

# Urban biodiversity is affected by human-designed features of public squares

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Cities are designed primarily for the benefit of humans but also provide habitat for other species. However, understanding how different components of urban vegetation and other features of urban spaces enable different species or species groups to live in the city remains limited. Here we show that, for the City of Munich, designed features of public urban squares strongly determine the occurrence of different species groups. While taxon richness and abundance increased with increasing ‘greenness’ of the square, different taxa responded to different square features, such as the proportion of lawn, the volume of shrubs and the density of trees, as well as the number of people or pets on these squares. Our results highlight that urban design for human needs affects other species that may cohabit these spaces. Consequently, planning strategies for biodiverse cities that aim to enhance human–nature interactions need to be multifaceted, considering the needs of humans and other taxa to create diverse living cities.

The number of people who live and work in an urban environment is expected to increase further, exceeding 65% of the global population in the coming decades<sup>1</sup>. Even though the biodiversity in cities is generally lower than in the natural habitats replaced by the urban environment, a surprisingly high number of species can occur in cities<sup>2–5</sup>, providing an important habitat even for threatened species, particularly in biodiversity hotspots<sup>6</sup>. In addition, urban nature is the nature that city dwellers can experience in their day-to-day life<sup>7,8</sup> with multiple positive effects on urban inhabitants<sup>9,10</sup>. Therefore, there is widespread agreement today on the need to safeguard and increase biodiversity in cities<sup>11–13</sup>, which requires a better understanding of what drives biodiversity in the urban environment<sup>3,14</sup>.

Detailed assessments of plants and animals in the urban environment started only in the 1980s<sup>3,15,16</sup>, often using transects from outside

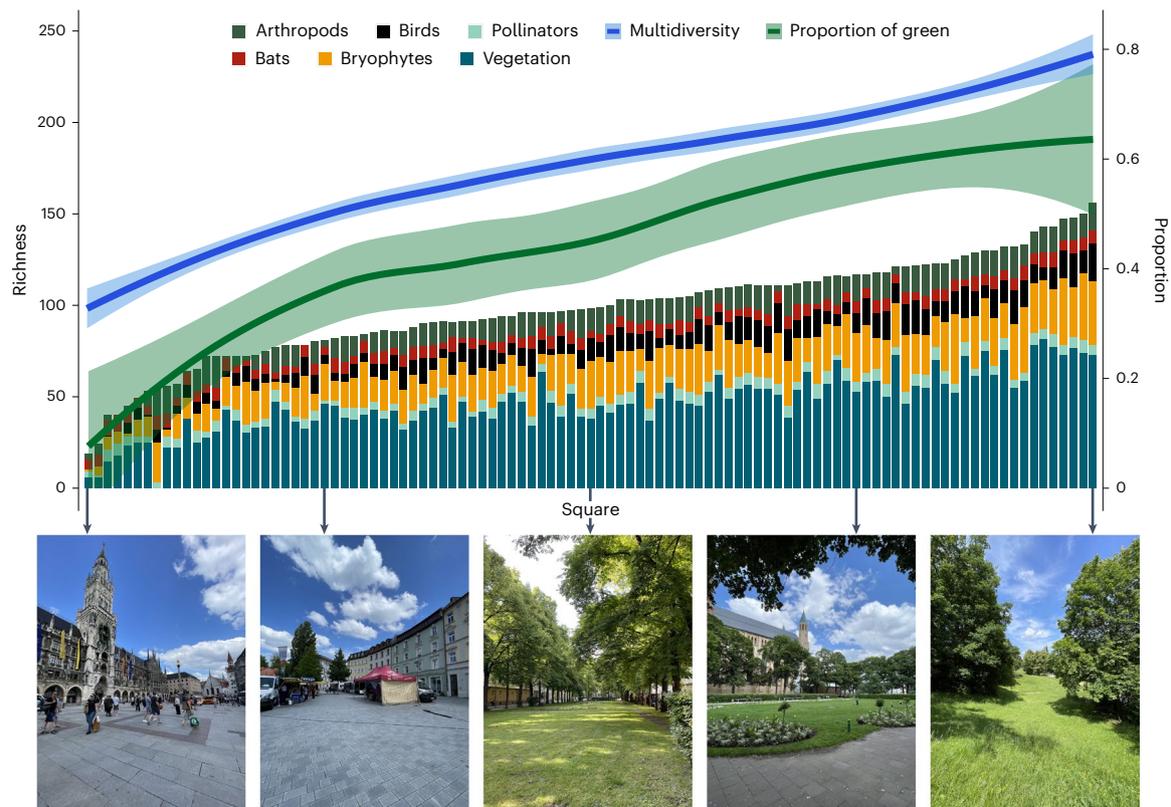
a city to the city center or comparing species compositions between urban and nonurban areas<sup>7,17,18</sup>. These comparisons have shown that urban communities differ from those outside the cities so that certain traits and taxa are overrepresented<sup>19</sup>, for example, the Fringillidae (finches) and Columbidae (pigeons) among birds<sup>20</sup>. More recently, studies have begun comparing sites within cities and have found that urban communities are not homogeneous but that properties of the particular site in the urban environment determine what species can occur there<sup>14,21</sup>. In a large meta-analysis, the size of the green area within a city, the presence of corridors, that is, the surroundings of a site, and vegetation structure were important to explain local species richness for several taxa<sup>22</sup>. Importantly, taxa can differ in their responses to the features of urban sites<sup>23</sup> and investigating the effects of individual site

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**Fig. 1 | Biodiversity and variability of public urban squares in Munich.** Each stacked bar represents 1 of 103 public squares. Squares that are sorted by their total species richness and composed of six taxa are shown in individual colors (left, y axis). The blue and green lines are LOESS (locally estimated scatterplot smoothing) curves for multidiversity (summed, scaled richness of all taxonomic groups; right, y axis) and the proportion of green (right, y axis) with its 95%

confidence interval (light-shaded areas). Images of squares highlight the variability in square features. Images of squares, from left to right, include Marienplatz, Hans-Mielich-Platz, Schäringerplatz, Johannisplatz and Pfrontener Platz, and highlight the variability in square features. Square images were taken by Antonia Haberer, 2024.

features in addition to the effect of overall green cover or greenness<sup>24</sup> may allow a more detailed understanding of why certain taxa are common on certain sites.

Urban green spaces comprise a wide range of different forms and not only include large remnants of natural habitats and parks but also smaller vegetated areas such as backyards, gardens, neighborhood common areas, vacant lots and streets with trees, which have been shown to be important habitats for a variety of species<sup>25,26</sup>. Yet public green spaces in built-up areas are less intensively studied, so their contribution to urban biodiversity and which of their features affect different taxa remains to be investigated. This is an important knowledge gap because, in the built-up area of the city, that is, the area that is developed primarily for the needs of humans, biodiversity conservation competes with other priorities of city planning, such as economic growth, transport infrastructure and housing development<sup>27</sup>.

Here, we investigate how different features of urban squares affect the diversity of different taxa living on the squares. We focus on public squares (open spaces in a city without housing that are publicly accessible<sup>28</sup>) as a core element of cities that serve as important public spaces where city dwellers have gathered since ancient times<sup>29</sup>. Urban squares are characteristic of European cities established while these cities grew. However, urban squares also occur in cities on other continents, for example, in South America where they were established under European influence, in New Zealand and the United States, but also in Asia in countries such as China. Particularly in North America, where many cities were planned as a grid, urban squares are rare as public spaces such as town squares mostly consist of entire grid cells and often, but not always, have a park-like appearance. However, analogs to urban squares studied here occur frequently, for example, publicly accessible

spaces in front of buildings or even shopping malls, that are not called a square but resemble the squares studied here in their features.

For our study, we selected 103 squares in Munich, Germany, differing in both the total amount and composition of urban vegetation, in particular trees, shrubs, grass and flower beds (Fig. 1, Methods and Extended Data Fig. 1). We characterized squares by a number of different features, including both vegetation-related variables and 'gray' characteristics relating to square design, including artificial light at night (ALAN) (Table 1 and Methods). Human usage of squares and the presence of domestic animals were quantified by counting humans on several days and times of the days using photographs. Because connectivity and habitat availability in the surrounding area have been shown to be important for biodiversity in urban environments<sup>22</sup>, we also calculated the percentage of green area in a buffer of 1,000 m around the border of each square. The squares investigated ranged from very 'gray', that is, being completely sealed, to very 'green', park-like squares, with different composition of urban vegetation, all a consequence of human design (Supplementary Figs. 1 and 2). In addition, squares differed widely in their attributes such the number of people.

In a second step, we quantified the abundance and richness of birds (separately considering the feral pigeon), pollinators and other arthropods, the richness and activity of bats, the activity of small mammals, pest small mammal species (mice and rats), the richness of bryophytes (including mosses and liverworts) and spontaneous herbaceous vegetation on each square, using taxon-specific sampling methods (Methods). As a measure of overall diversity, we calculated a multidiversity index, summing the scaled richness of all taxonomic groups (Methods).

**Table 1 | Summary of features and biodiversity of 103 public squares in Munich**

Square features			
Variable	Mean±s.d.	Min	Max
Surrounding greenness	0.44±0.13	0.174	0.757
Square size (ha)	0.92±0.98	0.09	6.71
Distance from center (km)	4.26±2.43	0	10.88
Proportion of lawn	0.21±0.16	0	0.66
Shrub volume (m <sup>3</sup> )	0.17±0.28	0	1.46
Area of flowers (m <sup>2</sup> )	18.04±67.61	0	460
Tree richness	6.92±5.96	0	25
Tree density	0.64±0.47	0	2.52
Median DBH (cm)	27.92±13.44	0	76
Variability of DBH	0.42±0.22	0	1.07
Old tree abundance	4.23±9.72	0	65
Old tree proportion	0.07±0.13	0	1
Number of people	18.69±32.97	0	262
Number of streets	4.16±2.09	0	11
ALAN (gray value)	34,825.19±25,701.5	5,912	178,530
Water (binary)	NA	0	1
Flower abundance	190.59±326.97	0	2,831.333
Flower richness	2.5±2.03	0	10.333
Number of pets	1.1±0.84	0	4.286
Biodiversity			
Multidiversity	0.59±0.13	0.23	0.85
Arthropod abundance	359.53±491.09	1	2,427
Arthropod richness	11.23±3.79	1	17
Bat activity	157.09±128.26	4	545
Bat richness	5.91±1.5	3	9
Pigeon abundance	11.92±28.45	0	143
Bird abundance	71.67±53.16	0	292
Bird richness	10.23±4.61	0	21
Bryophyte richness	19.58±7.85	1	38
Pollinator abundance	27.51±16.94	0	78
Pollinator richness	4.98±1.54	0	8
Pest mammal activity	0.12±0.2	0	0.84
Small mammal activity	0.14±0.18	0	0.81
Vegetation richness	47.25±15.74	6	82

Square features were assessed using maps and other digital resources and on-site visits. The biodiversity of different taxa was assessed using taxa specific methods. Name, unit and summary statistics are provided for each variable. Biodiversity metrics are combined by square. NA, not applicable.

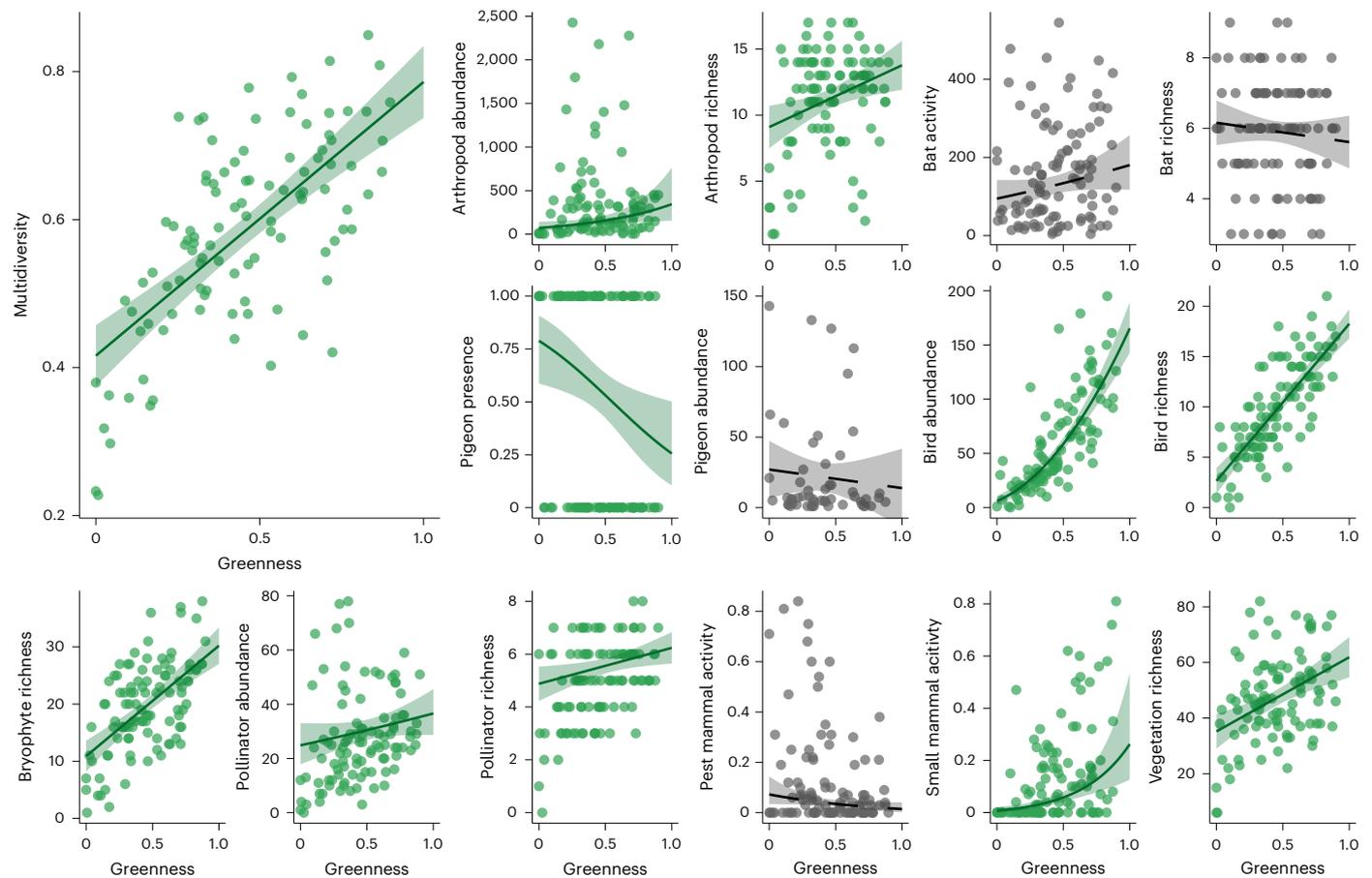
Squares differed greatly in biodiversity and the taxon richness of the most diverse square was almost eight times the richness of the biodiversity-poorest square (Table 1 and Fig. 1). Some species occurred on all or almost all squares, such as the flowering plants *Plantago major* and *Taraxacum officinale* (all squares), the silver bryophyte *Bryum argenteum* (93 squares) and the bird species carrion crow *Corvus corone* (92 squares) and great tit *Parus major* (94 squares). However, the vast majority of taxa occurred on a subset of squares, including species that are considered to be 'urban species'. For example, among birds, the feral pigeon, *Columba livia f. domestica*, and the house sparrow, *Passer domesticus*, occurred only on 54 and 10 squares, respectively.

Given the good coverage of the sampled communities (Supplementary Information 4), the observed variations in taxa distribution across the sampled areas suggest distinct ecological preferences.

As a first test for drivers of the biodiversity of squares, we fit linear models for the effect of greenness (proportion of green cover; Methods). Greenness on the squares positively affected both diversity and abundance/activity of all taxa, except for the abundance of feral pigeons, bat activity and richness, and pest mammal activity (Fig. 2). For taxa where both abundance (or activity) and richness were measured, the relationship to richness was stronger (Extended Data Table 1). Multidiversity was most strongly affected by greenness ( $F_{1,101} = 79.01$  and  $P < 0.001$ ; Fig. 2). These results emphasize the important role of planted vegetation for urban diversity, despite the fact that this urban vegetation was created predominately with human use in mind. Thus, the greening of cities benefits not only humans through better provisioning of ecosystem services<sup>30</sup>, but also other organisms, which in turn will enhance human–nature interactions<sup>31,32</sup>. Both the scatter around the regression lines and the differences in slopes between greenness and abundance/diversity of individual taxa suggest, however, that greenness is a coarse measure of the suitability of squares for organisms and that individual square features may offer better explanations as to where certain taxa occur. In addition to multidiversity, we also investigated the community composition of squares, based on all taxa studied (Methods), we found that while community composition changed along the green-to-gray gradient, there was ample additional variability in the occurrence of taxa, both among the greener squares as well as among the grayer squares (Extended Data Fig. 2). This also confirms the need to investigate the effects of individual features.

To test the effects of individual square features on urban biodiversity, we fit separate random forest models for multidiversity and each taxon's richness and abundance/activity (Methods and Extended Data Table 2). These models, which excluded overall greenness, explained, on average, almost twice as much variance in the response variables compared with models with greenness only (greenness models:  $r^2 = 0.239$ , Extended Data Table 1; random forest models:  $r^2 = 0.433$ , Extended Data Table 2). Additionally, random forest models predicted the observed diversity well (Supplementary Figs. 3–16), confirming the hypothesis that the individual components of urban vegetation explain biodiversity better than overall greenness. Our analysis found that each taxon was affected by several square features (Fig. 3). To rank variables by the strength of their effects on biodiversity, we calculated importance scores (percentage increase in mean square error (m.s.e.); Methods) for each square feature. The proportion of green in the 1,000 m buffer around the squares positively affected only some of the taxa, including bat richness. For most taxa, however, local square features were more important for their abundance and diversity. This shows that the design of an urban square is pivotal for the biodiversity that can be found there. The proportion of lawn, shrub volume and tree density affected most biodiversity variables and were the strongest drivers of a square's overall greenness (Fig. 3).

The proportion of lawn on a square affected most taxa positively and was the most important explanatory variable for multidiversity, bryophyte richness, arthropod abundance, arthropod richness and bird richness (Fig. 3). Lawns in the city are generally highly managed and therefore only occasionally allow taller plants to flower or set seeds; hence, they do not allow insect species that feed on shoots, flowers and flowerheads to complete their life cycles. However, they do provide habitat for soil-dwelling organisms and species living close to the surface, and hence also provide food for arthropod-feeding guilds, including birds, predatory arthropods, mammals such as the hedgehog<sup>33</sup> and some bats, for example, *Pipistrellus kuhlii* and *Pipistrellus pipistrellus*<sup>34</sup>, both common in our study. We found lawns to have the highest abundance and second-highest richness of arthropods and the highest richness of spontaneous vegetation.



**Fig. 2 | Effect of greenness on biodiversity on public squares in Munich.** Each dot represents 1 of 103 public squares sampled between 2017 and 2018. The green graphs indicate a significant ( $P \leq 0.05$ ) relationship between how green a square is and the biodiversity measure. The gray graphs indicate no significant

relationships. The lines represent the predicted values from linear models and the shaded areas are 95% confidence intervals (Extended Data Table 1). For effects of not-shown covariates, refer to Extended Data Table 1.

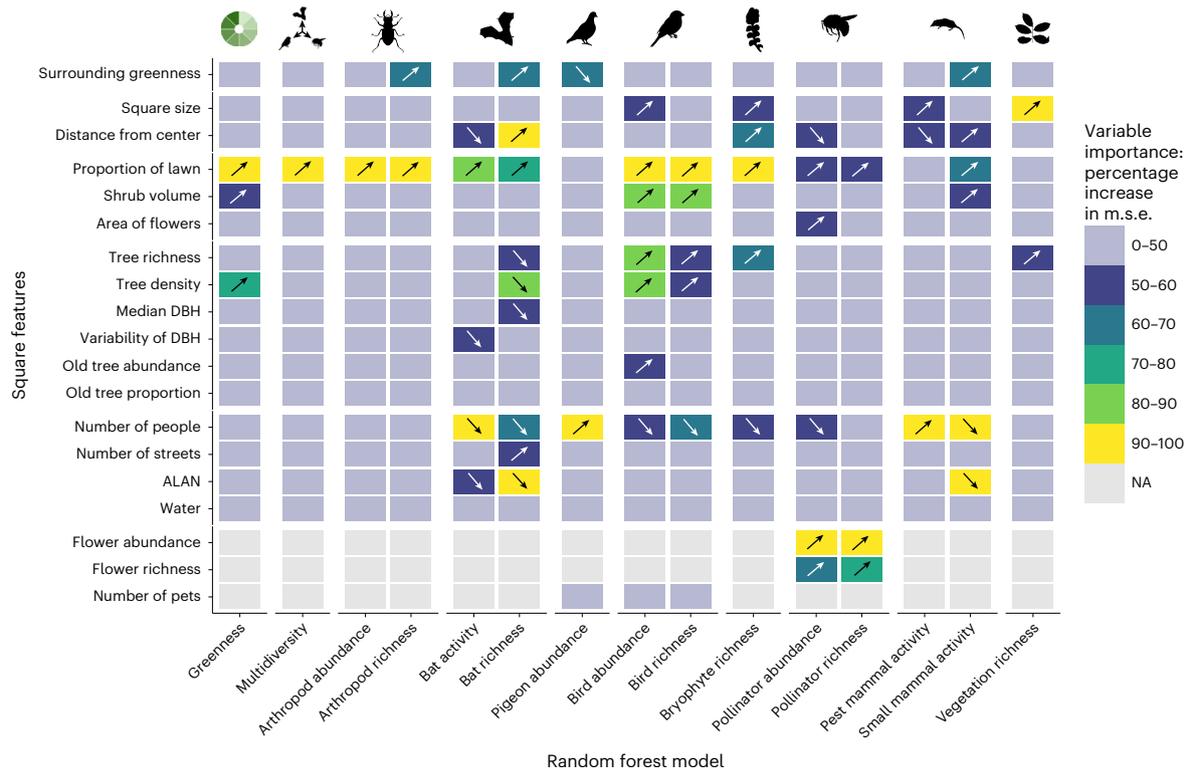
Several tree-related variables positively affected the biodiversity of the squares, in particular, tree richness and tree density (Fig. 3), both of which were also significant drivers of change in community composition as indicated by significant correlations among these environmental variables and the position of the square in the ordination of the biotic communities (Extended Data Fig. 2). Trees offer the highest vegetation biomass in cities and tree species differ in the resources they provide to different organisms. In our study, there were up to 25 species of trees on a square, whereby Norway maple (*Acer platanoides*;  $n = 1,179$ ) and small-leaved linden (*Tilia cordata*;  $n = 1,044$ ) were the most abundant. Interestingly, the proportion of old trees was not an important variable, despite old trees being disproportionately important for biodiversity worldwide<sup>35</sup>. There are several potential reasons for this. First, our definition of old trees (diameter at breast height (DBH)  $\geq 60$  cm) includes trees that are  $<100$  years old, that is, they are still relatively young; among all squares, there were only 17 trees with a DBH  $>100$  cm. Second, the management of old trees in highly accessible urban areas dictates the premature removal of the tree or management of deadwood for public safety<sup>36</sup>, and this deadwood is one of the most important features of old trees for many species<sup>37</sup>.

Shrubs were the third most important feature on a square predictive for overall greenness and affecting biodiversity. Strong effects were found for the abundance and richness of birds and small mammals. Like trees, shrubs offer biomass, structure, resources and habitats in a city<sup>38</sup>. These can result from the shrubs themselves (for example, nesting sites in the shrub, flowers and berries) or from shielding areas inside

or below the shrubs from disturbance or management (for example, for spontaneous herbaceous vegetation).

Features not related to the overall greenness of a square also affected several taxa. Square size, that is, total area, influenced the richness of spontaneous vegetation and bryophytes and the density of birds and small mammals, supporting the importance of urban patch size as found in previous studies<sup>22</sup>. Larger areas generally provide more and more diverse local habitats (that is, the species–area hypothesis<sup>39</sup>) and this may also hold for squares. Distance from the city center negatively affected pollinator abundance, pest mammal and bat activity, and positively affected bryophyte, small mammals and bat richness. Bryophytes, for example, are sensitive to the effects of urbanization, such as the heat island effect<sup>40</sup> and air pollution<sup>41,42</sup>, both of which increase closer to city centers. In contrast, pest mammals are positively associated with the built-up areas of cities<sup>43</sup>. ALAN had negative effects on small mammal activity, bat activity and bat richness, that is, nocturnal taxa. While under certain circumstances, some bat and small mammal species may be able to exploit opportunities created by ALAN<sup>44,45</sup>, ALAN is agreed to negatively impact biodiversity<sup>46</sup>.

The number of humans visiting a square negatively affected a number of taxa and positively affected only feral pigeon abundance and pest mammal activity. The presence of humans has been shown to have negative effects even on highly urbanized species<sup>47,48</sup>, while some species, such as the pest mammals in our study, rely almost entirely on the resources created by humans. Community composition on squares was also significantly affected by ALAN and the number of people (Extended Data Fig. 2). While squares with the highest human



**Fig. 3 | Scaled importance of square features and biodiversity of multiple taxa in Munich.** The rows represent the square features. The columns are the biodiversity measurements for eight taxa, multidiversity and greenness. The variable importance scores, percentage increase m.s.e. from the

random forest models (Extended Data Table 2) are binned to six categories. Light gray represents NA values. Arrows represent the direction of the relationship. NA, not available. Icons reproduced from PhyloPic under a Creative Commons license [CC0 1.0](https://creativecommons.org/licenses/by/4.0/).

disturbance were mostly completely sealed, we find that at intermediate greenness, squares characterized by high human disturbance, had different communities than squares with intermediate green but a smaller number of people active on the square (Extended Data Fig. 2). Water sources were rare on the squares ( $n = 18$  squares) and the presence of water was not selected as important for any of the taxa.

Our results demonstrate that important features differ markedly between taxa and that there is not a single set of features that are optimal for all urban biodiversity. Some taxa, in particular birds and small mammals, were affected by a larger number of square features, while others, such as the richness of spontaneous vegetation and arthropods, only by a few variables (Fig. 3). While several taxa were strongly affected by variables related to shrubs, trees and lawns, birds were most influenced by several other green features. In contrast, small mammals were the least affected by the greenness variables of a square but were negatively influenced by the number of people on squares and ALAN, both indicative of disturbances. Similarly, bats showed a limited, negative effect of the greenness variables with the strongest influence being from disturbance variables. This suggests that for some taxa, either local green is not a factor, or some additional feature is more important, for example, connectivity (demonstrated to be important for common urban bats, for example, *P. pipistrellus*<sup>49</sup>).

While our study shows the potential of designing for both humans and biodiversity, there are also trade-offs and limits resulting from the different associations between features and taxa. For example, only some species benefit from increased tree density, and if high tree density implies a low proportion of open grassy areas, other species will be less likely to occur (Fig. 3). Further, lighting (ALAN) required to make people feel comfortable and safe during the night will negatively impact light-sensitive species such as small mammals and bats. As both the human use of squares and ALAN are related (Supplementary Figs. 1 and 2), implementing smart or wildlife-friendly lighting systems could

provide people with the safety they need while reducing the impact on wildlife<sup>50</sup>. There are also limits to the simultaneous use of squares by both wildlife and humans, as indicated by the negative effect of human presence on the community composition and the abundance and richness of several taxa.

### Conclusion

Our findings add to the growing body of evidence that urban vegetation benefits biodiversity in general. Thus, the replacement of sealed surfaces with grass or other vegetation by urban planners will result in immediate biodiversity benefits<sup>51</sup>. Extending beyond the general ‘green in cities begets biodiversity’, we showed that differences in square design and the type and amount of vegetation planted affected what organisms could live on the squares, ranging from bryophytes and flowering plants to arthropods, birds and small mammals. This is important, as in the discussion of creating a green infrastructure for cities, ‘green’ is often not qualified, suggesting that it does not matter what is grown. Although we often used coarse categories (trees, shrubs, lawns and flower beds), our study found striking differences in the effect of these different components on the biodiversity of the square. It is likely that describing the urban form in more detail, in particular the planted vegetation, but also other structures such as nesting possibilities for animals in buildings, will unravel further relationships between the design of a particular site in the city and the associated biodiversity. As our study was restricted to Munich, we recommend that comparable studies be carried out in other regions to determine how local biodiversity responds to the urban form.

Our study emphasizes that in the city, plants and wildlife not only occur in remnants of natural habitats or large parks but also in the built-up area of the city<sup>12,25</sup>. Our analysis showed that the way humans design a public urban square, a structure made for human use and central to urban life, strongly influences the biodiversity inhabiting these squares.

Importantly, our findings are not limited to the biodiversity on public squares in Europe but are expected to be valid in other regions of the world where forms of public squares also exist, and they are likely to apply also to other categories of public and potentially private spaces. The square features included in our study were planned and implemented by humans for humans; all other organisms, including spontaneous vegetation, assembled on the square as a consequence of this design. The strong effects we found of this design on the biodiversity of urban squares emphasize that urban planners and landscape architects have an important role to play in creating biodiverse cities where human–nature interactions are possible. Embracing different greens in urban planning and design by creating diverse and heterogeneous sites will benefit various taxa, thus contributing to maintaining and increasing city-wide biodiversity.

## Methods

### Square selection

We calculated the size of 354 public squares ('Platz' in German) in the City of Munich, Germany (48.1372, 11.5761) using Google Earth and ArcGIS. As size was log-normally distributed, we conducted a stratified random sampling using five equally sized classes (Supplementary Information 1), resulting in 95 squares. Characterization of the squares using Google Earth and ArcGIS showed that they had good distribution in their distance to the city center (Marienplatz) and the presence of trees. As squares without tree cover were underrepresented, an additional eight were manually selected, resulting in 103 squares (Extended Data Fig. 1).

### Square characterization

Squares were characterized by their features used as explanatory variables for the analysis of biodiversity on the squares (Extended Data Table 1). First, we delineated the borders of each square (far edges of roads, private property boundaries, walls and adjacent buildings) using aerial images and land register maps (Supplementary Information 1). We then calculated the size of each square (0.086–6.71 ha) using ArcGIS. Distance from center was calculated as the direct line distance from Marienplatz to the center of each square. Using the aerial images, we calculated the normalized difference vegetation index for each 20 cm pixel and determined the area and proportion of greenness of each square (normalized difference vegetation index with a threshold  $\geq 0.2$ ). To understand whether there was an influence of green in the surroundings of each square, we calculated a buffer of 1 km from the edge of each square. We used the same method above to determine the surrounding greenness (proportion of green).

Using aerial images, land register maps and Google Earth, we determined the proportions and areas of different surface cover types. We calculated the area and proportion of lawns (grass), area of shrubs, proportion of flowers (flowering plants), gravel and sand. The total unsealed surface area was calculated by adding the different surface cover types and the sealed surface area by subtracting the unsealed surface area from the total area (Supplementary Information 1).

Vegetation was further characterized by measuring on-site shrub volume ( $\text{m}^3$ ), tree (species) richness and abundance. We also calculated tree density per  $100 \text{ m}^2$  (tree abundance  $\times 100/\text{area} (\text{m}^2)$ )<sup>52</sup>. Each tree's DBH was measured to derive the median DBH and variability of DBH (coefficient of variation) (Supplementary Information 1). We determined old trees to be those with a DBH greater than 60 cm and then calculated the old tree abundance and old tree proportion (proportion of all trees with a DBH greater than 60 cm) for each square.

To assess human disturbance and impact on each square, we measured the number of people on each square, the number of streets associated with a square and ALAN. To assess the number of people, we took four photos from the center of each square, one in each cardinal direction. Photographing was repeated on three different days, each covering a different time (morning, midday and afternoon).

The number of people in each photo was then summed and the mean total for all days was calculated. Using Google Earth, we counted the number of streets touching the boundaries of each square. Finally, we calculated the ALAN as the average gray value per square using Luojia-1 satellite images (Supplementary Information 1).

While reviewing the satellite imagery and visiting the squares, it was additionally noted whether a square contained a water source as the presence of water (for example, fountains).

### Biodiversity assessment

**Multidiversity.** We calculated a multidiversity index<sup>53</sup> for all the richness variables (arthropods, bats, birds, bryophytes, pollinators and vegetation) as the average proportional species richness across taxonomic groups. To ensure equal weight for all taxonomic groups, we standardized the species richness values by scaling them to the highest observed value across all squares. The scaling ensures that undue weight is not given to taxonomic groups with higher species richness. The average by square is then calculated as multidiversity.

**Arthropod abundance and richness.** We collected arthropods between May and July 2017 on five habitats per square: sealed surfaces (paved or tarmac), grassy areas, flower beds (not planters or raised beds), shrubs and trees. All habitats on a square were sampled once at a single point on the same day between 09:00 and 19:00 (Supplementary Information 2). Surface habitats were sampled by suction sampling<sup>54,55</sup> using a battery-operated leaf blower outfitted with a gauze filter using a cage covering an area of  $0.25 \text{ m}^2$  (Supplementary Fig. 2.1). Trees and shrubs were sampled using knockdown sampling and collecting the arthropods in a funnel attached to a sample jar. In the laboratory, all individuals were sorted to order level (Supplementary Table 2.1)<sup>56</sup>. We then calculated the taxonomic group richness per square and the abundance per square as the total number of arthropods for each taxonomic group collected across all sampled habitats.

**Bat activity and richness.** We undertook bat sampling on single nights, from 1 h before sunset to 1 h after sunrise, between June and October 2017. All squares were sampled four times in clusters of 2–15 squares using ultrasonic recorders (ecoObs Batcorder 3.1 (quality of 20, threshold of  $-36 \text{ dB}$ , post trigger of 800 ms and critical frequency of 14 kHz (ref. 57))). Clusters were chosen so there was a minimum of 500 m between squares and formed a gradient from the city center to the edge. Recordings were automatically identified using the software suite from ecoObs (bcAdmin (version 3.9), bcAnalyze (version 3.0) and batIdent (version 1.0)) and manually checked by an expert (K.J.) (Supplementary Information 2). Bats were identified to species level where possible or recorded in a species group (Supplementary Table 2.2). Species richness was calculated as the total number of species or species groups identified across all rounds. To be conservative, if a species group and a species from that group were identified in the same recording period, this was only considered one species. Activity was determined by calculating the total, across all rounds, number of minutes per sampling period in which a call of that species was recorded.

**Bird abundance and richness.** Birds were recorded visually and aurally along transects, sampled three times in spring (April to July) 2017, once in fall (October) and three times in winter (December 2017 to February 2018)<sup>52</sup>. The sampling order of the squares was randomized. In ArcGIS, we manually created transects (ranging from 1.5 m to 1,279.35 m) to cover the whole area of each square with a 25 m radius around the route<sup>58</sup>. Survey time per square was standardized to 20 min as it allowed each square to be fully surveyed but was short enough that all squares could be surveyed within 2 weeks. All species detected within a 25 m radius around the observer were recorded. Each individual's location and movement direction was recorded to reduce double counting. Feral pigeon (*Columba livia f. domestica*) abundance was determined

as the total of observations across all rounds. Bird abundance was determined as the total of all observations across all rounds, minus pigeons. Bird species richness was calculated as the total number of species detected per square across all rounds, minus feral pigeons (Supplementary Information 2).

**Bryophyte richness.** We collected mosses and liverworts between October 2017 and January 2018 on three different substrate types on all squares: wood, soil and stone (Supplementary Information 2). Species on vertical structures such as walls or trees were collected up to 2 m above ground level. We sampled each square for a maximum of 60 min (20 min for each substrate type). When moving between patches of a substrate, the timing was paused. If a substrate type was missing, it was skipped, and the sampling time was reduced by 20 min. We stopped sampling a habitat once no new species were found for several minutes. Samples were dried overnight at 50 °C before identification. Species were identified as species, species groups or morphospecies using relevant guidebooks and comparison with herbarium specimens based on macro- and microscopical characteristics (Supplementary Information 2 and Supplementary Table 2.3). Bryophyte richness was calculated as the total number of species, morphospecies or species groups identified per square. If a species group and a species contained in the group were both identified on a square, then this was only counted as one species.

**Pollinator abundance and richness.** Pollinators were sampled on each square three times between May and July 2018, using five annual ornamental plants as phytometers (standardized plants used to measure ecosystem traits; Supplementary Information 2). We changed the time of day a square was sampled each round so that squares were sampled once in the morning, at midday and once in the afternoon (between 08:30 and 16:30). The phytometers were placed 25 cm apart in a random order as close as possible to the center of the square, ensuring they were in an open, sunny spot. Observations began 30 min after placing the phytometers and continued for 30 min (a total of 90 min during the three sampling periods per square). Any pollinators that interacted with the reproductive parts of the phytometers were recorded. Multiple visits of the same individual to different flowers on one phytometer were counted as one visit. If a pollinator flew to another phytometer and interacted, it was counted as a new visit. Additionally, the abundance, number of racemes, spikes and umbels, and richness of flowers in a 3 m radius around the phytometers were recorded<sup>51</sup>.

Pollinators were identified in the field. If immediate identification was not possible, the insect was captured with an aspirator and stored in a jar for later identification in the laboratory. Sampled (observed or captured) pollinators were classified into functional groups representing bees (Apoidea), which were grouped into three body size classes: honeybees (*Apis mellifera*, containing the classical European honeybee but also other similarly sized and easily confused bees), bumblebees (*Bombus* sp. and individuals from the family Megachilidae) and small bees (other Apoidea) (Supplementary Table 2.4). We calculated the functional group richness and the total abundance (total number of observations per functional group) across all rounds for each square.

**Pest and small mammal activity.** We sampled pest and small mammals using footprint tunnels<sup>59</sup> baited with cat food (Supplementary Information 2 and Supplementary Fig. 2.2) over 9 weeks between June and September 2017. Sampling was done on five consecutive nights (one sampling session) per square. A maximum of 12 squares, forming a transect from the city center to the edge, were sampled simultaneously each week. We placed five tunnels per square at five locations on combinations of surface type (sealed or gravel and grass) and linear structures (hedge and wall). Four tunnels (two on grass and two on sealed surface) were placed in the middle of, adjacent and parallel to the linear structures (two along walls and two along hedges) to avoid

disturbances of traffic or pedestrians and encourage target species that were moving along the structures to enter the tunnel. A fifth tunnel was placed in the center of the largest grassy, open area away from linear structures (Supplementary Fig. 2.3). Where all five surface and structure types were not present on a square, we reduced the number of tunnels accordingly.

We checked the tunnels daily; bait and ink were replaced if necessary and the tracking sheets were collected and replaced. Each sheet represents 24 h of activity. After collection, the track sheets were photographed. Tracks were then identified to species level or allocated to a species group (Supplementary Table 2.5) based on the size, shape, length and width of the print and the number of toes, in addition to the arrangement of tracks<sup>60</sup>. Identified species and groups were then categorized as either ‘pest mammals’ (predominately rats (8.8%) and mice (83.4%)) or ‘small mammals’ (predominately hedgehogs (98.8%) and shrews (1%); Supplementary Table 2.5). Pest and wild mammal activity were calculated as the proportion of valid track sheets (between 7 and 50 per square) of which a pest or wild small mammal was detected.

**Vegetation richness.** In June and July of 2020, we recorded the spontaneous vegetation (all apparently unplanned or unplanted vegetation) diversity on eight different surfaces (frequently mown grass (<15 cm), infrequently mown grass (>15 cm), tree plates, woody structures other than trees, planting beds, planters, pavement cracks, unsealed surfaces and additional furnishings, for example, benches) of each square (Supplementary Information 2). Each surface, structure or furnishing type was observed for 15 min per square until all types of surfaces were observed. All observed plants were identified to the species. If a species was unidentifiable, we recorded it as such, and these were later removed for analysis. We combined all observations across surfaces, structures and furnishings and calculated the total species richness per square (Supplementary Information 2).

### Statistical analysis

All analyses were conducted in R (version R-4.1.1)<sup>61</sup> using R-Studio (version 2021.09.0)<sup>62</sup>.

**Effects of greenness on abundance and diversity.** To test the effect of greenness on each taxa’s abundance and richness, we fit linear regression models for each taxon and the proportion of green on each square. For birds and pollinators, where additional covariates were collected in conjunction with the biodiversity observations (domestic animals for birds and flower richness and abundance for pollinators), these were included and fit first in the model.

**Importance of individual square features on abundance and diversity.** To characterize individual square features’ effects on each taxa’s abundance and richness, we calculated variable importance scores. This was done using the random forest method from the caret package<sup>63</sup> by growing forests with 1,001 trees for each taxon. To improve model interpretability and reduce bias in importance scores<sup>64</sup>, we removed highly colinear predictors (tree abundance, unsealed surface area, area of green and shrub area; variance inflation factor  $\leq 5$ , vifstep in the package usdm<sup>65</sup>), resulting in a final list of 14 predictors (Table 1 and Supplementary Fig. 1.1). We conducted a principal component analysis using prcomp of the final 14 predictors to illustrate the relationships of the square features (Supplementary Figs. 1.2–1.6). Final models were created using tenfold cross-validation with three repeats<sup>66</sup> and by tuning mtry using the tuneRf function from the RandomForest package<sup>67</sup>. Variable importance was calculated using the varImp function in caret, which calculates the percentage increase in mean squared error (m.s.e.). The percentage increase in m.s.e. score for a variable is the difference between the final model m.s.e. and the m.s.e. after permuting the order of the values of that predictor. Variables with higher values of percentage increase in m.s.e. have a larger effect on

the predictive performance of a model. The variable importance was then scaled, ranging from 0 to 100. Finally, the direction of the effect (positive or negative) was determined by inspection of the partial plots (Supplementary Figs. 3.1–3.14).

**Community composition of squares.** We conducted a nonmetric multidimensional scaling analysis to further investigate the different species occurring on the squares using the metaMDS function in the vegan package<sup>68</sup>. To illustrate how the communities vary with the square features, we fit them using the envfit function of the vegan package.

### Reporting summary

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

### Data availability

The square features and biodiversity data are publicly available via Dryad at <https://doi.org/10.5061/dryad.bcc2fqzq> (ref. 69).

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## Author contributions

These authors contributed equally: A.J.F. and S.T.M. S.T.M., M.M., W.W.W. and A.J.F. developed the research goal and aims. Field data were collected and processed by B.A., K.J., M.M., K.B., A.F., L.G., J.J., K.K., N.M., C.O., M.U., J.W., J.M., P.D. and S.T.M. A.J.F. and S.T.M. analyzed the data. The manuscript was written by A.J.F., S.T.M. and W.W.W., with contributions from all co-authors.

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## Competing interests

The authors declare no competing interests.

## Additional information

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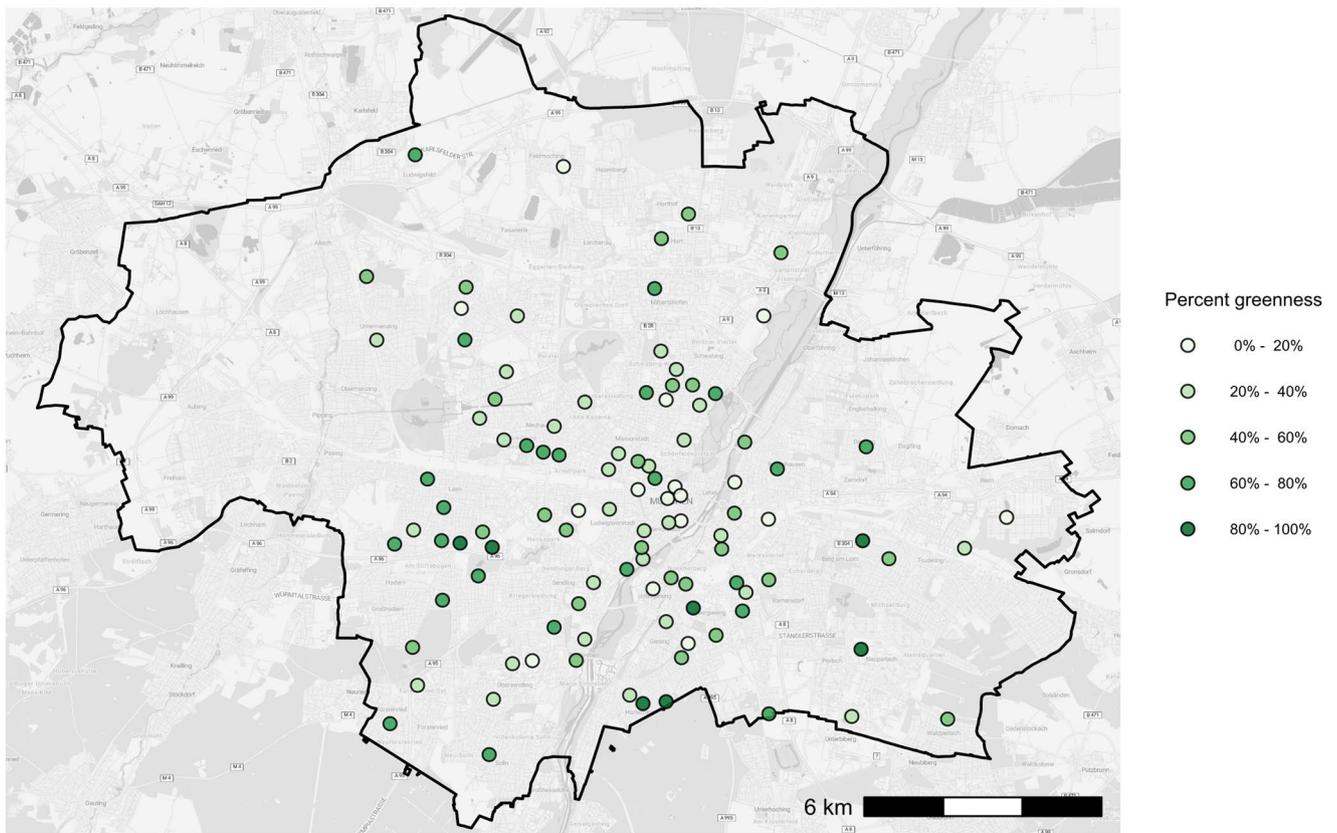
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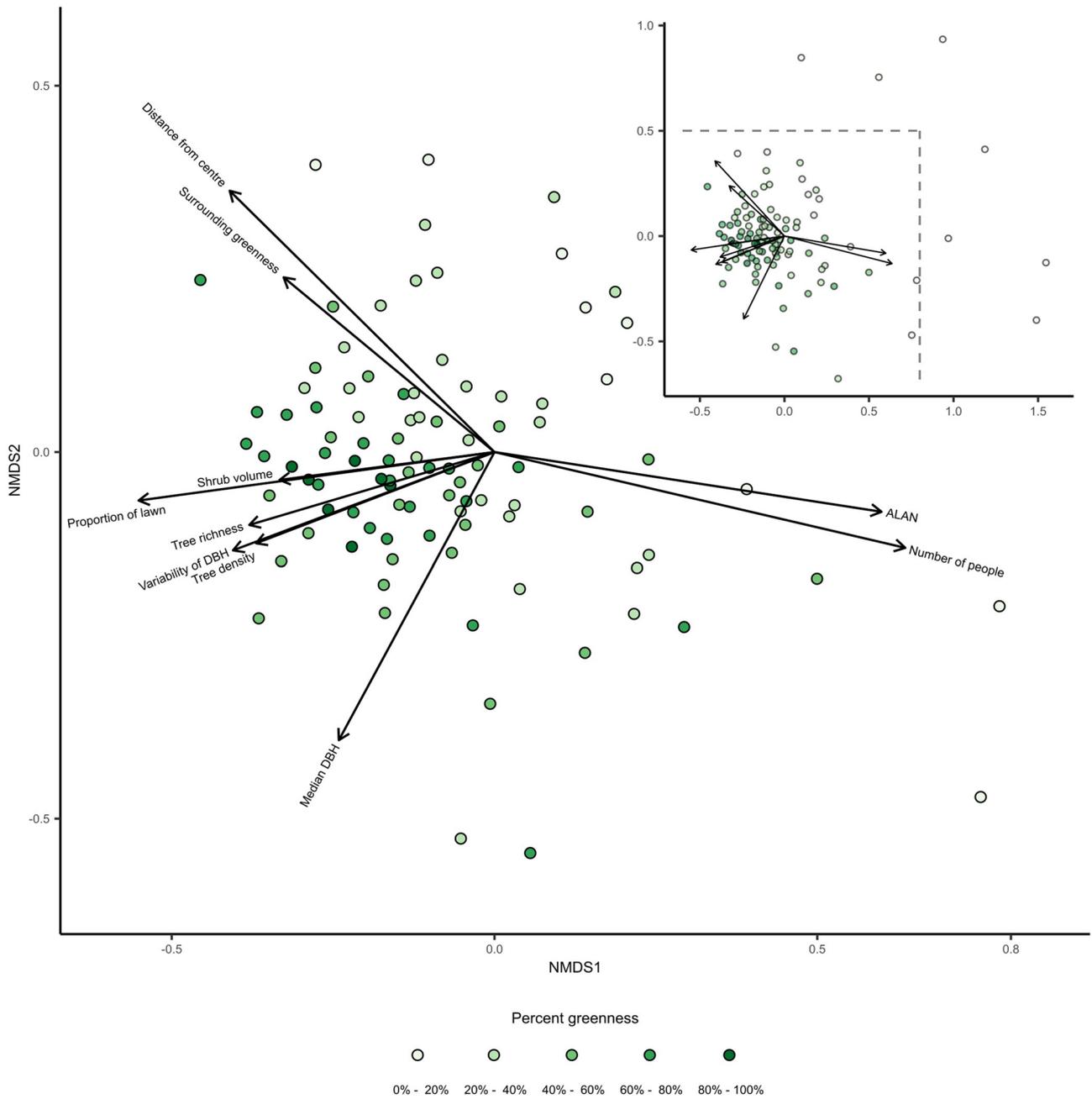
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**Extended Data Fig. 1 | Location of public squares in Munich and their greenness.** The circles represent the location of 103 public squares in the city of Munich, Bavaria, Germany. Colour represents the percentage of green cover on each square based on the Normalized Difference Vegetation Index

with a threshold of 0.2. Percent greenness is continuous and binned for display purposes. Map tiles by Stamen Design, under a Creative Commons license [CC BY 3.0](https://creativecommons.org/licenses/by/3.0/). Map data © OpenStreetMap contributors under a [CC BY-SA 2.0](https://creativecommons.org/licenses/by-sa/2.0/).



**Extended Data Fig. 2 | NMDS biplot indicating the community composition of public urban squares in Munich.** Each circle represents one of the 103 public squares in the city of Munich, Bavaria, Germany. Colour represents the percent of green cover on each square based on the Normalized Difference Vegetation Index

with a threshold of 0.2. Percent greenness is continuous and binned for display purposes. Shown vectors are the square features with significant relationship to the ordination ( $p \leq 0.5$ ). Inset shows how very grey squares have very different communities to greener squares.

## Extended Data Table 1 | Greenness linear model results

Taxonomic group	Covariates	Greenness	Adjusted R2
Multidiversity		<b>F<sub>1,101</sub>=79.01; p&lt;0.001</b>	0.436
Arthropod abundance*		<b>F<sub>1,98</sub>=5.36; p=0.023</b>	0.042
Arthropod richness		<b>F<sub>1,98</sub>=8.76; p=0.004</b>	0.073
Bat activity°		F <sub>1,101</sub> =2.867; p=0.094	0.018
Bat richness		F <sub>1,101</sub> =0.754; p=0.272	-0.002
Pigeon presence	<b>Domestic animals*: z<sub>1,101</sub>=2.848; p=0.0044</b>	<b>z<sub>1,100</sub>=-2.524; p=0.012</b>	NA
Pigeon abundance	(Domestic animals*: F <sub>1,51</sub> =1.22; p=0.274)	F <sub>1,51</sub> =0.364; p=0.549	-0.008
Bird abundance*	(Domestic animals*: F <sub>1,100</sub> =0.06; p=0.803)	<b>F<sub>1,100</sub>=67.40; p&lt;0.001</b>	0.391
Bird richness	(Domestic animals*: F <sub>1,100</sub> =1.20; p=0.275)	<b>F<sub>1,100</sub>=167.9; p&lt;0.001</b>	0.621
Bryophyte richness		<b>F<sub>1,101</sub>=52; p&lt;0.001</b>	0.336
Pollinator abundance°			
Pollinator richness	<b>Local flower abundance*: F<sub>1,99</sub>=33.07; p&lt;0.001</b> (Local flower richness*: F <sub>1,99</sub> =0.13; p=0.718)	<b>F<sub>1,99</sub>=19.09; p&lt;0.001</b>	0.326
	<b>Local flower abundance*: F<sub>1,99</sub>=33.03; p&lt;0.001</b> (Local flower richness*: F <sub>1,99</sub> =0.0046; p=0.946)	<b>F<sub>1,99</sub>=33.03; p&lt;0.001</b>	0.418
Pest mammal activity*		<b>F<sub>1,101</sub>=22.4; p&lt;0.001</b>	0.027
Small mammal activity*		F <sub>1,101</sub> =3.861; p=0.052	0.173
Vegetation richness		<b>F<sub>1,100</sub>=18.9; p&lt;0.001</b>	0.151

\*log-transformed, °square-root transformed

Results of linear models examining the relationship between the proportion of green on 103 urban squares in Munich and seven taxonomic groups plus multidiversity. For models with covariates, a two-way ANOVA was used, while a one-way ANOVA was used for the rest. The tests were two-sided. Bolded results are significant ( $p \leq 0.05$ ; no correction for multiple testing).

## Extended Data Table 2 | Random forest model results

Taxonomic Group	mtry	% Variance explained	RMSE	R Squared	MAE
Greenness	7	75.3	0.12	0.77	0.09
Multidiversity	5	71.28	0.07	0.74	0.06
Arthropod abundance*	7	30.03	1.34	0.33	1.04
Arthropod richness	5	26.5	3.14	0.35	2.49
Bat richness	5	7.95	1.4	0.16	1.14
Bat activity°	4	4.54	5.11	0.16	4.27
Pigeon abundance	4	12.97	24.21	0.3	14.65
Bird abundance°	5	50.19	2.12	0.58	1.66
Bird richness	7	71.62	2.44	0.74	2.05
Bryophyte richness	5	36.57	6.69	0.44	5.51
Pollinator abundance°	4	23.36	1.42	0.32	1.15
Pollinator richness	4	29.57	1.24	0.41	1.04
Pest mammal activity*	7	22.78	1.25	0.37	1.08
Small mammal activity*	4	43.97	1.11	0.5	0.91
Vegetation richness	7	49.88	10.95	0.53	8.91

\*log-transformed, °square-root transformed

Random forest model performance metrics for seven taxonomic groups plus greenness and multidiversity. Mtry represents the number of variables selected at each split. Performance was evaluated using percent variance explained, root mean squared error (RMSE), R-squared, and mean absolute error (MAE) through repeated cross-validation with 10 k-folds and three repeats.

## Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

### Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- | n/a                                 | Confirmed  |
|-------------------------------------|--|
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement  |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly   |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> The statistical test(s) used AND whether they are one- or two-sided<br><i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i>   |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> A description of all covariates tested   |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons  |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> For null hypothesis testing, the test statistic (e.g. $F$ , $t$ , $r$ ) with confidence intervals, effect sizes, degrees of freedom and $P$ value noted<br><i>Give <math>P</math> values as exact values whenever suitable.</i>                            |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings  |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes  |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Estimates of effect sizes (e.g. Cohen's $d$ , Pearson's $r$ ), indicating how they were calculated  |

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

- |                 |  |
|-----------------|--|
| Data collection | <input type="text" value="No software was used."/>   |
| Data analysis   | <input type="text" value="All analyses were done in R (version R-4.1.1) using R-Studio (version 2021.09.0), including the packages random forest (tuneRF, partialPlot), caret (train, varImp), vegan(metaMDS, envfit), and usdm (vifstep). Initial bat identification and data management were done using EcoObs bcAdmin (Version 3.9), bcAnalyze (Version 3.0) batIdent (Version 1.0)."/> |

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

### Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

author upon reasonable request.

## Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	N/A
Reporting on race, ethnicity, or other socially relevant groupings	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences     Behavioural & social sciences     Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	N/A
Data exclusions	N/A
Replication	N/A
Randomization	N/A
Blinding	N/A

## Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	N/A
Research sample	N/A
Sampling strategy	N/A
Data collection	N/A
Timing	N/A
Data exclusions	N/A
Non-participation	N/A
Randomization	N/A

# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	To understand how design features of urban spaces influence biodiversity, we collected biodiversity and feature data on 103 public urban squares in the city of Munich, Germany. Data on seven taxonomic groups (arthropods, bats, birds, mosses, pollinators, small mammals, and spontaneous vegetation) were collected between April 2017 and July 2020. Squares were characterized by their features and surroundings using digital assets. Squares covered a gradient in vegetation cover (greenness derived from NDVI) and distance from the city centre (Marienplatz). To first understand how overall greenness drives biodiversity on the squares we created linear models for each of the taxonomic groups and the greenness measure. To understand more in-depth how the individual features of a square drive its biodiversity, we produced random forest models and calculated the importance scores for each square feature.
Research sample	Urban squares that cover a gradient in green cover and distance from the city centre. On each square design features as explanatory variables and the richness and abundance (or activity) of the seven taxonomic groups (arthropods, bats, birds, mosses, pollinators, small mammals, and spontaneous vegetation) were measured. For arthropods, this is insects collected on five habitats: sealed surfaces (paved or tarmac), grassy areas, flower beds (not planters or raised beds), shrubs, and trees at a single point over an area of 0.25 m <sup>2</sup> . For bats, a sample represents the activity and richness from four sampling nights using one ultrasonic recorder. For birds, a sample represents the richness and combined abundance from observations covering a square's whole area over seven periods (three in spring and summer, once in fall and three times in winter). A moss sample represents all species collected from three substrate types (wood, soil, stone) on each square. For pollinators, a sample represents the combined richness and abundance from five phytometers and three rounds on each square. For small mammals, a sample represents activity from a maximum of fifty footprint sheets over a five-day period. A vegetation sample represents all unplanned or planted species observed during a fifteen-minute period on eight different surfaces (frequently mown grass (<15cm), infrequently mown grass (>15cm), tree plates, woody structures other than trees, planting beds, planters, pavement cracks, unsealed surfaces and additionally furnishings, e.g., benches) per square.
Sampling strategy	<p>Based on a list of 814 open spaces in Munich, we chose squares by only considering street names containing the term "Platz" (square) in German. This resulted in a list of 354 squares. As square size was log-normally distributed, we then divided the squares into five size bins (on a log scale: (maximum size-minimum size)/5). Using stratified random sampling, we randomly drew a proportional number from each bin, redrawing if a square was less than 200m from another square (n=95). As squares without tree cover were underrepresented, an additional eight were manually selected, resulting in 103 squares.</p> <p>Arthropods on surfaces were collected using a battery-operated leaf blower outfitted with a gauze filter using a cage covering an area of 0.25 m<sup>2</sup>. Trees and shrubs were sampled using knockdown sampling and collecting the arthropods in a funnel attached to a sample jar. In the laboratory, all individuals were sorted to order level. Bats were sampled four times in clusters of 2-15 squares using ultrasonic recorders. Clusters were chosen so there was a minimum of 500 m between squares and formed a gradient from the city centre to the edge. Birds were recorded visually and aurally along manually created transects to cover the whole area of each square with a 25 m radius around the transect and transects were covered in a period of 20 minutes. Mosses were observed or collected on different substrates on each square for a maximum of 60 minutes per square (20 minutes per substrate type) or until no new species were observed. Pollinators were sampled by observing interactions with five phytometers during three rounds covering different periods of the day (morning, midday, and afternoon). Small mammals were observed by identifying footprints left behind on track sheets from five footprint tunnels placed on different combinations of surface types on each square. Spontaneous vegetation was recorded by identifying species on eight different substrate types. Substrates were observed for a maximum of 15 minutes until all substrate types on each square were observed.</p>
Data collection	All data was collected in the field by trained ecologists or students. Bryophyte samples were collected and brought back to the lab for identification using relevant guides. Acoustic recordings and automatic identification of bats were manually checked by a bat expert.
Timing and spatial scale	We collected arthropods between May and July 2017. We undertook bat sampling on single nights, from one hour before sunset to one hour after sunrise, between June and October 2017. All squares were sampled four times. Birds were recorded visually and aurally along transects, sampled three times in spring (April to July) 2017, once in fall (October) and three times in winter (December 2017 to February 2018). We collected mosses and liverworts between October 2017 and January 2018. Pollinators were sampled on each square three times between May and July 2018. We sampled pest and small mammals on five consecutive nights over nine weeks between June and September 2017. In June and July of 2020, we recorded the spontaneous vegetation.
Data exclusions	Data from all squares was included in the analyses. Some square features were excluded from the analysis due to collinearity with other features. Features removed were chosen based on a variance inflation factor $\leq 5$ .
Reproducibility	All methods used for quantify the square features and monitoring the taxonomic groups so that repeated data measurement would be possible in Munich or other cities.
Randomization	We generally had a systematic rule for placing the sampling site at the centre of the square and when there were multiple potential sites fulfilling the rule, we randomly chose between these.
Blinding	Data collection was undertaken using field observations, however, those collecting the biodiversity data in the field were not aware of the square features describing the sites.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	<input type="text" value="The field conditions for biodiversity recording were standardized for the individual taxonomic groups measured."/>
Location	<input type="text" value="Our data were collected in Munich, Germany (48.1372, 11.5761)"/>
Access & import/export	<input type="text" value="Field sites were publicly accessible urban spaces."/>
Disturbance	<input type="text" value="Field work was conducted in public urban spaces where disturbance is a regular component."/>

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input type="checkbox"/>	<input checked="" type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern
<input type="checkbox"/>	<input checked="" type="checkbox"/> Plants

### Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

## Antibodies

Antibodies used	<input type="text" value="N/A"/>
Validation	<input type="text" value="N/A"/>

## Eukaryotic cell lines

Policy information about [cell lines and Sex and Gender in Research](#)

Cell line source(s)	<input type="text" value="N/A"/>
Authentication	<input type="text" value="N/A"/>
Mycoplasma contamination	<input type="text" value="N/A"/>
Commonly misidentified lines (See <a href="#">ICLAC</a> register)	<input type="text" value="N/A"/>

## Palaeontology and Archaeology

Specimen provenance	<input type="text" value="N/A"/>
Specimen deposition	<input type="text" value="N/A"/>
Dating methods	<input type="text" value="N/A"/>
<input type="checkbox"/> Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.	
Ethics oversight	<input type="text" value="N/A"/>

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Animals and other research organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

Laboratory animals	<input type="text" value="This study did not involve laboratory animals."/>
Wild animals	<input type="text" value="For all sampling methods, arthropods were killed on site using ethanol. Identification of most arthropods requires killing and transport to a lab where they can be observed under a microscope."/>
Reporting on sex	<input type="text" value="No sex based information was collected."/>
Field-collected samples	<input type="text" value="Samples were stored in 98% ethanol during transport, sorting and identification."/>
Ethics oversight	<input type="text" value="Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not."/>

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Clinical data

Policy information about [clinical studies](#)

All manuscripts should comply with the ICMJE [guidelines for publication of clinical research](#) and a completed [CONSORT checklist](#) must be included with all submissions.

Clinical trial registration	<input type="text" value="Provide the trial registration number from ClinicalTrials.gov or an equivalent agency."/>
Study protocol	<input type="text" value="Note where the full trial protocol can be accessed OR if not available, explain why."/>
Data collection	<input type="text" value="Describe the settings and locales of data collection, noting the time periods of recruitment and data collection."/>
Outcomes	<input type="text" value="Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures."/>

## Dual use research of concern

Policy information about [dual use research of concern](#)

### Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Public health
<input checked="" type="checkbox"/>	<input type="checkbox"/>	National security
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Crops and/or livestock
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Ecosystems
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Any other significant area

### Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Demonstrate how to render a vaccine ineffective
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Confer resistance to therapeutically useful antibiotics or antiviral agents
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Enhance the virulence of a pathogen or render a nonpathogen virulent
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Increase transmissibility of a pathogen
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Alter the host range of a pathogen
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Enable evasion of diagnostic/detection modalities
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Enable the weaponization of a biological agent or toxin
<input checked="" type="checkbox"/>	<input type="checkbox"/>	Any other potentially harmful combination of experiments and agents

## Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A

## ChIP-seq

### Data deposition

- Confirm that both raw and final processed data have been deposited in a public database such as [GEO](#).
- Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links <i>May remain private before publication.</i>	N/A
Files in database submission	N/A
Genome browser session (e.g. <a href="#">UCSC</a> )	N/A

### Methodology

Replicates	N/A
Sequencing depth	N/A
Antibodies	N/A
Peak calling parameters	N/A
Data quality	N/A
Software	N/A

## Flow Cytometry

### Plots

Confirm that:

- The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).
- The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).
- All plots are contour plots with outliers or pseudocolor plots.
- A numerical value for number of cells or percentage (with statistics) is provided.

### Methodology

Sample preparation	<i>Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.</i>
Instrument	<i>Identify the instrument used for data collection, specifying make and model number.</i>
Software	<i>Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.</i>
Cell population abundance	<i>Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.</i>
Gating strategy	<i>Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.</i>

- Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

# Magnetic resonance imaging

## Experimental design

Design type	Indicate task or resting state; event-related or block design.
Design specifications	Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.
Behavioral performance measures	State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).

## Acquisition

Imaging type(s)	Specify: functional, structural, diffusion, perfusion.
Field strength	Specify in Tesla
Sequence & imaging parameters	Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.
Area of acquisition	State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.
Diffusion MRI	<input type="checkbox"/> Used <input type="checkbox"/> Not used

## Preprocessing

Preprocessing software	Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).
Normalization	If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.
Normalization template	Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.
Noise and artifact removal	Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).
Volume censoring	Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.

## Statistical modeling & inference

Model type and settings	Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).
Effect(s) tested	Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.
Specify type of analysis:	<input type="checkbox"/> Whole brain <input type="checkbox"/> ROI-based <input type="checkbox"/> Both
Statistic type for inference	Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.
(See <a href="#">Eklund et al. 2016</a> )	
Correction	Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).

## Models & analysis

n/a	Involvement in the study
<input type="checkbox"/>	<input type="checkbox"/> Functional and/or effective connectivity
<input type="checkbox"/>	<input type="checkbox"/> Graph analysis
<input type="checkbox"/>	<input type="checkbox"/> Multivariate modeling or predictive analysis
Functional and/or effective connectivity	Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).
Graph analysis	Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph,

Graph analysis

*subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*

Multivariate modeling and predictive analysis

*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*