Bees need larger brains to thrive in urban environments

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Abstract

The rapid conversion of natural habitats to anthropogenic landscapes is threatening insect pollinators worldwide, raising concern on the consequences for their fundamental role as plant pollinators in natural and agricultural systems. However, not all pollinators are negatively affected by habitat conversion, as some find in anthropogenic landscapes appropriate resources to survive and reproduce. Why some animals can thrive in anthropogenic environments that most species cannot tolerate remains insufficiently understood, but it might in part reflect enhanced behavioural plasticity to exploit new resource opportunities. This theory -known as the cognitive buffer hypothesis- has received ample support in studies of vertebrates. However, it is less obvious whether the tiny brain of insects can similarly buffer individuals against the many challenges of anthropogenic habitats. To address this issue, we measured brains for 384 individuals from 116 species of bees, the most important group of pollinators, and evaluated the association of their brain sizes with detailed information on habitat preferences. Our analyses revealed that bees that prefer forested or agricultural habitats had smaller brains relative to their body size than those who prefer urban habitats. In addition, urban bees also tend to have larger body sizes, and hence, show larger absolute brain sizes. Our results provide the first empirical support of the cognitive buffer hypothesis in invertebrates, suggesting that a large brain in bees could confer behavioural advantages to tolerate urban environments.

Keywords: relative brain size, habitat preference, Apoidea, urbanisation. [a]

1. Introduction

Pollinators deliver a fundamental ecosystem service on which the earth's vegetation and human economy depend [1]. Regrettably, there is increasing evidence of recent declines in pollinator populations [2–4]. One of the main contributing factors to the current pollinator declines is the alteration and loss of their habitat due to human activity [5,6]. Anthropogenic landscapes present new challenges for survival and reproduction of organisms, increasing their risk of extinction [7,8,9]. Yet, not all pollinator species are negatively affected by land use change. For instance, some bee species are able to tolerate human-altered environments [10–12] or even to thrive such as *Bombus terrestris* [13]. However, we still lack generalizable information about the functional and ecological consequences of inhabiting these novel environments [14].

Human-dominated habitats —notably cities— drastically modify the original conditions where pollinators evolved, but can also offer unique ecological opportunities in the form of new nesting spots, reduced predation pressure and high food availability associated with non-indigenous plants [7,12,15]. The question is then why only some species are able to tolerate urban environments. The "cognitive buffer hypothesis" provides an explanation for this conundrum, suggesting that in novel environments the chances to successfully survive and reproduce depends on cognition [16], that is, the processes involved in gathering, storing and reacting to environmental information [17]. While the "cognitive buffer hypothesis" receives ample support from studies of vertebrates [18–21], similar evidence is lacking for insects. [b]

Insects have been long associated with the most basic types of learning due to their miniature brain [22,23]. However, numerous studies have shown that bees and other insects have sophisticated cognition [24–26]. For instance, some social insects can learn by observing other individuals how to use tools to solve complex tasks [[27]][c]. In addition, there is also evidence for substantial variation across species in brain size—both in absolute terms and relative to body size— with species that have larger brains also exhibiting enhanced cognitive performance [28]. Therefore, we can ask whether the varying success of insects in human-altered habitats might be explained by variation in brain size.

Here, we report the first test of the "cognitive-buffer hypothesis" in insects. Our test is based on a unique database of brain measures for 116 European and North American bee species. By means of detailed information of geographic distribution (GBIF; http://www.gbif.org/), we characterise habitat preferences for all the species, and use a phylogenetically-informed comparative analysis to assess whether bees that proliferate in human-altered habitats have enlarged brains compared to those that avoid them.

2. Methods

(a) Bee species dataset

Our dataset contains measurements of brain and body size for bee specimens captured on flowers by hand netting in different areas of the East Coast of the United States and Europe (Spain and the Netherlands). The dataset includes information of 384 female individuals from 116 species that represent 6 families and 31 genera. We only considered female specimens because: (i) females are involved in a greater diversity of tasks than males, and hence are expected to experience greater selective pressures from the environment; and (ii), there are evident behavioural and morphological differences between sexes that are associated with the size and structure of the brain [29,30]. Brain size was measured as the weight of fixed brains[d] and body size as intertegular[e] span (see supplementary text). Because brain size scales allometrically with body size, we considered for our analysis the size of the brain relative to the body.

We estimated brain size relative to body size through modelling the log-transformed association between brain weight and intertegular span. For this, we specified a Bayesian linear model with the function *brm* from the package *brms* version 2.18 [31] where brain weight was the response variable and intertegular span the predictor. To correct for the non-independent evolutionary histories among species, we included the phylogenetic covariance matrix as a random factor. Lastly, we extracted the differences between the observed and predicted values (i.e., residuals) that represent the relative brain size. High values indicate larger brains than expected for their body size and low values denote smaller brains than expected. We found that brain size scaled allometrically with body size (Bayesian $R^2 = 0.9$) and that this relationship was constrained by the evolutionary history of the species (phylogenetic signal of relative brain size, $\lambda = 0.6$; $P < 0.01$). However, there were considerable variability in relative brain size within and across the different taxonomic groups (i.e., genera and subfamily level; Figure S1; Figure 1A)

(b) Occurrence data

We downloaded occurrence information for all species from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) for North America and Europe. The data was downloaded through R programming language with the help of the function *occ_download* from the package *rgbif* version 3.7.3 [32]. We selected the states or countries with the highest density of records for our set of species. For North America, we selected states located on the East Coast of the United States (Figure S2A), covering an approximate area of 136,937 km^2. For Europe, we selected countries located on the north and centre of the continent (Figure S2B), representing a total area of 600,497 km^2. To further reduce biases in the data, we only included species with a minimum number of 50 records and whose geographic distribution was larger than the sampled area (i.e., excluding species at the edge of their distributions). In addition, we optimised the match between species occurrence and the land cover data by only using georeferenced records obtained between 1990 and 2022 with a minimum of two decimals of latitude/longitude coordinates.

(c) Land cover classification

We assigned a habitat type to each GBIF occurrence by merging land cover information with the georeferenced records of species occurrences. The land cover classification was obtained from the 2006 online inventories of the National Land Cover Database (NLCD) for United States and the Corine Land Cover (CLC) for Europe. After downloading these inventories as raster files, we used the functions *rast* and *extract* from the *Terra* package version 1.6-41 [33] to read and obtain the cover classification of the different georeferenced records, respectively. To simplify the interpretation and conduct a joint analysis for both occurrence datasets, we divided the resulting cover classes into three single categories: (i) natural, (ii) agricultural and (iii) urban (see Tables S1 and S2 for details).

(d) Construction of the phylogenetic tree

We constructed a phylogeny with all studied species by using a previously published genus-level bee phylogeny [34]. For this, we first read the backbone phylogeny with the function *read.tree* and drop the missing genera with function *drop.tip* from the package *ape* version 5.6-2 [35]. Then, we selected as an outgroup a wasp genera (*Tachysphex*) and recalculated distances to the root with the function *chronos* from *ape*. Species tips were added to genera nodes as polytomies of equal branch length relative to the genera branch length using the phytools package version 1.2-0 [36]. From the resulting tree, we created a scaled phylogenetic covariance matrix with the function *inverseA* from the package *MCMCglmm* version 2.33 [37].

(e) Analysis

Habitat preference was estimated by comparing species occurrences per habitat with the ones that we would expect if they occur at random. For this, we generated 10,000 randomised matrices based on the occurrence matrix (i.e., species in rows and habitats in columns) with the function *nullmodel* from the package *bipartite* version 2.16 [38]. We implemented this function with the method 'r2dtable', which maintains row and column sums constant by using Patefield's algorithm [39]. This maintains the proportional dominance of the species and habitats constant but reshuffles their associations. We then estimated the percentage of simulated occurrences per species and habitat that were under the observed ones (i.e., percentile). Lastly, we considered that a bee species exhibited a "high preference" for any of the three studied habitats when the number of occurrences observed in this habitat exceeded the 80th percentile of the values obtained from the simulations. On the contrary, the species was considered to exhibit a "low preference" for the habitat when the observed occurrences were below the 20th percentile. To better understand if our findings are affected by the evolutionary histories of the species, we estimated the phylogenetic signal of relative brain size and habitat preference across habitats for our set of species with the help of the function *phylosig* from the *phytools* package.

To evaluate how the association between habitat preference and relative brain size changed by habitat type, we modelled with Bayesian generalised linear models their association. For this, we first joined the resulting habitat preference and relative brain size datasets by species and

extracted those with statistical habitat preference on any of these three habitats. Because we assessed habitat preference as binary (low or high), we specified a Bernouilli distribution where habitat preference was the response variable and relative brain size the predictor. Again, we included the phylogenetic covariance matrix as a random factor. Moreover, we also explored how habitat preference changed by brain weight and intertegular span independently. For this, we conducted two analogous models with these two different predictors. In addition, we also investigated the different trends for the United States and Europe separately.

All our models were run with 4,000 iterations with previous 1,000 warm up iterations, usingnon-informative or weakly informative priors [31]. Further, the different posterior predictive checks were conducted with the function *pp_check*, also from the *brms* package. All our analyses were undertaken in R version 4.0.5 [40], and all data processing and graphics were done with the set of packages from the tidyverse version 1.3.0 [41].

3. Results

Habitat preference varied substantially across species (Figure 1B) but showed none (i.e., preference for agricultural and rural habitats) or moderate phylogenetic signal (i.e., preference for natural habitat; $\lambda = 0.38$; $P = 0.02$). In general, most bee species preferred one or two habitat types but more rarely occurred indistinctly in the three habitats (Figure 1B). The most preferred habitats were the agricultural and natural ones with 49 and 48 species over 80% of the values from null models, respectively (Figure 1B and Figure S3). In contrast, most species avoided or had low preference for urban habitats (56 species under the 20th percentile) and just 28 species showed high preference for this habitat type (Figure 1B and Figure S3). The resulting distribution of habitat preferences for each of the habitats analysed followed a zero-one inflated beta distribution (Figure S3), indicating that there were high frequencies of habitat preferences close to 0 or 1 but low frequencies of intermediate values between 0 and 1. Hence, in our analyses we only modelled the extremes of the distribution (i.e., species classified as avoiding or preferring a given habitat).
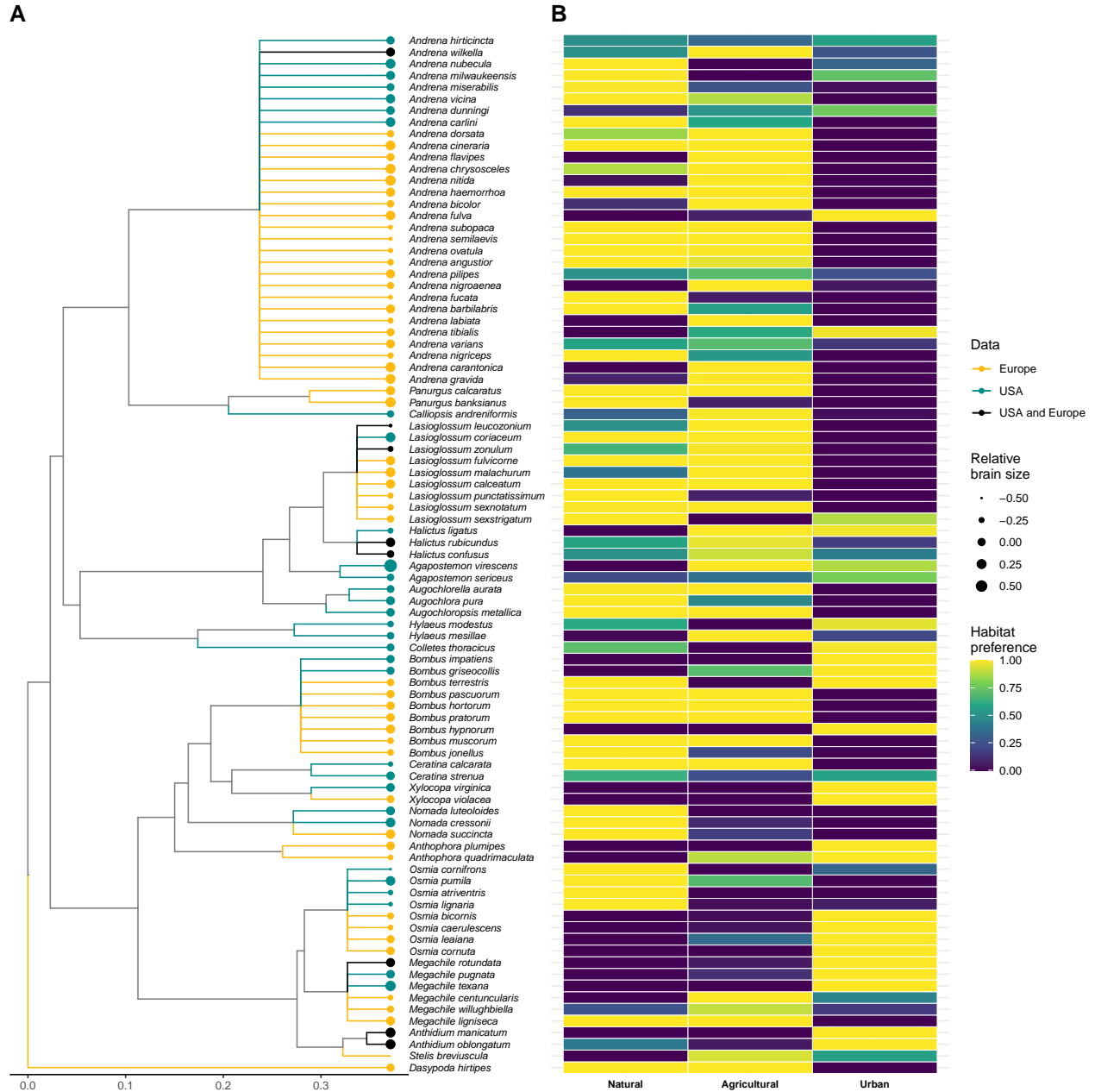
Figure 1. Phylogenetic relationship and habitat preferences for the selected bee species with brain weight and intertegular distance information (N=89). A) Phylogenetic tree at the genus level. Tree branches are coloured based on the geographical location of the different bee species (North of Europe, East Coast of United States or from both regions). The deviation of the brain size in relation to the body (i.e., residuals) is indicated with weighted points at the end of the tip branches. Larger points indicate larger brains in proportion to their body size and vice versa. B) Heatmap showing the habitat preference for each bee species. The columns delimit the habitat type (i.e., natural, agricultural, semideveloped and urban) and the rows the different bee species.

Although our model evaluating how relative brain size was associated with habitat preference explained little of the overall variance (Bayesian $R^2 = 0.11$), we found differences when we explored this association by habitat type (Figure 2A). Specifically, we found that bees with larger brains relative to body size showed a higher preference for urban habitats than bees with smaller relative brain sizes (Figure 2A). Contrarily, bees with smaller relative brains showed higher preference in natural and agricultural habitats than bees with larger relative brain sizes (Figure 2A). Although the models of the association between absolute brain size and intertegular span with habitat preference captured also little of the overall variance (Bayesian $R^2 = 0.25$; Bayesian $R^2 = 0.23$, respectively), we found marked differences between habitat types (Figures 2B and 2C). Specifically, we found that bees with larger brains and body sizes tend to appear more in urban habitats and bees with smaller brains and body sizes are more common in natural and agricultural ones (Figures 2B and 2C). These findings were consistent with the analogous analyses separated by geographical regions (United States and Europe; Figure S4).
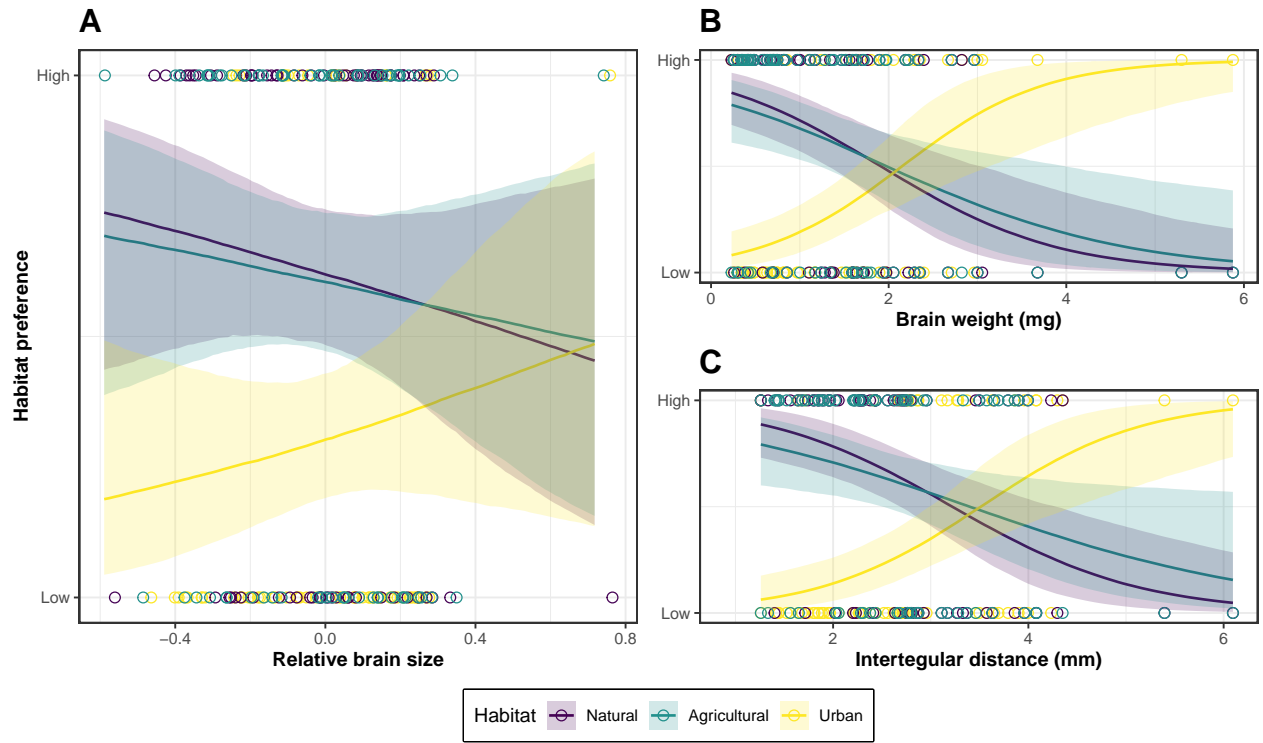
Figure 2. Association between relative brain size (A), brain weight (B) and intertegular distance (C) with habitat preference by habitat type (i.e., natural, agricultural and urban). The shaded and coloured areas by habitat type represent 95% credible intervals.

4. Discussion

Bees with a preference for inhabiting urban habitats tended to have larger brains relative to their body, and those with forest or agricultural preferences had relatively smaller brains. These results are in line with the cognitive buffer hypothesis [16], which predicts that novel environments should select for larger brains. In urban environments, individuals are frequently exposed to a variety of new challenges such as novel resources or human disturbances that can change fast in time and space [42]. In such scenarios, a large brain could confer the behavioural flexibility needed to efficiently exploit novel resources or avoid novel predators. Our findings are also consistent with previous evidence found in vertebrates that having a large brain size can allow survival in urban environments [43,44], and suggest that, in bees, urban dwellers may need to have better cognitive abilities and flexibility in their behaviour than forest or agricultural bees.

The exact mechanism that allows large-brained bee species to prefer urban habitats is still unclear. However, there are some examples of novel behaviours that might be needed to survive in urban environments, such as the use of human-made materials to nest [45] or being able to collect pollen and nectar from exotic flowers [46]. In addition, despite the lack of broad consensus of the functional consequences of urbanisation [14]], there is support to the idea that cities select against small body sizes [47,48]. We also found larger bees in urban areas using data from two different continents and over 100 bee species. This may be a consequence of the patchy resource distribution as the foraging distance in bees is positively associated with body size [49,50]. Further, the patchiness of urban resources might also favour species that are already adapted to look for target resources (i.e. specialist bees), which tend to have relatively larger brains [51]. However, this hypothesis requires that the needed resources are present. In any case, this idea would need to be properly tested for bees, as there are also shreds of evidence that associate increasing urbanisation with wider ecological niches [14,52,53].

Our analyses focused on brain size mainly for reasons of data availability. The use of brain size is based on the existence of previous evidence that enlarged brains enhance cognitive performance in bees [28] and is justified because the brain is less subject to measurement error or context-dependent biases than are experimental measures of cognition [54]. However, the use of brain size as a proxy for cognitive performance is not exempt from criticism [24,55]. Thus, finer brain measurements like neuropils size or mushroom bodies [the suspected centres of cognitive processes in bees; 56,57,58] are likely to help improve our understanding of bee cognitive abilities in relationship to urbanization. Overall, our findings highlight the importance of behavioural responses for understanding the dynamics of insect populations in altered environments, and stresses the need to avoid viewing them as passive agents of external factors.

Data accessibility

All occurrence data used in this study can be downloaded from https://doi.org/10.15468/dl.5s5kuf. In addition, bee trait data and code can be found in the online repositories of

Zenodo XXXXXXXXXXX and Github https://github.com/ibartomeus/declines_brain.git.

Authors' contributions

MAC, IB and JBL designed the study. MAC and FS collected the data. JBL led the analysis with help from MAC and IB. JBL and IB wrote the manuscript with contributions from all authors.

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Conflict of interest declaration

We declare we have no competing interests.

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Supplementary material

Brain and body size measurements

Brain size was measured as the weight of the fixed brain for each specimen. First, all collected individuals were kept in cold and sent to the laboratory where they were identified by expert taxonomists and anesthetized in cold. Then, heads were removed with a scalpel and placed in a fixative solution (4% paraformaldehyde in 0.1 M phosphate-buffered saline -PBS- pH = 7.4) to avoid degradation. Subsequently, brains were extracted from the head capsule and placed on a petri dish after removing the retina from the optic lobes and cleaning the entire brain of all tracheae and fat bodies. By doing this, we ensured that our brain measurements mainly accounted for neural tissue. We then placed the brains on a small piece of Parafilm® and dried the exceeding fixative solution with Kimwipes® tissues. Then, within 4 seconds of the liquid removal, we weighted the brains with the help of a microbalance Sartorius Cubis®. Finally, we calculated the average weight for the species with more than one specimen. Because weighing bee brains is a highly error-prone task, we excluded values that were under or above 1.5 times the interquartile range for each species.

We considered as a proxy of body size the average intertegular span (ITS) per species. ITS represents the distance between the base of the wings (tegulae) on the bee thorax and has been shown to accurately predict body size as it is highly correlated with dry body weight (Cane et al., 2006; Kendall et al., 2019). All ITS measurements were conducted with a stereomicroscope (magnification 16x or 80x) with a calibrated ocular micrometre (resolution down to 0.02 mm).

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Table S1. Original downloaded cover classes for United States with the respective assigned cover classes and number of bee occurrences found on each of them.

| Original NLCD Cover class	Occurrences	Assigned cover class
Hay/Pasture	3837	Agricultural
Developed, Open Space	3470	Urban
Developed, Low Intensity	2844	Urban
Deciduous Forest	2825	Natural
Developed, Medium Intensity	2320	Urban
Cultivated Crops	1038	Agricultural
Mixed Forest	1017	Natural
Woody Wetlands	989	Natural
Developed, High Intensity	962	Urban
Shrub/Scrub	492	Natural
Evergreen Forest	395	Natural
Herbaceous	353	Natural
Open Water	293	Discarded
Emergent Herbaceous Wetlands	278	Natural
Barren Land	143	Discarded

Table S2. Original downloaded cover classes for Europe with the respective assigned cover classes and number of bee occurrences found on each of them.

Original CLC Cover class	Occurrences	Assigned cover class
Discontinuous urban fabric	109779	Urban
Non-irrigated arable land	60722	Agricultural
Pastures	52571	Agricultural
Complex cultivation patterns	20975	Agricultural
Broad-leaved forest	15013	Natural
Land principally occupied by agriculture	10400	Agricultural
Sport and leisure facilities	9534	Urban
Industrial or commercial units	9258	Urban
Mixed forest	8513	Natural
Coniferous forest	7308	Natural
Green urban areas	5924	Urban
Natural grasslands	2900	Agricultural
Moors and heathland	2826	Natural
Water bodies	2578	Discarded
Vineyards	2191	Agricultural
Continuous urban fabric	1875	Urban
Water courses	1848	Discarded
Road and rail networks and associated land	1731	Discarded
Inland marshes	1611	Natural
Mineral extraction sites	1248	Discarded
Fruit trees and berry plantations	1192	Agricultural
Peat bogs	1092	Natural
Construction sites	1085	Urban
Transitional woodland-shrub	1067	Natural
Beaches, dunes, sands	696	Natural
Intertidal flats	576	Natural
Sea and ocean	426	Discarded
Estuaries	422	Discarded
Port areas	376	Urban
Airports	371	Urban
Dump sites	285	Discarded
Salt marshes	166	Natural
Sparsely vegetated areas	33	Natural
Coastal lagoons	23	Natural
Bare rocks	8	Discarded
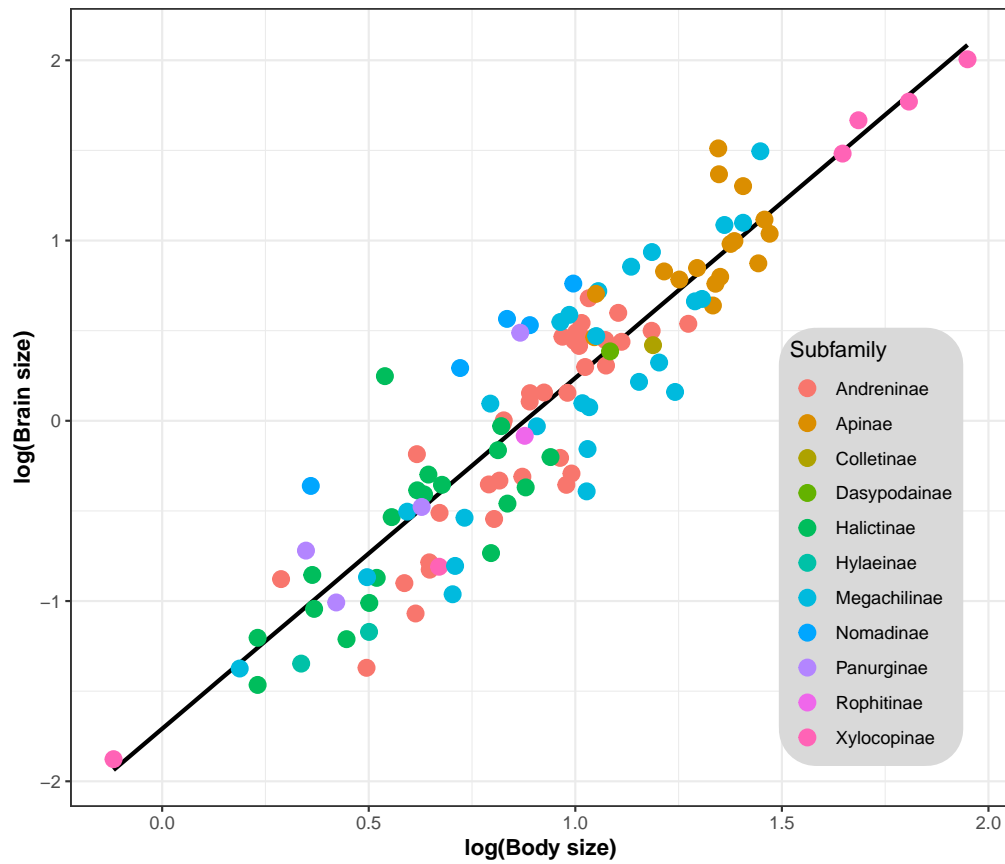
Figure S1. Association between the log-transformed values of brain and body size (N = 116). The different raw values or points are coloured by the subfamily taxonomic rank.
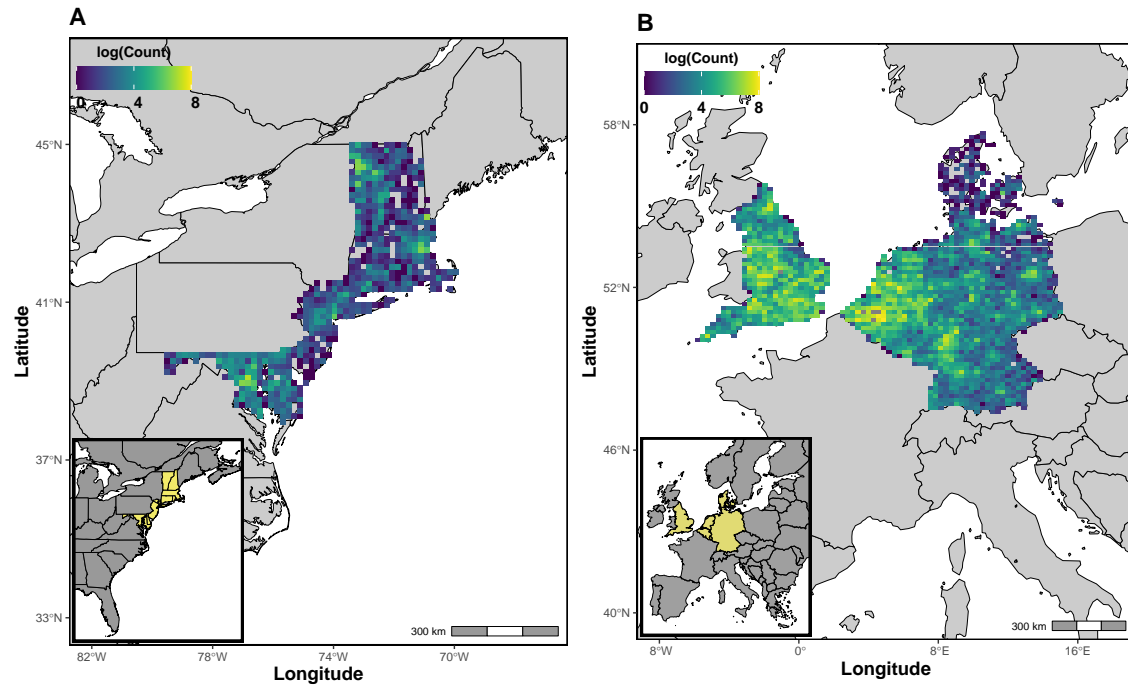
Figure S2. Maps showing the study areas and the number of GBIF occurrences in logarithmic scale for the selected bee species. A) East Coast of United States with records for Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York metropolitan area, New Jersey, Delaware and Maryland. B) European continent with records downloaded for England, Belgium, Netherlands, Germany and Denmark.
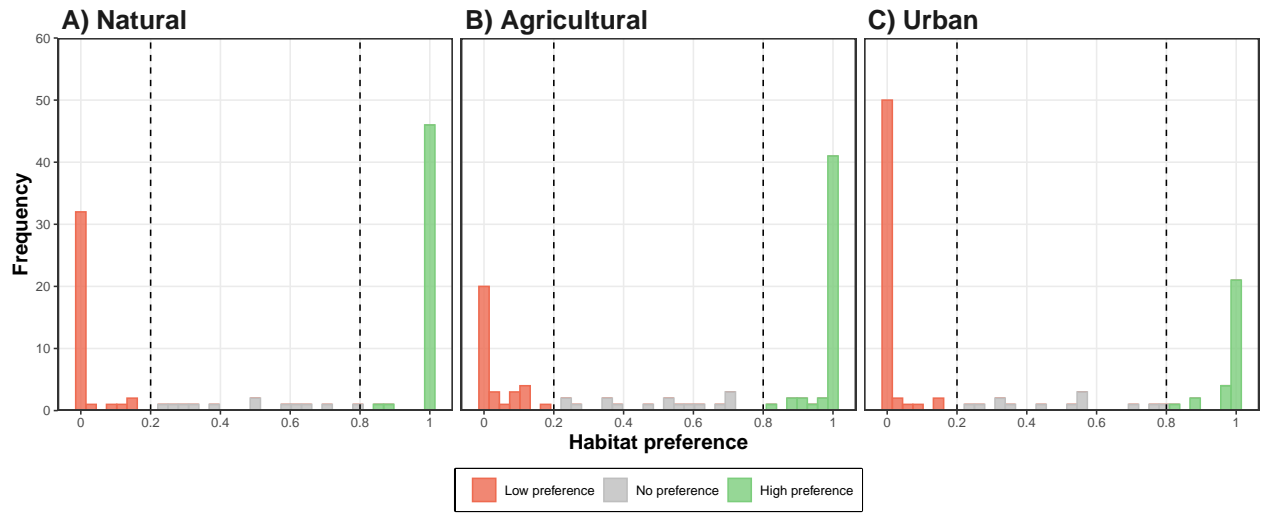
Figure S3. Frequency distribution of the bee preferences for each habitat type (i.e., natural, agricultural and urban). The different habitats are reclassifications from the 2006 land use categories of the Corine Land Cover (CLC) inventory for Europe and the National Land Cover (NLC) database for Unites States.

[a]Quizá completar el cupo de keywords? propongo Urban habitats, pollinators, cognitive buffer hypothesis. [b]Tenemos alguna forma de dar pruebas de esto? Sé que demostrar la no-existencia de algo es muy difícil, pero se me queda un poco cojo afirmar esto sin nada más. No he encontrado nada. Supongo que si hay problemas con esto los revisores lo indicarán. [c]El artículo de los bombus jugando llegó al mainstream, quizá sería buena estrategia citarlo, además así tenemos una cita de algo actual!

https://www.sciencedirect.com/science/article/pii/S0003347222002366?via%3Dihub [d]cita sayol aqui. [e]citar Kendall aqui [f]Qué pondrías aquí? [g]puedes rescatar los proyectos del mineco que agradece MA en sus papers? Survive_change, creo. Nada más por mi parte. [h][**xmiguelangelcolladox?**][**gmail.com?**] podrías rescatar el funding que creas más oportuno?

United States occurrences (N = 21,256)
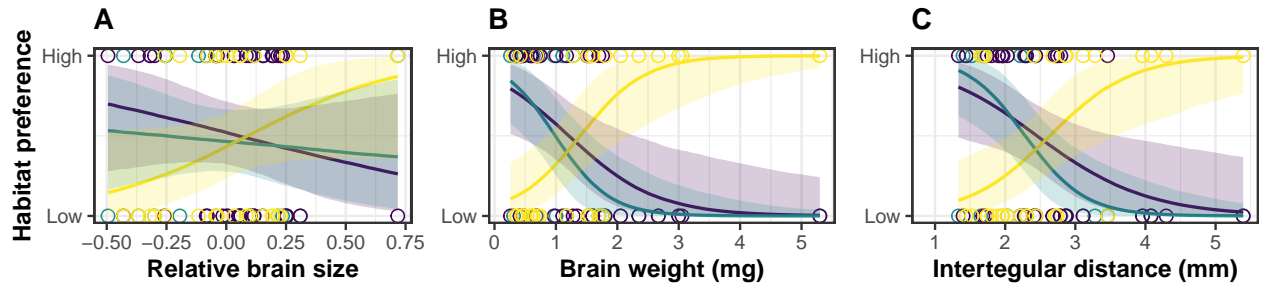
Europe occurrences (N = 336,623)
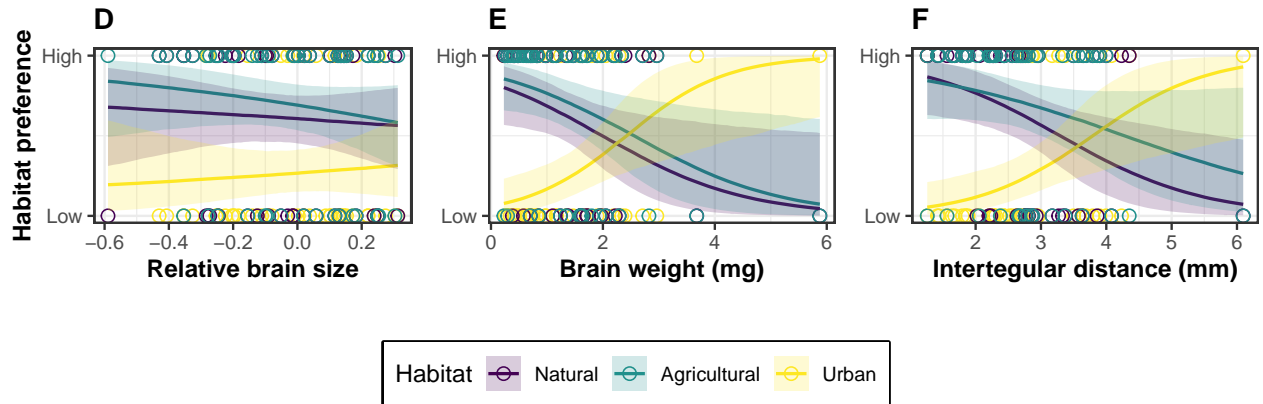
Figure S4. Association between relative brain size (A and D), brain weight (B and E) and intertegular distance (C and F) with habitat preference separated by habitat type (i.e., natural, agricultural and urban) and geographical region (USA in the upper panel and Europe in the lower one). The shaded and coloured areas by habitat type represent 95% credible intervals.