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# Luxury and legacy effects on urban biodiversity, vegetation cover and ecosystem services

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Socio-economic and historical drivers shape urban nature distribution and characteristics, as luxury (wealth-related) and legacy (historical management) effects. Using remote sensing and census data on biodiversity and socio-economic indicators, we examined these effects on urban biodiversity and vegetation cover in Vitoria-Gasteiz (Basque Country). We also tested the luxury and legacy hypotheses on regulating ecosystem services (ES) and explored predictor interactions. Higher educational attainment positively correlated with urban biodiversity, confirming the luxury effect, but had no effect on vegetation cover or ES. Older areas had higher vegetation cover and ES evidencing a legacy effect with an inverse response on biodiversity, attributable to more recent management strategies promoting biodiversity in green spaces. Habitat quality amplified the luxury effect, while population density strengthened the legacy effect. Our results suggest that urban biodiversity is mainly driven by socio-economic factors, while vegetation cover and ES are influenced by management legacies in interaction with population density.

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## INTRODUCTION

Urban green spaces (UGS) and their associated biodiversity are key to urban residents' health and quality of life[1,2]. Green infrastructure, including parks and street trees, is increasingly considered in urban planning as nature-based solutions (NbS) for climate change adaptation and mitigation[3–5]. UGS provide multiple ecosystem services (ES) and functions, such as habitat maintenance, local climate regulation, air quality improvement, runoff control, and spaces for people to relax, exercise, socialise, among others[6–8]. These benefits are influenced by the characteristics of the UGS, such as their structure, size, connectivity, and biodiversity[9,10]. For instance, tree diversity and vegetation structure can affect the amount of shade reducing the urban heat island effect, its quantity can influence the amount of carbon sequestration, and connectivity can promote wildlife movement in the landscape[11]. Additionally, different taxonomic groups can further contribute to plant pollination, providing food and other resources, improving soil and water quality, and control pests.

Classical approaches in ecological research have largely focused on climatic and other natural or semi-natural factors as local biodiversity determinants[12]. However, socio-economic factors related to wealth or urban form and development are increasingly being recognised as key drivers of biodiversity patterns in cities[12–14]. The effect of urban development and social dynamics in cities lead to heterogeneous urban landscapes by influencing the spatial distribution and proportion of impervious surfaces, availability of resources, and environmental quality factors like water, soil or air quality[1,15]. In this context, urban residents with higher socio-economic status, have a greater capacity to allocate resources towards vegetation and habitat, thereby influencing the overall UGS dynamics[1,15,16]. In addition, wealthier residents can have greater influence and agency over public and private decisions, including land use planning and investments in their neighbourhoods, due to their lobbying capacity, as well as access to decision-makers, including public and private investors[7,16]. Their political connections, social capital, knowledge, and access to information further strengthen their ability to advocate for their own interests, which can ultimately shape urban biodiversity and vegetation patterns over time[2,16–18]. Driven by the lifestyle choices, social status, and ability to invest in environmental management options, the influence of wealthier residents can ultimately contribute to environmentally driven neighbourhood differentiation[16,19]. These factors collectively contribute to the complex dynamics of urban ecosystems and their biodiversity[2,19]. Thus, urban residents may have differential access to nature and its associated benefits, including situations where disadvantaged communities may often experience deprived access to those benefits[20]. Human-driven uneven distributional patterns of vegetation and biodiversity can shape ecological patterns underpinning ecosystem functions and ES in urban contexts[15]. People's exposure to nature and its related benefits has been increasingly constrained to urban contexts with advancing urbanisation[9,21]. Since urban nature and biodiversity tend to be unevenly distributed across social groups, it is key to address its distribution in urban contexts from an environmental justice dimension[7,22].

Wealthiest areas have been spatially related to higher biodiversity, a pattern defined as 'luxury effect', and proxied by plants[12,23,24], birds[14,24,25] and to mammals, lizards and arthropods to a lesser extent[1,14,26]. This pattern has also been analyzed regarding urban green cover inequalities using remote sensing[27–29]. Thus, lower household income and individual educational attainment have been associated with low abundance of trees within urban areas[30]. However, the exclusive use of

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conventional economic indicators, such as income, as proxies for social status in studies of the luxury effect is a topic of debate. These indicators oversimplify complex social concepts, making accurate quantification challenging. Recent meta-analysis has indicated that income might be an incomplete predictor of ecological communities' patterns[31]. Therefore there is a strong need to include alternative indicators that consider individual development opportunities, capabilities, and other factors for a comprehensive understanding of the luxury effect. In this regard, education is an alternative descriptor that may capture a broader range of socioeconomic variation and improve the ability to explain the luxury effect[1,23,31,32]. Previous research has shown that people with higher educational attainment are more likely to prefer and have the economic means to live in areas with more UGS in cities[32–34]. Such wealthier groups may also exert a higher influence on urban environmental management, tending to demand higher environmental quality in their neighbourhoods, e.g. by supporting vegetation cover in neighbourhoods where they live[32]. Although income and higher educational attainment have been associated with urban biodiversity patterns in the literature, their correlation does not imply a causation. This is because urban socio-ecological systems are shaped by a myriad of biophysical and social factors, and their interactions, including population dynamics, biogeographical filters, socio-cultural aspects, habitat fragmentation and land uses[9,11,13,35].

The way vegetation cover and biodiversity are spatially distributed in urban landscapes is further influenced by the legacies of past land use policies, including UGS management practices and urban planning strategies[15,17,23,36]. This is defined as 'legacy effect' and is often explained by higher plant diversity in older neighbourhoods (i.e. areas with older housing and urban development), and reflects the longer-term trajectory of management practices[2]. For instance, longer development periods will allow for a higher tree diversity due to extended successional times, several establishment of different tree species by multiple managers, and adequate timeframes for species with long lifespans to reach their full size[2,19,23]. Since legacy effect can uphold biodiversity patterns driven by luxury effect over time, both luxury and legacy effects may result in additive responses[12].

Understanding the consequences of luxury and legacy effects on spatial patterns of urban biodiversity and their cascading effects on human well-being may contribute to better management practices and strategies towards environmental justice. Hence, we here analyse how luxury and legacy effects influence the spatial distribution of vegetation cover, biodiversity and their associated regulating ES in urban landscapes. Our study contributes to the limited existing knowledge about the role of luxury and legacy effects on the provision of ES in urban landscapes. We focus our study on the mid-size European city of Vitoria-Gasteiz (248,087 inhabitants[37]), located in the Basque Country. In the 1990s, Vitoria-Gasteiz implemented an ecological restoration initiative to create a green belt in its degraded peripheral areas. In 2012, the city was awarded as the European Green Capital, recognising its greening efforts. Following that, during 2014, a green infrastructure plan was designed to further increase UGS towards the urban core, promote urban wildlife, and enhance ES[9,38]. We here: i) test for the luxury and legacy effects by assessing the relationship between urban residents' high educational attainment and urban development age, respectively, regarding biodiversity and vegetation cover; and ii) assess how luxury and legacy effects influence the supply of regulating ES, by focusing on those provided by public urban trees. We expect to evidence the presence of luxury and legacy effects, which are associated with increased biodiversity and vegetation cover, thereby enhancing the capacity to provide regulating ES. However, we expect these effects to be influenced by additional socio-environmental factors and their interaction, such as population density, vegetation cover, and habitat quality, which are often overlooked in the analysis of these effects. By integrating these factors and their interactions, our research contributes to a more comprehensive understanding of the complex dynamics shaping urban environments.

## RESULTS

### Luxury and legacy effects on biodiversity

Biodiversity, as proxied by tree and bird species richness, was positively associated with high educational attainment, as an indicator of the luxury effect ($R^2 = 0.25$, $F = 10.01$, $p < 0.01$, Fig. 1, Table 1). Conversely, biodiversity was negatively associated with the indicator of legacy effect: neighbourhood development age ($R^2 = 0.22$, $F = 8.61$, $p < 0.01$, Fig. 1, Table 1). Neighbourhoods with higher biodiversity corresponded to those which underwent significant urban development between the late 1970s and the late 1990s (See Supplementary Table 2). Furthermore, species richness was positively correlated to habitat quality ($R^2 = 0.45$, $F = 22.85$, $p < 0.001$, Fig. 1, Table 1) with a logarithmic response, vegetation cover ($R^2 = 0.16$, $F = 6.35$, $p < 0.05$, Fig. 1, Table 1) and negatively to neighbourhood´s population density ($R^2 = 0.34$, $F = 14.92$, $p < 0.001$, Fig. 1, Table 1).

Apart from these direct effects, we also found significant effects on the interaction between variables correlated to species richness. Urban biodiversity was correlated with the interaction of high educational attainment and habitat quality, where biodiversity increased with high educational attainment, particularly so in neighbourhoods with higher habitat quality ($R^2 = 0.53$, $F = 31.09$, $p < 0.001$, Fig. 2A, Table 1). In addition, urban biodiversity was negatively correlated with the interaction between neighbourhood development age and population density, where biodiversity decreased with neighbourhood age, particularly so in more densely populated neighbourhoods ($R^2 = 0.38$, $F = 17.92$, $p < 0.001$, Fig. 2B, Table 1).

Furthermore, neighbourhood age and population density were highly correlated in Supplementary Fig. 4 ($R = 0.64$; $p < 0.01$).

### Luxury and legacy effects on vegetation cover

Vegetation cover, including both herbaceous and canopy cover, showed no significant relation to higher education attainment, as an estimator of the luxury effect (Table 1). Furthermore, it was positively correlated with habitat quality ($R^2 = 0.29$, $F = 12.23$, $p < 0.01$, Table 1), showing a logarithmic response, and negatively correlated with population density at neighbourhood scale ($R^2 = 0.39$, $F = 18.36$, $p < 0.001$, Table 1). Yet, vegetation cover decreased with neighbourhood age, as an estimator of the legacy effect, particularly so, in areas with higher population density, where older and more populated neighbourhoods tend to have lower vegetation cover ($R^2 = 0.15$, $F = 5.97$, $p < 0.05$, Fig. 1, Fig. 3, Table 1). Newly developed neighbourhoods typically with lower population densities showed a high share of vegetation cover (Supplementary Fig. 2 and Supplementary Table 1). Habitat quality also showed a positive logarithmic response to vegetation cover ($R^2 = 0.29$, $F = 12.23$, $<0.01$).

### Luxury and legacy effects on ecosystem services

The estimated provision of regulating ES based based on the application of the i-Tree tool[39] for in Vitoria-Gasteiz in 2015, indicated that urban trees accounted for 185,145 $m^3$/yr. of transpired water, 30,652 $m^3$/yr. of avoided runoff, 14.1 ton/yr. of removed air pollutants and 617.0 ton/yr. of carbon sequestration respectively (Supplementary Table 3). Since these four regulating ES were spatially co-ocurrent, we aggregated them into a single ES index with a value ranging from 0 (no provision) to 100 (highest provision). Moran's I showed no significant autocorrelation in the

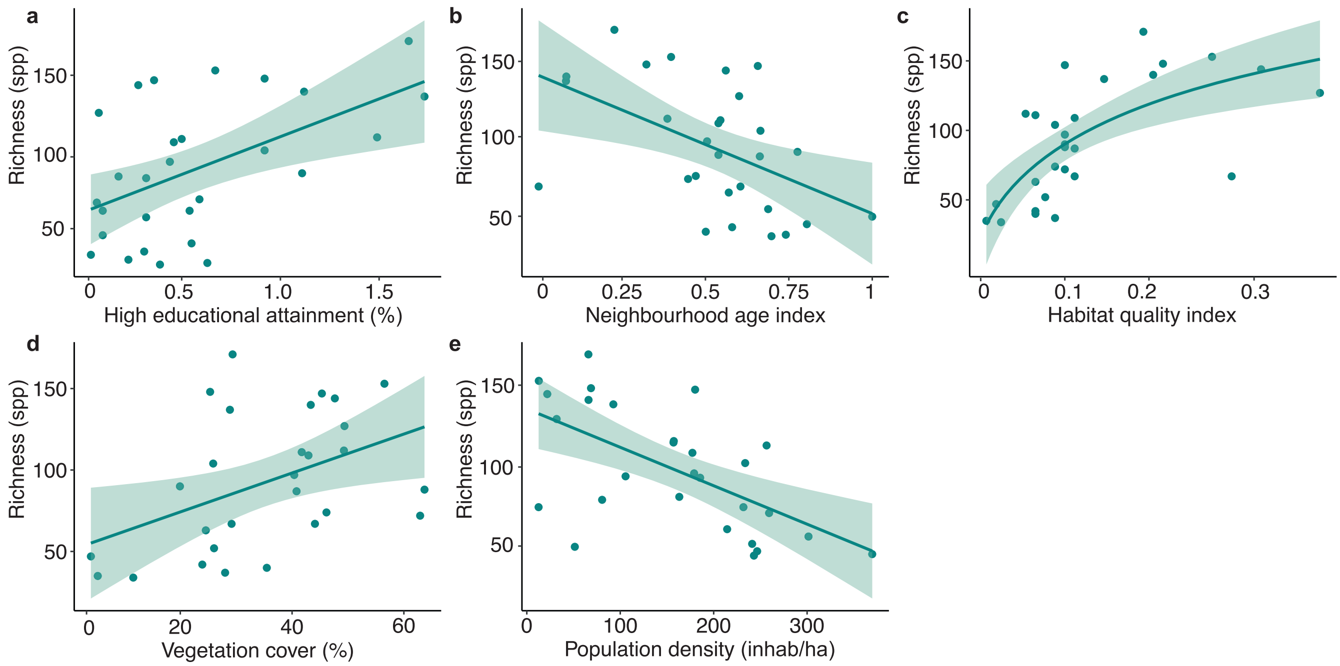


**Fig. 1 Urban biodiversity responses to socio-environmental characteristics.** Linear models of biodiversity, expressed as tree and bird species richness, in response to **a** high educational attainment (% of the population with high education attainment by neighbourhood over the total population, proxy of luxury effect), **b** neighbourhood development age index (values ranging from 0 – newest to 1 – oldest), **c** habitat quality index (values ranging from 0- lowest to 1- highest), **d** vegetation cover (% by neighbourhood) and **e** neighbourhood population density (inhab/ha). Shaded areas represent the 95% confidence interval. Model information provided in Table 1.

**Table 1.** Linear models of urban biodiversity and vegetation cover to socio-environmental characteristics.

| Model | Adj. $R^2$ | F | *p* | Std.Error |
|---|---|---|---|---|
| Biodiversity *(Species richness)* | | | | |
| *Richness = 66.05 + 46.32 * High education* | 0.25 | 10.01 | <0.01 | 36.09 |
| *Richness = 140.68 - 91.70 * Neighbourhood age* | 0.22 | 8.61 | <0.01 | 36.82 |
| *Richness = 202.40 + 52.89 * log(Habitat quality)* | 0.45 | 22.85 | <0.001 | 30.99 |
| *Richness = 50.34 + 1.19 * Vegetation cover* | 0.16 | 6.35 | <0.05 | 38.08 |
| *Richness = 133.87 - 0.26 * Population density* | 0.34 | 14.92 | <0.001 | 33.86 |
| *Richness = 63.44 + 355.11 * High education:Habitat quality* | 0.53 | 31.09 | <0.001 | 28.67 |
| *Richness = 124.64 - 0.33 * Neighbourhood age:Population density* | 0.38 | 17.92 | <0.001 | 32.68 |
| Vegetation cover (%) | | | | |
| *Vegetation cover = 39.07 - 6.35 * High education* | 0.00 | 1.03 | n.s. | 15.44 |
| *Vegetation cover = 50.84 - 29.46 * Neighbourhood age* | 0.15 | 5.97 | <0.05 | 14.2 |
| *Vegetation cover = 69.04 + 16.21 * log(Habitat quality)* | 0.29 | 12.23 | <0.01 | 12.98 |
| *Vegetation cover = 51.68 - 0.10 * Population density* | 0.39 | 18.36 | <0.001 | 12.05 |
| *Vegetation cover = 48.53 - 0.14 * Neighbourhood age:Population density* | 0.48 | 26 | <0.001 | 11.13 |
| *Vegetation cover = 35.44 - 0.33 * High education:Habitat quality* | −0.04 | <0.001 | n.s. | 15.74 |

Model and parameters of urban biodiversity (tree and bird species richness) and vegetation cover (% per neighbourhood) in response to: high educational attainment (% of the population with high education attainment by neighbourhood over the total population, proxy of luxury effect), neighbourhood development age index (values ranging from 0 – newest to 1 – oldest), habitat quality index (values ranging from 0- lowest to 1- highest), population density (inhab/ha), vegetation cover (only for biodiversity), and interactions of high educational attainment with habitat quality and neighbourhood age with population density. Model formula for each predictive variable, adjusted variance explained ($R^2$), F-statistic (F), significance level (p) and standard error (Std. Error). $N = 28$, n.s.: non-significant.

spatial distribution of the aggregated ES index (Moran's I: z-score = 0.34, $p = 0.72$).

The regulating ES index was higher in older neighbourhoods surrounding the historical mediaeval neighbourhood of Casco Viejo (old town) (Fig. 4) with higher canopy cover (Supplementary Fig. 1 and Fig. 2). Conversely, the lowest share of the urban tree canopy, and thus the lowest provision of regulating ES was registered in Casco Viejo, and newer neighbourhoods located on the outskirt's areas of the city where tree-based green infrastructure is more recent (Fig. 4).

The ES index was positively correlated with vegetation cover, including trees and herbaceous vegetation (Table 2). We found no

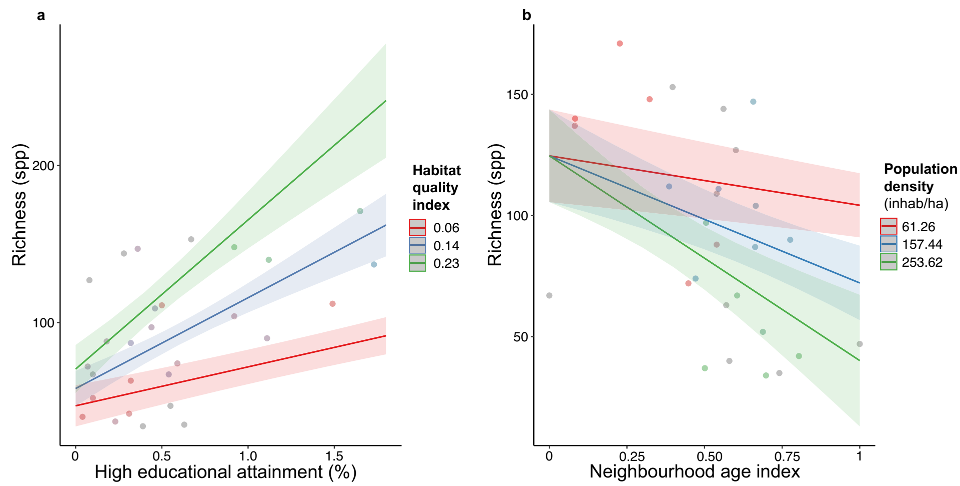


**Fig. 2 Urban biodiversity responses to proxies of luxury and legacy effect.** Linear models of biodiversity, expressed as tree and bird species richness, in response to **a** high educational attainment (% of the population with high education attainment by neighbourhood over the total population, proxy of luxury effect), by levels of habitat quality index (values ranging from 0 - lowest to 1 - highest), and **b** neighbourhood age index (values ranging from 0 – newest to 1 – oldest, proxy of legacy effect) by levels of population density (inhab/ha). Shaded areas represent a 95% confidence interval. Habitat quality and population density are grouped into three categories defined by the mean value and +/-1 standard deviation[78]. Model information provided in Table 1.

**Table 2.** Linear models of regulating ecosystem services index to socio-environmental characteristics.

| Ecosystem Services | | | | |
|---|---|---|---|---|
| Model | Adj. $R^2$ | F | *P* | Std.Error |
| *ES = 50.95 - 15.87 * High education* | 0.05 | 2.65 | n.s | 24.05 |
| *ES = 27.05 + 28.22 * Neighbourhood age* | 0.03 | 1.85 | n.s | 24.39 |
| *ES = 57.50 - 108.29 * Habitat quality* | 0.10 | 4.03 | n.s | 23.49 |
| *ES = 15.11 + 0.75 * Vegetation cover* | 0.19 | 7.39 | <0.05 | 22.28 |
| *ES = 37.84 + 0.02 * Population density* | -0.02 | 0.25 | n.s | 25.12 |
| *ES = 7.47 + 2.0 * Neighbourhood age:Vegetation cover* | 0.57 | 37.2 | <0.001 | 16.19 |

Model and parameters of regulating ecosystem services index (ES) in response to: high educational attainment (% of the population with high education attainment by neighbourhood over the total population, proxy of luxury effect), neighbourhood development age index (values ranging from 0 – newest to 1 – oldest), habitat quality index (values ranging from 0 - lowest to 1 - highest), vegetation cover (% per neighbourhood), population density (inhab/ha), and interactions of vegetation cover with population density. Model formula for each predictive variable, adjusted variance explained ($R^2$), F-statistic (F), significance level (*p*) and standard error (Std. Error). *N* = 28, n.s.: non-significant.

direct correlation between the ES index regarding luxury or legacy effect predictors alone, *i.e.* high educational attainment and neighbourhood age, respectively (Table 2). Yet, we found a legacy effect on regulating ES mediated by vegetation cover. That is, the regulating ES index was positively correlated with neighbourhood age when interaction with vegetation cover is included, where older neighbourhoods provide more regulating ES, especially in neighbourhoods with more vegetation cover ($R^2 = 0.57$, $F = 37.2$, $p < 0.001$, Fig. 5, Table 2).

## DISCUSSION

Our results support the 'luxury effect' hypothesis, which suggests that urban biodiversity is associated with wealthier neighbourhoods, which tend to have higher education attainment[15,30]. Species richness is positively correlated with high educational attainment (Table 1, Fig. 1). This correlation is particularly strong in neighbourhoods with higher levels of educational attainment and higher-quality habitats, emphasising the luxury effect. Previous research suggests that this luxury effect can be attributed to human and other species' preferences for environmentally desirable areas while avoiding environmental burdens such as pollution[1,15]. Wealthier social groups, proxied as those group with higher educational attainment in this study, hold significant influence over local UGS investments and have the capacity to shape land use planning according to their interests[16]. The greater resources of wealthier households enable them to allocate more towards private green spaces, resulting in enduring legacy effects that reinforce the luxury effect and bring about long-term changes in UGS composition[12,36].

We also found an inverse legacy effect on urban biodiversity, with declining species richness as neighbourhood development age increases (Fig. 1). This is likely attributable to the dynamic influence of neighbourhood development on the quality of urban ecosystems. UGS are inherited in the landscape, reflecting legacies of past management, greening movements, and changing socio-economic conditions, that affect neighbourhood development and people's behavioural changes[36]. The historical decisions and urban planning employed in the past have a lasting effect on current vegetation cover patterns, which may not be easily predicted based on present data[19,30,32]. Vitoria-Gasteiz has historically prioritised the conservation of older neighbourhoods while preserving the design and medieval architecture of the old town, with the creation of UGS being a more recent priority (since the 1990s). Evidence from the city shows that, although it has a relatively long history of green planning, UGS close to the urban core, where older neighbourhoods are located, has resulted in lower ecological quality, but still provides multiple ES such as recreation, cooling or runoff control[9,38]. Other landscape descriptors were found to influence urban biodiversity, in particular, habitat quality, vegetation cover, and population density at neighbourhood scale (Fig. 1). These are key factors that had an effect on the magnitude of both luxury and legacy effects: while the luxury effect on biodiversity was stronger in areas of high habitat quality, the inverse legacy effect was more pronounced with increased population density. This implies complex socio-ecological interactions that influence luxury and legacy effects,

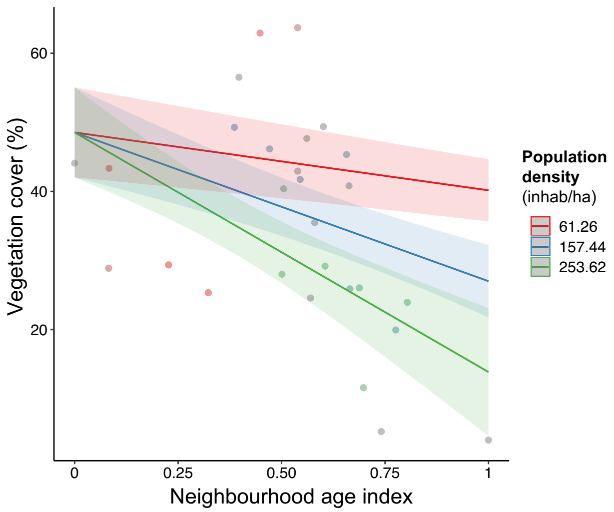


**Fig. 3 Vegetation cover (% of neighbourhood area) linear models in response to the interaction of neighbourhood age index and population density.** Shaded areas represent the 95% confidence interval. Population density (inhab/ha) categories grouped by three terms defined by the mean value and +/−1 standard deviation[78]. Model information provided in Table 1.

including discourses, narratives about environmental management, and the role of social power and political influence. Hence, it is essential to understand the socio-political context of the city in order to gain insight into the ideological motivations behind greening efforts[13,40].

Our findings provide useful information on how both effects can be further influenced by ecological and social descriptors. In order to improve habitat quality and greening to enhance biodiversity, urban management should focus on the ecological status of older neighbourhoods in the urban core. Given the logarithmic response of habitat quality to species richness (Fig. 1), increases of habitat quality at the lowest ranges would have comparatively higher effects on species richness than at higher ranges. The most biodiverse neighbourhoods (Fig. 2), were mainly developed between the late 1970s and early 2000s (Supplementary Fig. 1 and Fig. 2). During this period, urban policies were implemented to drive greening strategies to reverse the damage from industrial activities and urban expansion (Supplementary Table 2)[40]. This suggests that past management practices and planning history continue to strongly influence present outcomes. Time is a key factor in urban biodiversity dynamics, particularly for species with slower colonisation times[2]. Thus, legacy effects must be considered in a broader context, incorporating land-use management history to understand how past management actions has shaped current landscape characteristics[36].

Our findings also indicate that, when solely considering vegetation cover (in both public and private land), there is no evidence to support the luxury effect hypothesis observed in previous studies[23,28,30,32]. This suggest that greener neighbourhoods do not necessarily attract residents with higher educational attainment, nor do they have increased habitat quality due to their ‘green’ character (Table 2). Hence, we infer that biodiversity was a better indicator than vegetation cover when analysing the luxury effect. This could be attributed to other factors not taken into account here, such as management choices involving the selection of native or non-native plant species, or preferences of some species over others.

We found that population density negatively affects species richness (Fig. 1) and exacerbates the negative effects of neighbourhood age on biodiversity and vegetation cover (Fig. 2). Population density and neighbourhood age are correlated (Supplementary Fig. 4), suggesting that older neighbourhoods tend to be more densely populated, having a detrimental effect on biodiversity and vegetation cover. This can be attributed to the design of historical old towns, like our case study, characterised by narrow streets and compact forms, compared to later developments like suburbs and urban sprawl areas, which tend to be less dense[41]. Population density influence vegetation trends over time, by affecting available canopy space and limiting the growth of new individuals of trees[2,42]. The relationship between population density and vegetation cover is complex, with both positive and negative associations observed[16,42]. For instance, while population density and income have been negatively correlated with vegetation cover[2], vegetation cover has been positively linked to more housing units[16]. These mixed outcomes suggest the importance of considering multiple factors and their interactions, such as education, land use management legacies, and income, when examining population density. Our study highlights that population density not only directly affects biodiversity negatively but also amplifies the negative impact of neighbourhood age on biodiversity and vegetation cover (Figs. 1, 2, 3).

We also found an inverse legacy effect between vegetation cover and neighbourhood age, that as per species richness was mediated by population density (see Fig. 3), implying that older and more populated neighbourhoods have less vegetation cover. Additionally, there was a decreasing trend of herbaceous vegetation cover towards the urban core (Supplementary Fig. 1), possibly due to urban densification[2,23]. Less populated areas, with lower housing density maintain a relatively high percentage of both herbaceous and tree cover (Fig. 3). Given these findings, urban planners should prioritise strategies that conserve and enhance vegetation in older and more compact areas. This is particularly crucial considering the effects of climate change in cities, which lead to environmental burdens like air pollution and heat stress, exacerbating environmental and climate injustices[43]. Implementing interventions such as green roofs, green walls, and street trees becomes key, especially in densely populated urban areas with limited space[44]. These interventions not only mitigate the challenges but also contribute to tackle the unequal distribution of greening. Moreover, prioritising green over impervious cover is vital to prevent the negative impacts of urban densification on biodiversity and vegetation, which worsen environmental injustices. To guide evidence-based strategies in sustainable urban development, further research is needed to understand how population density, land use, and neighbourhood age influence biodiversity and vegetation cover.

Moving on to the effects on regulating urban ES, our research tested the luxury and legacy hypotheses for ES for the first time. Higher educational attainment and neighbourhood development age were not associated with regulating ES provision when considered as single terms (Table 2). However, we observed a strong association between vegetation cover and regulating ES provided by urban public trees. Nevertheless, there was no evidence that increased urban biodiversity leads to a larger flow of these regulating ES. The distribution of regulating ES seemed to be influenced by management and land use legacies, indicated by neighbourhood development age, in interaction with vegetation cover (Fig. 5). Our models that included richness and habitat quality were statistically non-significant (Table 2). This suggests that urban tree planting schemes in the past may have been focused at providing shading or aesthetic purposes rather than enhancing plant diversity. Our results support that older neighbourhoods with higher canopy cover yield more regulating ES, even if they have less biodiversity[7]. The i-Tree Eco accounts for tree structural traits (e.g. DBH, height, and crown size), which have a greater influence on regulating ES than tree diversity[45]. Urban trees typically have an average lifespan of between 19 and 28 years, and the mortality rate of young trees is generally high[46]. As such, older neighbourhoods with larger, more mature trees

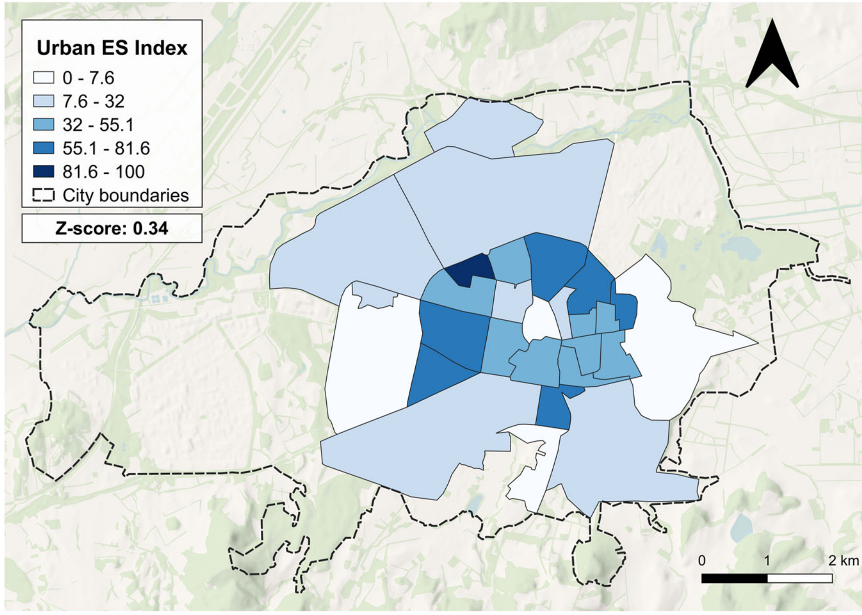


**Fig. 4 Spatial distribution of the regulating ES index supplied by urban trees at the neighbourhood scale.** Index values were classified using natural breaks for spatial representation: by maximising variance between classes and minimising variance within each class. Background from © MapTiler (www.maptiler.com) and © OpenStreetMap (CC BY-SA 2.0).

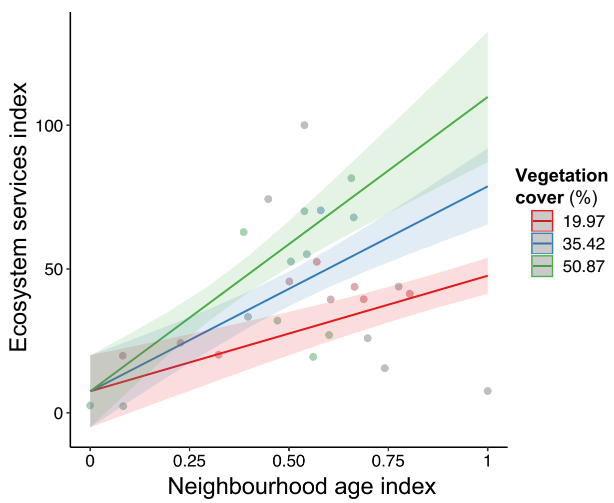


**Fig. 5 Ecosystem services (ES) linear models in response to the interaction of neighbourhood age index and vegetation cover (% per neighbourhood).** Shaded areas represent the 95% confidence interval. Neighbourhood development age is grouped by three terms defined by the mean value and +/−1 standard deviation[78]. Model information provided in Table 2.

provide higher regulating ES when compared to newer neighbourhoods with a higher proportion of young trees and herbaceous cover (Fig. 4). This pattern may be influenced by age, suggesting that the older and greener the neighbourhood, the stronger the relationship with regulating ES provision (Fig. 5). This could be due to the long-term establishment of trees[2], with large old trees being carefully maintained for their cultural and heritage values[47,48]. Our findings suggest that ES provision is concentrated in areas surrounding the urban core, where a higher proportion of public older trees are located. However, this also implies that newer neighbourhoods offer potential opportunities to enhance green cover, biodiversity conservation and ES provision in the future, as tree canopy cover increases with age. Together, these findings suggest that UGS identity is markedly different between older and newer neighbourhoods, reflecting relevant legacy effects patterns.

This research illustrates the multidimensional character of the socio-economic attributes associated with urban biodiversity, vegetation and ES. While the associations described here are correlative and do not infer direct causation, our findings emphasise the relevance of the luxury effect phenomenon. We have also shown that the legacy of prior investment and management of UGS has a considerable effect on how benefits from the urban canopy are distributed within a city. Urban planning and the implementation of green infrastructure must consider these effects to address climate adaptation, biodiversity conservation, and environmental justice. This is especially important as the people capable to pay the increased property and rent prices associated with more biodiverse and green areas, and thus investing in higher adaptive capacity to climate change, are high-income residents[2,49–51].

Our results support the notion that past land use planning and development, with or without planning, influence the availability and quality of UGS, thus impacting the potential effectiveness of green infrastructure, including the exposure and access to regulating ES, which are key for climate adaptation[3]. This has consequences for residential areas, which often reflect lifestyles associated with group identities and social status[16,19,52]. Management decisions, such as allocating resources for urban green infrastructure, can further drive neighbourhood differentiation and exacerbate existing environmental injustices[50]. This highlights the importance of considering luxury and legacy effects in urban planning strategies from an environmental justice perspective to achieve a better balance in the distribution of UGS and associated ES. This has important implications for environmental justice, as the way urban planning for green infrastructure is implemented will determine who ultimately benefits from urban investments. This includes recognising and accounting for the socio-economic structure embedded in urban planning practices, which can drive systemic and asymmetric power relationships that reproduce environmental injustices[50].

Expanding and conserving UGS as part of urban green infrastructure without prioritising access to their benefits for vulnerable groups can exacerbate environmental injustices and trigger luxury effects[53]. It is crucial to prioritise access to these benefits for those who need them the most, particularly for individuals and communities who are most exposed to hostile environmental conditions. Achieving this requires considering socio-environmental variables such as population density, which can affect the responses of luxury and legacy effects on the distribution of UGS and associated ES. Therefore, these variables should be included in management strategies to better predict the impact of these effects on the distribution of UGS and ES[2]. This, in turn, can have an effect on the success or failure of biodiversity and ecological quality enhancement policies across urban green infrastructure and multiple ES[54,55]. Urban managers often perceive biodiversity conservation as a co-benefit of other actions (e.g. opportunities for recreation, or mitigating extreme events), rather than a strategic priority systematically planned to enhance ecological integrity in the urban context[4].

Planning urban green infrastructure becomes a key determinant of biodiversity patterns and ecosystem functions, as well as providing access to and exposure of urban nature and its associated ES. Older neighbourhoods with early designed UGS have distinct structural and natural features that influence their ability to support biodiversity and provide ES. Thus, UGS should be evaluated based on their specific characteristics and capacity to support ES, which are influenced by historical perceptions of green spaces. In the context of Vitoria-Gasteiz, the city's urban form and historical characteristics present a challenge when it comes to integrating green infrastructure into older areas. This demands the implementation of green-grey infrastructure integration approaches. However, in newer areas of the city, there is an opportunity to prioritise a higher coverage of trees to facilitate a greater flow of ES in the future[7]. By doing so, both the legacy effect and the population density effect can be taken into account, leading to a more equitable distribution of UGS and their associated ES throughout the city.

To reduce inequalities, strategies should focus on increasing learning opportunities in and about nature, amplifying its social value, investing in long-term biodiversity enhancement plans, and implementing conservation and restoration actions to protect and improve vegetation cover. These measures could foster community engagement in the creation and preservation of UGS, while also mitigating the impacts of population density and supporting the success of ecological quality enhancement policies. However, it is important to acknowledge that social inequalities may persist. Residents in economically disadvantaged areas may have limited resources to allocate towards private green spaces, hindering their participation in green initiatives. Addressing resource constraints alongside educational efforts is crucial to achieve equitable access to UGS and mitigate green inequalities. Further research is needed to identify the specific types of regulating ES provided by different tree species, which could help prioritise tree planting schemes in coordination with urban biodiversity enhancement plans. With these considerations in mind, our study opens up new avenues to consider luxury and legacy effects and unravel the relationship between urban biodiversity, ecological functions, and ES, along with its cascading effects on urban dwellers' well-being.

## METHODS

### Study site

Vitoria-Gasteiz is a middle-sized city (248.087 inhabitants[37]), located in the Basque Country and is internationally recognised as the 2012 European Green Capital. Located in the North of the Iberian Peninsula, Vitoria-Gasteiz has a considerable share of publically-accessible green infrastructure, including urban parks, forests, wetlands and canopy (Fig. 6)[9]. From the mid-1980s, the city committed to a consistent urban greening strategy encompassing a planned urban network of green infrastructure[40]. The latter included the restoration of multiple ecosystems towards the urban fringes of the city which aimed at limiting urban expansion and slowing industrial activity. The most remarkable outcome of these greening policies was a 731-ha and 35 km long greenbelt delimiting the urban core. The urban green areas of Vitoria-Gasteiz harbour more than 381 different species of trees and shrubs with more than 130,000 trees distributed around the city as well as 12,160 shrub masses[38]. Vitoria-Gasteiz is one of the European cities with a greener surface area (20 $m^2$) per inhabitant. Despite the consistent efforts towards greening the city, smaller-sized centrally located UGS has been recently associated with low

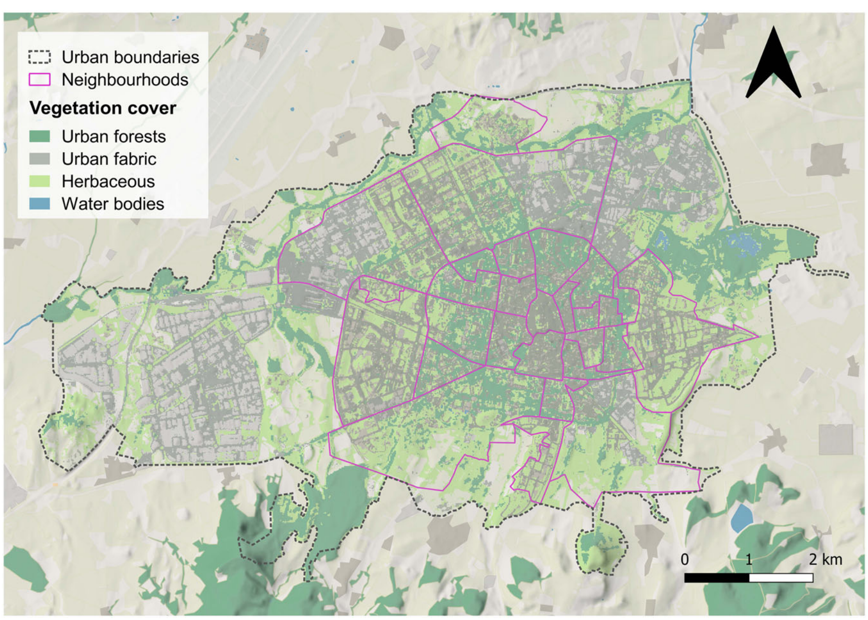


**Fig. 6 Study area.** Location of Vitoria-Gasteiz city, neighbourhood delimitation and main land uses cover within urban boundaries defined by urban fabric, forests, water bodies and herbaceous cover. Own elaboration based on GEE random forest classifier and Sentinel -2 imagery (see Section 4.2. for methodology details). Background from © MapTiler (www.maptiler.com) and © OpenStreetMap (CC BY-SA 2.0).

habitat quality and urban biodiversity, as opposed to larger areas towards the outskirts of the city[9]. Vitoria-Gasteiz offers a unique and suitable case study to test if luxury and legacy effects influence the spatial distribution of urban vegetation, biodiversity and ES at the neighbourhood scale. This is due to its fine-scale urban public canopy coverage data (i.e. urban tree inventory), resulting from the implementation of a recent urban green infrastructure planning strategy[38,56], as well as a bird census database resulting from a consistent biodiversity monitoring programme.

### Indicators for luxury and legacy effects

We combined public biodiversity datasets with a remote sensing approach and socio-demographic variables to assess the luxury and legacy effects. We first compiled two biodiversity datasets as a measure of species richness: an inventory of trees located in public land including individual tree information provided by the City Council[56] and a bird census (10016 observations) consisting of 100 sampling points distributed across the public urban green space between 2017 to 2020 by the NGO SEO/BirdLife[57], with the data being provided by the City Council. We also used mean habitat quality values per neighbourhood as a complementary indicator for biodiversity, whose spatially explicit data was obtained from previous research in the study area[9]. Here, habitat quality refers to the capacity of urban ecosystems to provide the resources and conditions needed for wildlife. This indicator is influenced by the proximity to and the intensity of human land uses and is a continuous variable ranging from 0 – low to 1 – high.

To distinguish between different vegetation cover types (i.e. herbaceous and canopy cover), we described 'herbaceous' as all non-woody vegetation[2], while 'canopy' describes the layers of leaves and woody vegetation that cover the ground when viewed from above[17]. We used 'vegetation cover' to describe the combination of the above-mentioned cover types. To integrate vegetation cover from both, public and private spaces, we complemented the above-mentioned datasets with a land cover classification using Google Earth Engine (GEE) and Random Forest classifier, a machine-learning method for satellite imagery-based land use classification[58]. A key advantage of the Random Forest classifier includes its high accuracy, robustness and efficient handling of noise or overfitting[59]. Besides, RF is a non-parametric method, so it does not need input variables following a particular statistic distribution[60]. We used the Sentinel-2 (A level-2A) Multi-Spectral Instrument (MSI) with two imageries averaged from 2017/07/11 and 2017/07/18 and between 10 and 20 m spatial resolution. We used the following MSI spectral bands: B2, B3, B4, B5, B6, B7, B8, B8A, B11, and B12. Before using the imagery, we performed an atmospheric correction using the QA60 quality band from Sentinel-2 to mask the clouds and select the images with the least cloud cover. To differentiate build areas from vegetated areas, we first calculated the Urban Index (UI) (bands B12 and B8A) and Normalised Difference Vegetation Index (NDVI) (bands B8 and B4) as inputs to be included in our land use classification. Then, we added to our dataset a Digital Elevation Model (DEM, 30 m resolution) from SRTM V3/USGS available for our study site and in the products catalogue of GEE. The DEM was used to assess aspect, slope, and hill shade variables. We then defined 4 different land use classes to be used in our study area: urban forests, urban fabric, herbaceous and water bodies. Following previous studies' recommendations, we selected 100 decision trees ($n = 100$) to run the classification model. The RF was then trained to map the vegetation cover distribution in Vitoria-Gasteiz and validate the classification accuracy. The validation data was then used to calculate a confusion matrix and assess the method's overall accuracy and kappa index to quantify the performance of RF.

To assess the role of vegetation cover in terms of luxury and legacy effects on ES, we used our land cover supervised classification outcomes (10 m resolution) including both herbaceous and canopy coverage. The resulting spatial pattern of herbaceous and canopy coverage from GEE is shown in Supplementary Fig. 1 and green cover percentage at the neighbourhood level is shown in Supplementary Fig. 2. To complement the dataset containing the public canopy inventory, we focused on canopy and herbaceous cover results.

Once we had the vegetation cover from our land use classification mapping (Fig. 6), we selected socio-demographic variables indicating socio-economic status to test them against the vegetation cover and biodiversity data. We collected all the variables for the 2015 year from the Basque Statistics Office[61] at the neighbourhood level. As yearly median household income was not available for the year 2015, we used census data on the percentage of residents with high educational attainment by neighbourhood over the total population[32,62]. Specifically, 'high educational attainment' is defined as the completion of tertiary education, including university studies, higher engineering and similar, as well as postgraduate, master's, doctoral and specialisation studies[63]. This variable is used as a suitable proxy for socio-economic status given that it is a key human capital marker (and hence also of income levels)[64,65] (Supplementary Fig. 5), which in turn has been shown elsewhere to influence both species diversity and vegetation cover[2,30,32]. Given that education and income tend to be highly correlated, in most cases it is difficult to isolate the influence of both variables which results in most studies considering only income and excluding education level, leading to findings only related to income[1,2,14,23,32]. Since information on educational attainment is relatively easily accessible, using this variable may be particularly adequate for case studies with low census data availability. We also included residential housing by construction year to build our neighbourhood age index and population density (inhabitants/ha) as control variables for the statistical modelling. To account for legacy effects, we built a neighbourhood development age indicator (see Eq. 1):

$$\text{Neighbourhood age} = \sum(\text{at} * \%t) \quad (1)$$

The neighbourhood age is calculated by summing the age of the transformation (at) at different time periods, ranging from 1800 to 2015, multiplied by the percentage of the area built by neighbourhood and time period (%t) (i.e. built housing, refer to Supplementary Table 2). We then rescaled the indicator values to a 0-1 range. Therefore, the higher the indicator, the older the neighbourhood and land transformation. The spatial distribution of the considered socio-demographic variables is shown in Supplementary Fig. 2 and Supplementary Table 2 for the development age per neighbourhood.

### Ecosystem services modelling of urban tree canopy

We quantified four ES for our case study: urban temperature regulation, runoff control, air purification, and carbon offsetting. We used data from the city council that were analysed using the i-Tree Eco software programme (v.6, www.itreetools.org). The i-Tree Eco tool is a process-based suite of models developed by the US Forest Service and designed to quantify urban forest structure and functions, including its ES supply[39]. This tool operates at a local scale and requires standardized field data of individual trees (i.e. species name, tree height, diameter at breast height (DBH), land use, crown size and health indicators) from either complete inventories or plot-based sampling[7,66]. It then combines the tree measures with hourly air pollution and meteorological data to assess the forest structure and quantify ES provision[39,67]. The outcomes of i-Tree assessments have been addressing the value of urban canopy to improve the life quality

**Table 3.** ES indicators quantified by i-Tree Eco and ES index considered in the assessment of public canopy.

| Ecosystem services (ES) | Indicator | Units |
|---|---|---|
| Temperature regulation | Transpiration | $m^3$/ha/year |
| Runoff control | Avoided runoff | $m^3$/ha/year |
| Air purification | Pollution removal is the sum of the removal rates:<br>$O^3$<br>$NO^2$<br>CO<br>$SO^2$<br>$PM_{2.5}$ | kg/ha/year |
| Carbon sequestration | Carbon storage | ton/ha |
| Urban ES Index | The scaled sum of the four combined indicators | 0 to 100 |

of urban residents through the supply of multiple ES such as air quality regulation, carbon storage, runoff control and heat mitigation (e.g. [7,68]). Further, i-Tree applications have contributed to exploring the relationship between urban forest management and environmental quality, along with identifying urban environmental justice issues[7,69,70].

From the complete inventory of urban public trees provided by the Vitoria-Gasteiz city council (originally containing 135,560 trees), we excluded trees from the modelling due to inaccuracies such as missing geolocation and structural variables, trees located in rural areas, inaccurate identification and removed trees, which finally resulted in 89,001 individuals for a clean version of the dataset. We confirmed the structural variable measures used for the assessment with an expert on tree physiology, (see Supplementary Table 4).

Given the limitations of i-Tree Eco to update the system's pollutant concentrations and precipitation data, such measures had to correspond to 2015 as the most recent year and be derived from the average values of four monitoring stations. Pollution removal is processed by i-Tree Eco for ozone (O3), nitrogen dioxide (NO2), carbon monoxide (CO), sulphur dioxide (SO2), and particulate matter of fewer than 2.5 microns (PM2.5)[70]. The i-Tree Eco indicators are presented in Table 3. Our modelling assessed urban temperature regulation by considering transpiration as an indicator of tree canopies' cooling effect on air temperature[71]. We estimated runoff control by considering rainfall infiltration, evaporation and water intercepted by the tree canopy as the total amount of avoided runoff[72]. Meanwhile, we estimated air purification from the dry deposition of air pollutants following Nowak et al. (2008) approach[73]. We stratified the analysis of all the indicators at the neighbourhood level ($n = 28$) to allow statistical analyses with the sociodemographic variables. Then, given that the distributive patterns of the four ES mapped were co-occurrent, we aggregated the ES outcomes to one single ES index value, following Baró et al. 2019[7]. To this, we re-scaled each one of the four regulating ES values in a range from 0 to 100 as the minimum and maximum values and then summarised the result without the application of weights. The final result was also rescaled to the 0 to 100 range.

### Data analysis

The scale of our statistical analyses was defined at the neighbourhood level ($n = 28$) as it was the finest scale for which the considered socioeconomic data was available. The socioeconomic data used was from the 2015 year to pair it with i-Tree Eco modelling. To account for legacy and luxury effects, we examined the contributions of both, high education attainment and urban development age (i.e. as explanatory variables), on biodiversity, vegetation cover and the four regulating ES along with other control variables such as population density, habitat quality and neighbourhood area (in ha) (Supplementary Table 1).

Initially, we computed all pairwise Spearman correlations (Supplementary Fig. 4) to see how our selected variables correlated with each other using the 'corrplot' package in R[74]. Then, we tested for spatial autocorrelation of the considered variables using Global Moran's I in ArcGIS v.10.7.1 (Supplementary Fig. 2). We used generalised linear models (GLMs) to assess biodiversity, vegetation cover and ES in relation to our selected explanatory and control variables. For each explanatory variables considered (i.e. high educational attainment, neighbourhood development age, habitat quality, vegetation cover, population density), we performed a separate linear regression. When finding strong and significant correlations, we tested for interactive effects between variables such as the case for i) high educational attainment and habitat quality, ii) neighbourhood age and population density, and iii) neighbourhood age and vegetation cover. We selected the models based on statistical significance ($p$ values $< 0.05$) and F-test and adjusted $R^2$ for goodness of fit, following the principle of parsimony. We assessed the performance of the selected models by testing for normality and good fit, influential observations and visual inspection of diagnostic plots. Statistical analyses were conducted using R v.4.2.2 and the 'tidyverse'[75], 'performance'[76] and 'SjPlot'[77] R packages.

### Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## DATA AVAILABILITY

Data that support the findings of this study are presented within the main text, figures and supplementary material. Raw data on biophysical variables (tree inventory, bird data) were provided by the Vitoria-Gasteiz city council upon request. Raw data on socio-economic variables were obtained in the following sites: Population density - https://www.vitoria-gasteiz.org/docs/j34/catalogo/00/89/densidadpoblacion16.7z Educational level https://www.eustat.eus/estadisticas/tema_303/opt_0/tipo_1/ti_nivel-de-instruccion/temas.html The data for habitat quality estimations can be found at: https://doi.org/10.1016/j.landurbplan.2022.104570.

## CODE AVAILABILITY

The data analysis in this study was performed using R version 4.2.2 (R Core Team, 2021) and several R libraries within RStudio, including 'tidyverse' (Wickham et al., 2019), 'performance' (Lüdecke et al., 2020), and 'sjPlot' (Lüdecke, 2021). Land cover classification using the Random Forest classifier was conducted using Google Earth Engine. Visualising and processing of spatial data were carried out using QGIS version 3.18.2. The quantification of ecosystem services was performed using i-Tree Eco software program version 6 (US Forest Service). The code that supports the findings of this study is available from the corresponding author upon reasonable request.

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C.A.; Conceptualisation, Methodology, Data curation, Validation, Formal analysis, Investigation, Visualisation, Writing–original draft, Funding acquisition. J.C.S.; Conceptualization, Methodology, Resources, Supervision, Writing–review & editing. J.P.P.; Conceptualization, Methodology, Formal analysis, Validation, Writing–review & editing. F.B.; Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. F.H.K.; Conceptualization, Methodology, Formal analysis, Writing–review & editing. U.P.; Conceptualization, Methodology, Resources, Supervision, Writing–review & editing, Funding acquisition.

## COMPETING INTERESTS

The authors declare no competing interests.

## ADDITIONAL INFORMATION

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