of the same city: university buildings do not negatively affect bird diversity as other urban buildings do; the same value of grass cover holds higher levels of avian diversity in university campuses than in non-campus areas; and that the greener the area surrounding the campuses (but not so the inside one), the more diverse bird community.

Third, a series of predictors (tree cover, human presence and water cover) promoted certain aspects of avian biodiversity and could be used by city planners and managers to enhance birds in their cities ultimately increasing the human well-being of their citizens (Methorst et al., 2021).

Finally, our data also indicated that universities are designed in a more eco-friendly way than other urban areas, for example with a larger proportion of green areas that could be behind some of the observed patterns. Of course, there are still interesting and important research questions that need to be explored, such as the seasonal approach (e.g., Caula et al., 2014; Ibáñez-Álamo et al., 2020), or the effect on different taxonomic groups (e.g., insects due to their importance for global biodiversity) to understand whether our findings can be generalized or are taxon-dependent. Despite future contributions, we hope that our study helps appreciate university campuses as important conservation urban areas (at least in the Mediterranean region) that could be useful in minimizing the negative impact of urbanization on biodiversity.

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CRediT authorship contribution statement

Olivia Sanllorente: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Visualization. **Rocío Ríos-Guisado:** Methodology, Software, Formal analysis, Investigation, Data curation, Writing – review & editing. **Lucía Izquierdo:** Methodology, Investigation, Writing – review & editing. **José Luis Molina:** Writing – review & editing, Investigation, Writing – review & editing. **Emeline**

Mourocq: Software, Validation, Formal analysis, Data curation, Writing – review & editing, Visualization. **Juan Diego Ibáñez-Álamo:** Conceptualization, Methodology, Validation, Resources, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition.

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.

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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.ufug.2023.128038.

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