

REVIEW

The impact of urbanisation on chipmunks, arboreal and flying squirrels: a global systematic review

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ABSTRACT

1. The current, rapid urbanisation process impacts global biodiversity and can be a driver for phenotypic changes in mammals that persist in cities. Animals display different response strategies in urban environments compared to natural areas, but patterns may differ among species. To better comprehend this process, we focused on a limited number of species that are present in many urban green spaces around the globe.
2. The aim of this systematic review is to investigate which response strategies chipmunks, arboreal and flying squirrels use to cope with urban environments, exploring whether there are general response patterns, and to reveal potential adaptations to life in urban areas. We included studies that compared trait differences among conspecifics living in different areas along an urbanisation gradient (rural–urban) and studies comparing individuals or populations between urban areas with different environmental characteristics.
3. The effects of urbanisation on chipmunks, arboreal and flying squirrels, at the individual and at the population levels, were identified in nine topics. Included articles explored at least one of these topics and their key findings were described.
4. Effects of urbanisation are evident in all considered topics. However, we found contrasting patterns between species or even among individuals of the same species studied in different geographical areas. Overall, we reported two knowledge gaps: some phenotypic traits were considered in few studies, and

many species, especially those living in the Global South, where urban growth rate is higher, have not been studied.

5. This systematic review suggests that urbanisation can be an important driver for adaptation in small mammals, underlining the complexity and differentiation of response patterns. Since target species have important ecological and social roles, additional comparative studies, increasing our understanding of processes that determine their presence in cities, are essential for urban green planning which aims to conserve biodiversity.

INTRODUCTION

The global population has recently surpassed 8 billion, and it is expected to reach 9 billion around 2037 and 10 billion around 2058 (United Nations 2022a). This continuous growth and the rural-to-city migration are predicted to cause an expansion of existing towns and the establishment of new ones, especially in less-developed regions (United Nations 2019, 2022b), ultimately impacting global biodiversity (McKinney 2008, Alberti et al. 2017, Li et al. 2021).

The study of urban wildlife ecology is a young field of research to which conservationists are directing their attention (Collins et al. 2021). Indeed, conservation of biodiversity is mandatory not only in the natural environment, where it contributes to ecosystem processes, but also in the urban context for protection of some endemic species (Aronson et al. 2014, Ives et al. 2016) as well as recreation and education of citizens (McKinney 2008). In a review, Dearborn and Kark (2010) explained seven motivations for conserving urban biodiversity, considering the benefits for nature as well as the benefits for humans. They highlighted the need of setting specific objectives before realising conservation actions and pointed out that each urban area is driven by different factors, such as culture or socioeconomics, that could result in a different motivation (and thus in different actions and consequences) to conserve biodiversity in each city. Thus, the need for globally comparative analyses arose to have a comprehensive view of this process.

Urban areas are characterised by different species composition than the nearby natural ones (Gallo et al. 2017, Leveau 2022). Among mammals, bats, rodents and carnivores are the most frequent orders present (as visitors or dwellers) in cities (Santini et al. 2019). Indeed, the response to urbanisation differs among species, varying from migration or local extinction to persistence and adaptation to this challenging environment (Sol et al. 2014, McDonnell & Hahs 2015). The ability to adjust the phenotype to environmental challenges in urbanised areas can enhance the probability of adapting

to novel conditions, which implies fitness advantages (McDonnell & Hahs 2015). Therefore, individuals can display response strategies in urban areas, which are generally related to morphology, behaviour and physiology, but they can also be associated with life-history parameters (e.g. McDonnell & Hahs 2015, Alberti et al. 2017, Johnson & Munshi-South 2017, Santini et al. 2019). Overall, studying animals' responses to challenges posed by anthropogenic pressures (e.g. infrastructures, noise, supplemental feeding) and evaluating whether they affect fitness provide an optimal opportunity to examine adaptation mechanisms in urban areas. However, to fully understand whether animals are advantaged in the urban environment, it is mandatory to compare individuals who live in cities with conspecifics occurring in rural habitats, evaluating both the effect at the individual level (e.g. behaviour, physiology) and at the population level (e.g. presence/absence, abundance). Additionally, studies that compare areas within the urban matrix, which differ in some environmental characteristics or pressures, could help to reveal potential adaptive mechanisms and/or determine the best management actions.

Arboreal and flying squirrels as well as chipmunks, included in this review even if phylogenetically more related to ground squirrels (Thorington et al. 2012, see also Appendix S1), are excellent models to study the effects of urbanisation on terrestrial mammals: in fact, these three taxa are present in urban green spaces around the globe, in both highly and less-developed regions, and either as native or invasive alien species (Koprowski & Nandini 2008, Bertolino 2009). These taxa use a three-dimensional environment, as they are, at least partly, arboreal or rely on food resources from shrubs. Hence, they exploit the habitat vertically as well as horizontally and use arboreal and shrub vegetation in natural forests, as well as in the urban context where they occur in city parks, lanes and public or private gardens, more or less isolated within the urban matrix (*Pteromys volans*, Mäkeläinen et al. 2016; *Tamias striatus*, Lyons et al. 2017; *Sciurus vulgaris*, Fingland et al. 2022). Understanding these species' potential adaptations in urban

environments has the ultimate goal of improving management and making urban areas suitable for their conservation. In fact, chipmunks and squirrels are important seed dispersers (Thorington *et al.* 2012), and some species also act as pollinators (Kobayashi *et al.* 2020), in urban as well as in natural habitats. Moreover, they often have an important social role in the urban environment becoming an attraction to citizens visiting greenspaces (in both public or private parks and gardens).

To better understand the capacity of wild animals to change phenotypic traits and, potentially, to adapt to the urban environment, we conducted a systematic review of the scientific literature to investigate response strategies to urbanisation and potential adaptations (fitness outcomes) of arboreal squirrels, flying squirrels and chipmunks. Particularly, we used studies 1) comparing rural/natural with urban areas, or analysing differences along the gradient, and 2) comparing different urban settings or analysing changes in relation to anthropic sources of disturbance (details below), to identify shifts in specific phenotypic traits and explore the pattern of these changes among species.

METHODS

Literature search and inclusion criteria

A systematic literature search was undertaken in December 2022 following the PRISMA protocols (Page *et al.* 2021). We conducted the literature search using Web of Science, Scopus and Google Scholar, applying the following terms: (squirrel* OR Sciurid* OR chipmunk*) AND (urban* OR anthro* OR town* OR city OR park* OR synurb*). We collected all the results listed on Web of Science and Scopus, while only the first 200 results from Google Scholar were included, which is the threshold of relevance used in other reviews (Razgour *et al.* 2016, Lisón *et al.* 2020, Fingland *et al.* 2022, Wauters *et al.* 2023).

We selected only English-written articles published in peer-reviewed journals, excluding book chapters, theses, reports, conference proceedings and news items. There were no restrictions regarding the year of publication.

After the identification phase, title and abstract of 1733 unique records were scanned for inclusion using the following criteria: 1) article must include at least one species of arboreal squirrel, flying squirrel or chipmunk; and 2) article must include at least one study site within an urban setting.

We obtained 109 articles whose full text was then assessed for eligibility, based on the following classification: 1) 'gradient rural-urban': studies that compare at least one rural with at least one urban area (either measured in the same study or reported from earlier literature) or that consider a variation along a rural-urban gradient; 2)

'gradient inside urban': studies within the urban environment that compare at least two areas or a gradient with different characteristics (e.g. urban park vs. urban forest, proportion built-up areas); 3) 'urban': studies in the urban setting without comparison, these studies were not discussed but only reported in Appendix S2.

Only 79 articles, which belong to the first two types, were retained. We excluded two review papers since they reported articles that were already included in the present systematic review. We added two articles that did not appear in our search but which were present in our personal libraries and relevant to the objectives of the present systematic review. The PRISMA flowchart is provided in Fig. 1.

Key findings from the included articles were described in nine broad topics and displayed responses to urban habitats were discussed. Each article explored at least one of the identified topics (Fig. 2). Distribution of included articles across years is presented in Fig. 3. The list of the articles included in the qualitative synthesis is presented in Appendix S3.

RESULTS AND DISCUSSION

Genetics

Genetic variation is often considered a factor of concern in urban settings, since populations are usually small and often partly isolated (reduced connectivity of green areas within cities and with surrounding woodlands or forests), which might result in lower genetic variability than in natural habitats. A study, considering only rural areas, reported lower genetic diversity in small and isolated populations than in larger and more connected populations of Eurasian red squirrels (*Sciurus vulgaris*; Wauters *et al.* 1994). In this review, we included two studies that compared the genetics of urban and rural Eurasian red squirrels. Rézouki *et al.* (2014) extracted DNA from hair samples (65 urban individuals and 13 forest individuals) and found a similar genetic diversity in the urban park and in the natural forest. In addition, they reported low levels of inbreeding at both sites (Rézouki *et al.* 2014). A study in Finland, collecting DNA from 47 urban squirrels and 46 rural individuals, also monitored natal dispersal of radio-tagged juveniles. Urban red squirrels were not genetically isolated from rural ones, but part of the same larger population with gene flow in and out from the city (Selonen *et al.* 2018). However, genetic distances were significantly higher within the city (increased genetic differentiation), medium between urban and rural individuals and lower among squirrels within the rural areas, indicating differences in spatial genetic structure between urban and rural

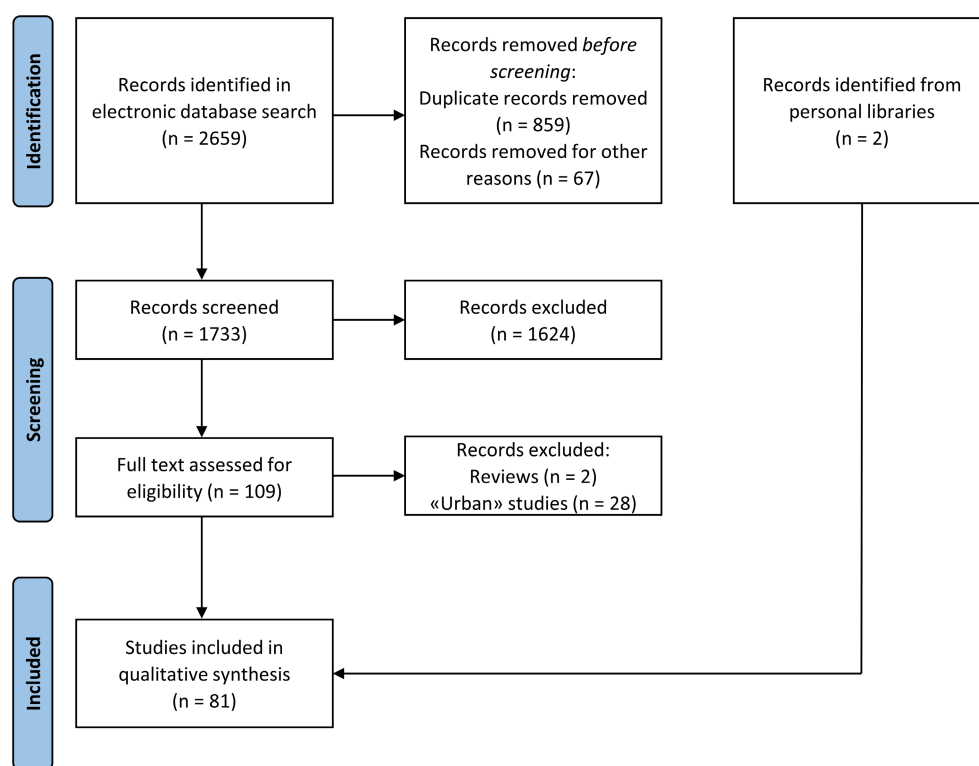


Fig. 1. PRISMA literature search flowchart.

populations (Selonen et al. 2018). These papers found that urban populations of red squirrels are genetically connected to nearby suburban or natural ones, which should improve their viability and persistence (Rézouki et al. 2014, Selonen et al. 2018).

Morphology

Morphological parameters, especially body mass and body size of wild mammals, can be easily measured and are related to habitat use and to several life-history traits (e.g. survival or reproduction; Wauters & Dhondt 1995, Wauters et al. 2007, Festa-Bianchet et al. 1997, Santicchia et al. 2018, Rode et al. 2020); in this way, they potentially have an effect on species adaptation. Considering mammals, Hantak et al. (2021) recorded body sizes of 100 North American species, reporting an increase in size with the proximity of urban areas for most of the included species, but they reported a greater increase for large than small mammals. From rural to moderately urbanised areas, the plant species' heterogeneity tends to increase, affecting the amount and the year-round presence of resources for rodents and bird species (McKinney 2008). In addition, cities are also often characterised by the availability of human-provided supplementary food, which could be the principal cause

for variation of morphological traits in urban areas (Bateman & Fleming 2012).

Comparing morphology of individuals living in rural and urban habitats, contrasting results emerged. Schmidt et al. (2022) did not find any significant difference in body condition or in body mass of Eastern grey squirrels (*Sciurus carolinensis*) between an urban area and a location in a rural hardwood forest. This study used small sample sizes: 20 individuals from the urban location and 8 from the rural. Small sample size will reduce the probability to detect significant differences, especially considering that differences in body mass among sexes, age classes (presence of juveniles), together with changes in body mass related to season and/or reproductive condition (e.g. Wauters & Dhondt 1989, Wauters et al. 2007) will further increase the variance in the dataset. However, a similar result was obtained in a study on Eurasian red squirrels (41 urban and 19 rural individuals), even if females appeared slightly heavier in the urban sites the difference between areas was not significant (Shimamoto et al. 2020).

A comparative study on chipmunks (*Tamias striatus*), with a larger sample size ($n = 140$), reported heavier females in urban than in natural populations but no differences in body mass among males (Lyons et al. 2017). This study highlighted the association of squirrels' body mass with

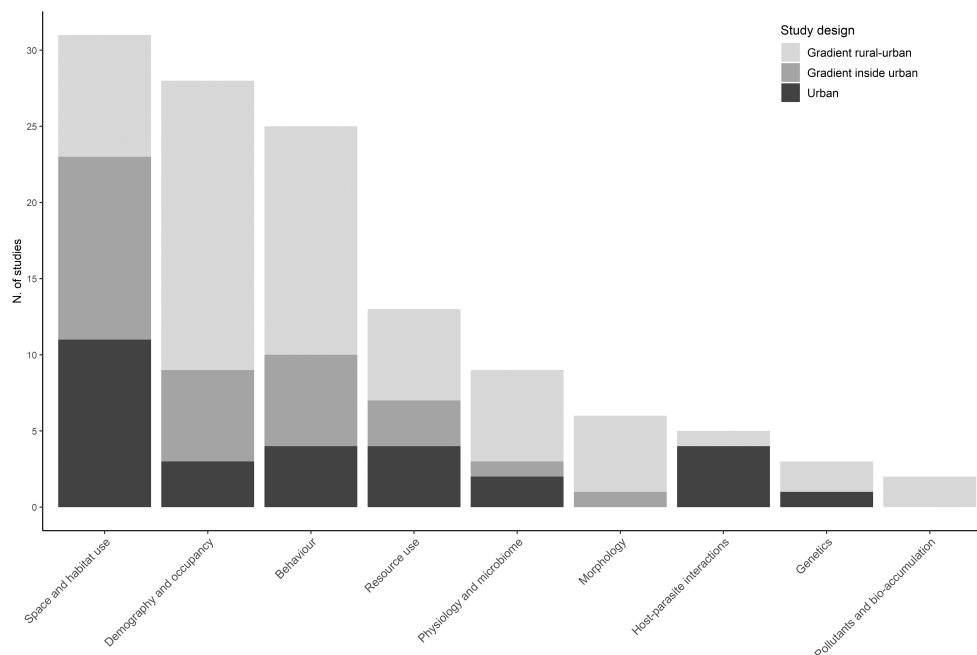


Fig. 2. Number of studies per topic, categorised following classification detailed in [Methods](#) section (gradient rural–urban, gradient inside urban, urban). Each article may belong to multiple topics.

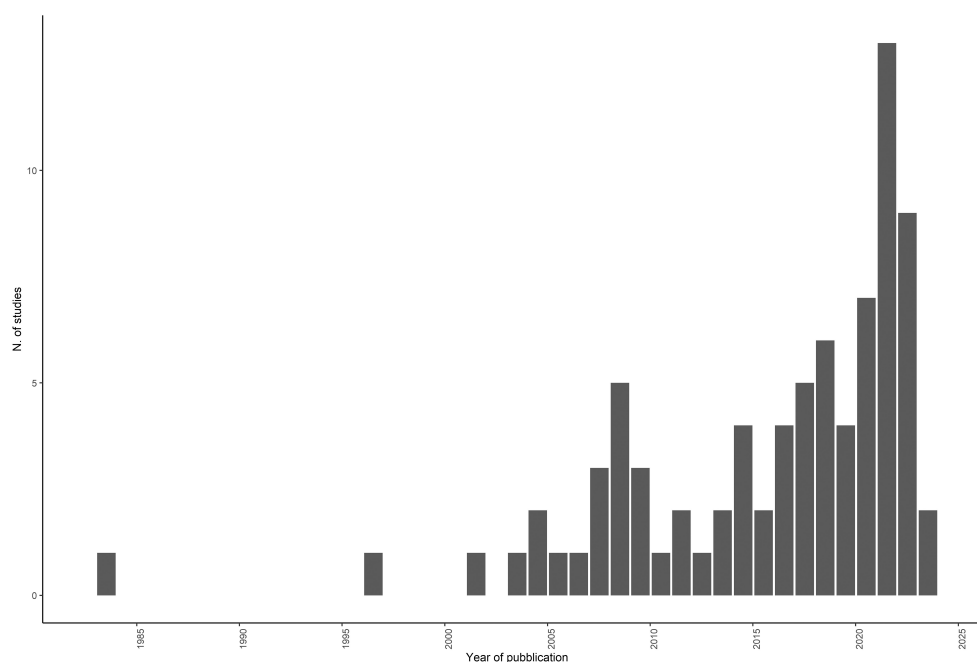


Fig. 3. Number of included studies published per year on chipmunks, arboreal and flying squirrels based on the list of discussed articles; each bar represents a single year's observations. The bar related to 2023 (after the literature search) indicates studies that were online first during the literature search and published in an issue in 2023.

reproductive success, thus suggesting that this species is adapted to the urban environment.

A contrasting pattern was reported for body mass and body condition of Eurasian red squirrels in two urban

areas: a park located in the city centre of Warsaw and an area described as an urban forest (Beliniak *et al.* 2022). Squirrels were heavier with better body conditions in the urban forest, although supplemental feeding was present

only in the other study area. Authors suggested that lower mass in the park could be due to the reduced necessity for individuals to accumulate fat where they have year-round access to food or, since in urban park population density was greater, to increased intraspecific competition (Beliniak et al. 2022).

While these studies measured body mass and body condition directly in the field, an alternative study design was used by Wist et al. (2022). They housed 13 urban and 7 rural adult male red squirrels and measured the individuals' body mass and condition at the trapping event and after around two weeks, at the end of the experiment, taking into account the energy intake and the diet composition. Their results suggest, contrary to the abovementioned studies, that urban individuals were significantly lighter than their forest counterparts at both times, but only urban squirrels significantly gained weight during the experiment (Wist et al. 2022).

These papers suggested that, next to intrinsic factors (e.g. genotype, basal metabolic rate), not only urbanisation level but also habitat characteristics of the urbanised areas can influence variation in body mass in different tree squirrel and chipmunk species (Lyons et al. 2017, Beliniak et al. 2022, Wist et al. 2022).

A different morphological trait was analysed by Cosentino and Gibbs (2022), melanism in grey squirrels, in 43 North American cities characterised by different degrees of urbanisation. Melanism, a Mendelian trait coded by a 24-bp deletion at locus *Mc1R12*, generally increased from rural to urban areas. This study suggests differential selection for certain phenotypes in urban than in rural areas, which could allow squirrels to persist or even thrive in urbanised landscapes.

Physiological response and microbiome

Environmental pressures and habitat modifications, including anthropogenic disturbances posed by urbanisation, can trigger physiological responses in animals which have to cope with such novel challenges (Bonier 2012, Boonstra 2013, Dantzer et al. 2014). Studies on urban endocrine ecology in arboreal squirrels and chipmunks have focused mostly on measuring concentrations of glucocorticoids, a downstream product of the hypothalamic–pituitary–adrenal (HPA) axis, which not only mediates the physiological stress response (Boonstra 2013, Wingfield 2013) but also regulates metabolic demand and energy acquisition (Romero 2004). However, measuring other facets, such as the immune response, stimulated by an acute HPA axis activity, as well as host microbiome variation, may widen the knowledge about the diverse physiological outcomes (Stothart et al. 2019, Stothart & Newman 2021). Indeed, measuring indices which detect

different timescale of the HPA axis activity (Palme 2019), such as plasma cortisol, hair/feather cortisol or faecal glucocorticoid metabolites, but also neutrophil:lymphocyte ratio (N:L) from blood samples, might provide a more comprehensive insight on the physiological response, which can be elicited by a batch of novel environmental stimuli ascribed to anthropogenic perturbations.

Hair cortisol concentrations (HCC) of samples collected from hair tubes (Cordeschi et al. 2021) were significantly lower in Eurasian red squirrels (*S. vulgaris*) inhabiting a city park than those in a natural unmanaged forest (Table 1). Unfortunately, in this study HCC measures were not controlled for possible confounding effects (i.e. individual, sex), due to the low sample size and methodological constraints (see Dantzer et al. 2014). Similarly, Stothart et al. (2019) found that HCC of Eastern grey squirrels (*S. carolinensis*), measured from samples collected directly from the animals during trapping sessions, were significantly lower in urban than in forest sites (Table 1). However, their models showed that HCC were significantly associated with some important bacterial families found in the microbiome (Akkermansiaceae and Lachnospiraceae abundance, negative and positive correlations, respectively: see fig. 2 in Stothart et al. 2019), which in turn differed between urban and forest environments (see fig. 1 in Stothart et al. 2019), apparently explaining the site differences observed for HCC. Conversely, in Eastern chipmunk (*T. striatus*), HCC from captured animals did not differ between urban and natural sites (Lyons et al. 2017).

Among studies measuring faecal glucocorticoid or cortisol metabolites (FGMs or FCMs) concentrations from samples collected during trapping sessions, Lyons et al. (2017) found that FCMs of Eastern chipmunks were significantly lower in urban than in natural habitats (Table 1). In contrast, FGMs of urban Eastern grey squirrels were higher than for forest residents (Stothart et al. 2019). Another pattern was documented in Eurasian red squirrels by Shimamoto et al. (2020) who, using a commercial kit not validated for the study species, did not find any significant difference in FCMs between urban and rural populations (Table 1). However, a study which considered variation of FCMs in this species only within an urban setting reported significantly higher FCMs in an area with increased human disturbance than in a low disturbance one (Haigh et al. 2017, see also Table 1).

Comparative studies that use FGM levels should also test for potential confounding factors, which might influence the physiological stress response to environmental challenges or anthropogenic disturbance (Dantzer et al. 2014). Rigorous studies must consider characteristics such as sex, age, reproductive condition, time of day when a sample is collected, or proportion of reactive vs. proactive individuals within a population (Dantzer

Table 1. Comparative studies which explored HPA axis activity in chipmunks and arboreal squirrels grouped by type of measure used. Unit of measurement between brackets. For each study details on species, author(s), year of publication, sampling method, urban setting (G, gradient rural–urban; GU, gradient inside urban) and physiological stress measures calculated in urban and, when applicable, rural (called ‘rural’ for simplicity, but see each study for other definition of the more natural/less urban setting) areas, have been reported. Symbols used: higher (+), lower (–), no difference (=). Unless otherwise indicated, values between brackets are represented as mean ± standard error (SE)

Type of measure			Urban setting	Urban	Rural
Species	Author(s), year	Sampling			
HCC (hair cortisol concentrations) (ng g ⁻¹ hair)					
<i>Tamias striatus</i>	Lyons et al. (2017) (FCMs)	Pellets from trapping	G	– (Overall mean ± SD: 274 ± 227)	+
<i>Sciurus carolinensis</i>	Stothart et al. (2019)	Hairs from trapping	G	– (54 ± 7)	+ (127 ± 34)
<i>Sciurus vulgaris</i>	Cordeschi et al. (2021, fig. 2a)*	Hair tubes	G	– (~80 mean)	+ (~105 mean)
FGMs or FCMs (faecal glucocorticoid/cortisol metabolites) concentration (ng g ⁻¹ dry faeces)					
<i>Tamias striatus</i>	Lyons et al. (2017) (FCMs)	Pellets from trapping	G	– (overall mean ± SD: 274 ± 227)	+
<i>Sciurus carolinensis</i>	Stothart et al. (2019) (FGMs)	Pellets from trapping	G	+ (784 ± 129)	– (349 ± 57)
<i>Sciurus vulgaris</i>	Haigh et al. (2017) (FCMs)	Pellets from trapping	GU	+ At high human disturbance (14300 ± 2640) – At low human disturbance (6350 ± 3340)	
	Shimamoto et al. (2020) (FCMs)	Pellets from trapping	G	= (96 ± 29)	= (143 ± 30)
N:L (neutrophil:lymphocyte) ratio					
<i>Sciurus carolinensis</i>	Stothart et al. (2019)	Blood from trapping	G	– (1.4 ± 0.3)	+ (2.9 ± 0.5)

*Only approximate means were available from this study.

et al. 2014, Palme 2019, Santicchia et al. 2022a), as well as appropriate methodological validation for each species (Palme 2019).

Using a different measure of acute HPA axis activity, Stothart et al. (2019) found that neutrophil:lymphocyte ratio (N:L), which is a direct immunological measure of stressor-induced (i.e. trapping) innate immunity, was significantly lower in urban Eastern grey squirrels than in forest ones, and positively correlated with the microbiome (Prevotellaceae abundance; see fig. 3 in Stothart et al. 2019).

Moreover, they also explored variation in coat colour and microbiome in response to urbanisation (broad and fine spatial scales), based on the assumption of the pleiotropic link between fur colour polymorphisms and vertebrate physiology, such as immunity and stress physiology, which are known to ultimately affect the microbiome (see Stothart & Newman 2021 and references therein). They found that urbanisation affected Eastern grey squirrel microbiome at landscape and intra-city spatial scales, and that coat colour differences, determined by a gene mutation, influenced the response of the squirrels’ microbiome to urbanisation. Also, as reported in previous studies, the observed patterns of colour phenotypes in populations in a heterogeneous landscape might have a physiological basis, which should be accounted for in further studies testing whether microbiome plasticity will be adaptive for hosts

in novel environments, such as urbanised areas (Stothart & Newman 2021).

Overall, we highlight that significant differences emerge from the studies reported in the present review; specifically, among patterns revealed by each biological matrix examined (i.e. hair, faeces, blood), which must be taken into consideration with regard to the timescale of the stress response that each index detects.

Pollutants and bio-accumulation

There is growing interest in using wildlife for monitoring environmental pollutants, in particular, heavy metals. The latter can accumulate in animal tissues, the so-called bio-accumulated substances (Suzuki et al. 2006). Their occurrence in wild animals can be determined from organ tissues, where it is necessary to kill the animals, or from hair, where non-invasive techniques can be used (Suzuki et al. 2006, Lurz et al. 2017). Heavy metals, released in the environment as a consequence of anthropogenic activities, have been demonstrated to have harmful effects on mammals, including humans, affecting their reproductive performance (Bhardwaj et al. 2021). Within rodents (rat, hamster, mice), several mechanisms of heavy metals (e.g. Cd, Pb, Hg) on the reproductive system have been investigated, but no studies tested these aspects, and their

effects on fitness, in squirrels and chipmunks. Indeed, we found only two studies in which concentrations of heavy metals were compared between squirrels from rural and urban areas. Alien Formosan squirrel (*Callosciurus erythraeus*) in Japan had high Cu concentrations in the liver and animals from the urban site had higher concentrations of trace elements from car exhausts [Vanadium (V), Zinc (Zn), Copper (Cu) and Arsenic (As)] than in the rural site (Suzuki et al. 2006). In Europe, mercury (Hg) concentrations in hair of red squirrels (*S. vulgaris*) were compared between two rural and one urban sites, the latter exposed to high levels of Hg from coal-fired power plants. Lurz et al. (2017) found that females from one of the rural sites had higher levels of Hg than either males or females from the other sites. They concluded that their study suggested that Hg accumulates not only in marine food chains and arctic ecosystems but also in species living in urban and rural terrestrial ecosystems.

Behaviour

Human-induced rapid environmental change (Sih 2013), such as natural habitat modifications and urbanisation, forces animals to cope with novel challenges shifting their behavioural responses (Lowry et al. 2013). For instance, foraging mode and temporal activity patterns, as well as personality traits, have changed along urbanisation gradients (Tuomainen & Candolin 2011, Lowry et al. 2013, Sol et al. 2013). Studies reported here are detailed in Table 2.

The majority of papers studied anti-predator behaviours, analysing flight initiation distance (FID) and/or vertical escape distance (VED) (but see Table 2). They reported a general trend of decrease in FID and VED in urban squirrels with respect to rural ones, using human and/or predator approach as a stimulus (McCleery 2009, Uchida et al. 2016, 2017, 2019, 2020, Kittendorf & Dantzer 2021) or in relation to degree of disturbance inside urban areas (e.g. human exposure; Engelhardt & Weladji 2011). Conversely, contrasting results were obtained by few studies, which observed a higher FID, in parklike areas (cemeteries, parks), than in forested areas (i.e. Engel et al. 2020), or a positive correlation among FID and human visitations (Uchida et al. 2021), as well as higher distance fled in response to a direct human approach (Bateman & Fleming 2014, but see Table 2). We also collected studies exploring vigilance behaviours, measured through alert distance and alarm, or directly observed vigilance behaviours, but among them no evident trend emerges. Indeed, in some studies, alert distance was lower in urban squirrels than in rural ones (Uchida et al. 2019), and it decreased with higher human-activity levels (Cooper et al. 2008), while, in other studies, it was higher in cases of a direct human approach (Bateman & Fleming 2014, but see Table 2). Also, squirrels exhibited more frequent alarm/

vigilance behaviours and mobbing calls in urban areas than in rural ones (Partan et al. 2010, Sarno et al. 2015, Uchida et al. 2020). Overall, but mostly in studies exploring anti-predator behaviours, we found differences in terminology to describe the measures used, which potentially detect the same facets of squirrels' behaviours (see Kittendorf & Dantzer 2021).

Considering studies which used OFT and MIS tests, chipmunks were less engaged in locomotion and grooming behaviours in urban than in rural areas (Lyons et al. 2017) while no differences in activity, exploration or sociability were found in red squirrels inhabiting urban or rural areas (Uchida et al. 2020). Also, red squirrels were found to have higher activity rates (radio-tracking data) in urban than in rural areas (Thomas et al. 2018), and day-round activity in urban respect to a bimodal activity pattern in rural areas (camera-trapping data, Beliniak et al. 2021). Moreover, grooming behaviour, considered a stress response by Uchida et al. (2020), was lower in urban than in rural red squirrels, while there were no differences in aggressive responses. Conversely, grey squirrels increased their aggression in urban areas in relation to conspecifics densities (Parker & Nilon 2012).

Resource use and the role of supplemental food

In urbanised habitats, the use of natural and supplemented food resources, as well as perceived predation risk linked to the distribution of (artificial) resources and/or human disturbance can strongly influence the behaviour, space use or dynamics of sciurids. Studies reported here used a variety of different approaches.

A cafeteria-type study using different bait types in three different habitat categories (urban, semi-urban and recreational forest) in Malaysia caught 537 small mammals from 15 species (4 belonging to Callosciurinae), and bait preferences differed among groups (Mohd-Taib & Ishak 2021). Species richness was higher in recreational (11 species) and semi-urban forest (13 species) than in the urban habitat (4 species), and in the latter no Sciuridae were trapped. Low numbers from four tree squirrel species were trapped in semi-urban and/or recreational forest (Mohd-Taib & Ishak 2021). In a residential area in Thailand, the frequency of detection of *Callosciurus finlaysonii* was higher than that of *C. caniceps* (Kobayashi et al. 2020). *C. finlaysonii* used buildings and electric wires as pathways in open areas, while the latter were avoided by *C. caniceps*. Finally, *C. finlaysonii* also consumed a greater diversity of food items than *C. caniceps* (Kobayashi et al. 2020).

Mammal-plant interactions can differ markedly between urban and natural areas, and this can have important effects on mammal-pollinated plants (Kobayashi et al. 2020). Comparing flower visitors of *Mucuna macrocarpa* between urban and natural areas in Japan and Taiwan,

Table 2. Studies on behavioural changes in chipmunks and arboreal squirrels in urban areas, respect to an anthropic source/cause, grouped by species and year of publication. For each study, details on author(s), year of publication, methods/variables measured, urban setting (G, gradient rural–urban; GU, gradient inside urban), observed change (reported for each method or variable) and summary of main measured differences among urban and, when applicable, rural (called ‘rural’ for simplicity, but see each study for other definition of the more natural/less urban setting) areas, have been reported. Symbols used: increase/higher (+), decrease/lower (–), no difference/change (=). Details between brackets

Species	Author(s), year	Methods/variable	Urban setting	Observed change	Urban	Rural
<i>Tamias striatus</i>	Lyons et al. (2017)	OFT (open field test)	G	OFT Chipmunks in urban habitats spend less time in locomotion and grooming, and more time latent (inside hollow tube) than in natural habitats	– Locomotion – Grooming + Time latent	+ Locomotion + Grooming – Time latent
<i>Sciurus carolinensis</i>	Cooper et al. (2008)	AD (alert distance)	GU	AD AD greater in sites with low human activity than in sites with high human activity; AD not different for squirrels approached by human alone and by human with dog on a leash AD (within site type) Presence of the dog increased AD in the high human-activity sites but had no effect in the low human-activity sites	+ AD (low human activity) = AD (human vs. human and dog) In high human activity sites: + AD (with dog)	
	Partan et al. (2010)	Alarm, vigilance and calm behaviours (mechanical squirrel model)	G	Alarm, vigilance and calm behaviour, higher in urban than rural habitats Alarm responses higher in the urban than in rural habitat for two conditions: Vm (Visual moving, in which the robot was uncovered and the tail flagged) and AVm (Audio Visual moving, in which the robot was uncovered, alarm calls played and the tail flagged)	+ Alarm + Vigilance + Calm + Alarm responses (Vm and AVm)	– Alarm – Vigilance – Calm – Alarm responses (Vm and AVm)
	Engelhardt and Weladji (2011)	FID	GU	FID FID increases as human exposure decreased	+ FID (lower human exp)	
	Parker and Nilon (2012)	Wariness Aggression	GU	Wariness Best model: wariness decreases with higher park canopy cover and higher population density Aggression Two most parsimonious models: aggression increases with increasing basal area, tree cover, squirrel density and is higher in smaller sized parks	Wariness and aggression vary with tree cover and squirrel density	
	Bateman and Fleming (2014)	AD FID (flight initiation distance) Distance fled	GU	AD Higher when pedestrians left footpath independent whether it looked or not at the squirrel FID and distance fled Squirrels most reactive (longer distances) when approached by a pedestrian that moved off the footpaths and looked at the squirrel as he approached	+ AD + FID + Distance fled (at higher human disturbance)	
	Sarno et al. (2015)*	Vigilance	G	Vigilance Vigilance differed across the rural–urban gradient with higher vigilance in the peri-urban than in the urban habitats and higher vigilance in urban and peri-urban with respect to semi-rural and rural habitats. No differences between rural and semi-rural habitats	+ Vigilance	– Vigilance

(Continues)

Table 2. (Continued)

Species	Author(s), year	Methods/variable	Urban setting	Observed change	Urban	Rural
<i>Sciurus niger</i>	Jagiello <i>et al.</i> (2019)	Behaviours observed (YouTube videos)	G	Feeding and movement were the behaviours most frequently recorded in both forest and urban habitats No difference in frequency of behaviour type between Eurasian red and Eastern grey squirrels in forest and urban habitats The probabilities of grooming and calling behaviours differed between habitats	Probability of: – Grooming – Calling + FID (cemetery, park) – FID (neighbourhood)	Probability of: + Grooming + Calling – FID (forest)
	Engel <i>et al.</i> (2020)	FID	G	FID Longer FID in cemetery and park than in neighbourhood and forest habitats. FID across all sites was negatively correlated with impervious surface cover and road extent, and positively correlated with greater amounts of residential land use		
	Chow <i>et al.</i> (2021a)	Novel food-extraction problem (easy and difficult) Recall test Spatial-learning task	G	Enhanced cognitive ability Comparison between rural and urban habitats in native and non-native squirrels. The four groups showed comparable performance in most measures	See paper for details	See paper for details
	McCleery (2009)*	FID Anti-predator behaviour (vigilance behaviours)	G	FID Mean distances were ~7 times greater on rural than urban sites. Difference between juveniles and adults in the urban site Anti-predator behaviour (human approaches) Increase ~3 times from urban to rural sites Anti-predator behaviour (natural predators) Responses to both coyote and hawk vocalisations on rural sites ~2 times more than in urban sites	– FID – Anti-predator behaviour (human) – Anti-predator behaviour (coyote, hawk)	+ FID + Anti-predator behaviour (human) + Anti-predator behaviour (coyote, hawk)
	Kittendorf and Dantzer (2021)	FID FAD (first alert distance) Probability of climbing a tree Latency to resume behaviour	G	Behavioural responses to human stimuli Urban squirrels exhibited greater tolerance to humans as they allowed a human observer to get closer to them before they exhibited vigilance (FAD, not statistically significant) or fled (FID, statistically significant) and tended to be less likely to climb a tree during the trial and more quickly return to typical behaviour following the trial compared to those in less urban sites Behavioural responses to stimuli from natural predators No difference between urban and less urban sites in the four response variables investigated when exposed to hawk and dog playbacks, or the control stimulus Behavioural responses within site type Differences in how squirrels responded to the playback treatments within each of the two types of study sites	– FID (human) = FAD = FID = Climb tree = Latency resume (hawk, dog, control)	+ FID (human) = FAD = FID = Climb tree = Latency resume (hawk, dog, control)

(Continues)

Table 2. (Continued)

Species	Author(s), year	Methods/variable	Urban setting	Observed change	Urban	Rural
<i>Sciurus vulgaris</i>	Uchida et al. (2016)	FID	G	FID Shorter FID in urban squirrels than in rural ones, regardless of season	– FID	+ FID
	Uchida et al. (2017)	VED (vertical escape distance) FID AD	G	VED VED was positively related to FID and shorter in urban than rural squirrels FID and AD FID was positively related to AD	– VED	+ VED
	Thomas et al. (2018)	Activity patterns (radio-tracking)	G	Activity Higher activity rate in semi-natural than in urban habitats and individuals in semi-natural habitat more consistently active throughout the day	– Activity	+ Activity
	Jagiello et al. (2019)	Behaviours observed (YouTube videos)	G	Feeding and movement were the behaviours most frequently recorded in both forest and urban habitats No difference in frequency of behaviour type between Eurasian red and Eastern grey squirrels in forest and urban habitats The probability of hoarding, grooming, calling, and interaction with people differed between habitat types	Probability of: – Hoarding – Grooming – Calling + Interact people	Probability of: + Hoarding + Grooming + Calling – Interact people
	Uchida et al. (2019)	AD FID	G	AD Shorter in urban than in rural habitats. No difference among different objects (human, fox, novel object) FID FID of urban squirrels was on average half that of the rural ones. Shorter FID in urban squirrels, in response to humans and predators, than in rural ones. FID in response to the novel object was not different between habitats. FIDs in response to humans were shorter than for the model fox and novel object in urban squirrels but no difference was observed among the objects in rural habitats	– AD – FID – FID (human, predators) = FID (novel obj)	+ AD + FID + FID (human, predators) = FID (novel obj)
	Uchida et al. (2020)	OFT and MIS (mirror image stimulation test) FID Mobbing calls	G	OFT and MIS Activity, exploration and sociability were not different between urban and rural squirrels Stress response (OFT) lower in urban squirrels than rural ones Aggressive responses to conspecifics (MIS) not different between the two area types VED Shorter VED in urban than in rural squirrels Number of mobbing calls Number of mobbing calls was almost three times higher in urban than in rural squirrels	= Activity = Exploration = Sociability – Stress response = Aggressive responses – VED + Mobbing calls	= Activity = Exploration = Sociability + Stress response = Aggressive responses + VED – Mobbing calls

(Continues)

Table 2. (Continued)

Species	Author(s), year	Methods/variable	Urban setting	Observed change	Urban	Rural
	Beliniak et al. (2021)	Activity pattern (camera trapping)	G	Activity Daily activity patterns differed seasonally and between the study sites. In the forest there were typically two activity peaks, one around the sunrise and second around the sunset; activity of park squirrels was more distributed throughout the day	Activity pattern: Day active	Activity pattern: Two peaks
	Chow et al. (2021b)	Novel problem-solving	GU	First success in solving the novel problem At the population level: increased proportion of first success in the novel problem was related to the decreased mean number of humans presented in a site per day, the number of buildings and squirrel population size Solving latency across successes Overall solving latency across success blocks was negatively related with the mean number of humans in a site per day and squirrel population size. Squirrels solved the novel problem quicker with increased human exposures and successful solving experience. At the initial learning phase: decreased solving latency across blocks was predicted by increased mean number of humans in a site per day	Direct human disturbance and squirrel population size affect novel problem-solving success	
	Uchida et al. (2021)	FID VED	GU	FID Negatively correlated with artificial feeding intensity, local tree density and proportion of green space around the park and human population density around the park. Positively correlated with number of human visitations, tree density in the park, pathway length, density of recreational equipment, proportion of green space, distance from a tree and local canopy cover VED Negatively correlated with artificial feeding intensity and population density around the park. Positively correlated with some of the other environmental variables (see fig. 3 and table 3 in the paper)	Park features (e.g. artificial feeding intensity, proportion of green space, tree density, density of recreational equipment) influenced FID and VED	

*Studies including also comparisons with an intermediate level along the rural–urban gradient (details not reported here).

Kobayashi et al. (2018) showed that flying foxes (Chiroptera, *Pteropus dasymallus*) were the main pollinator in both area types in Japan, while in Taiwan it was the sciurid *C. erythraeus*. Squirrels visited the plants at the same or even higher frequency in the urban than in the natural habitat. Overall, negative effects of animals' guilds on the success of *M. macrocarpa* pollination were lower in urban compared to forested areas (Kobayashi et al. 2018).

It is widely acknowledged that squirrels are likely to benefit from artificial food in urban and/or semi-urban areas, but this view has recently been challenged (e.g. Schmidt

et al. 2022, Wist et al. 2022). Serum biochemistry analysis could be an effective way to measure population-level health, as it should be a good indicator of disease state, nutritional status and habitat quality (Schmidt et al. 2022). Moreover, comparing body mass, food choice (nutrient intake) and diet composition between natural (rural) and urban areas could reveal adaptations to living in urban environments. A study that compared blood samples collected from urban and rural eastern grey squirrels showed that urban squirrels had higher glucose levels, but lower potassium, phosphorus, chloride and albumin:globulin ratios than those from rural

site (Schmidt et al. 2022). Although these preliminary results must be interpreted cautiously, they suggest that urban grey squirrels might be less healthy than rural ones, and that elevated blood glucose in urban squirrels is related to higher sugar intake coming from human waste or food types used to feed these animals in urban sites (Schmidt et al. 2022). A similar result was found in a study on Eurasian red squirrels: 13 males from a high-density ($5.1 \text{ squirrels ha}^{-1}$) small urban park and 7 males from a large natural forest were held for 13–18 days in outdoor enclosures to carry out cafeteria experiments (Wist et al. 2022). The animals were fed with four types of natural food and four types of typical supplemented food often observed being used in the park habitat. Urban individuals had a lower initial body mass but consumed significantly more food (in both weight and energy content) per day and significantly gained weight over the course of the experiment. Despite this increase, they remained of lower mass than the forest squirrels (Wist et al. 2022). All squirrels preferred (fat-rich) hazelnuts, but urban squirrels had a wider dietary range and consumed more non-natural food items, and, mainly by eating biscuits, urban squirrels had a higher sugar intake (Wist et al. 2022). Although on a small sample size, this study suggests that urbanisation affects foraging behaviour and food preferences, which might result in a nutritional mismatch or, at least, negative side effects (high blood glucose levels) due to the consumption of non-natural food items (Wist et al. 2022). Hence, both studies show that possible digestive and physiological costs induced by the use of supplemental food might reduce the health or even the fitness of squirrels living in urban areas.

Living in the city may also alter cost–benefits of foraging, in particular, when animals perceive the urban habitat as risky due to disturbance and/or predation risk. This can be investigated using comparative studies of the Giving-Up-Density (GUD, the density of resources in a patch at which an animal stops foraging, probably as a result of increasing costs), or by looking at space-use patterns in relation to human disturbance/presence (Reher et al. 2016). Van Der Merwe et al. (2007) compared food limitation, foraging cost related to predation risk and the importance of cacheable foods between a high-density urban residential area and a semi-natural habitat, measuring GUDs in depletable food patches. GUDs in urban area were higher in summer than in winter, the opposite than in the semi-natural habitat. There were no differences in GUD for safe and risky microhabitats between the two study sites, but differences in GUDs between cacheable and less cacheable food were lower in the semi-natural habitat. Note that in the urban sites both grey and fox squirrels were abundant, while at the semi-natural site, fox squirrels predominated. Hence, differences in the behaviour of squirrels between the two habitats were related

to a combination of seasonal fluctuations in the abundance of cacheable natural food and less cacheable human-derived food and higher perceived predation risk by more persistent harassment by pets and people in the residential urban sites.

GUDs, of artificial food (sunflower seeds in pans), were also used to assess anthropogenic impact on foraging of grey squirrels along a rural–urban gradient of 78 study sites (Bowers & Breland 1996). GUDs were lower (more seeds removed), and a higher proportion of pans were used in relatively high-density urban and suburban areas than in more rural areas, or forest controls. For the sites near or within human settlements, GUDs were higher where there was substantial ground cover and where domestic pets (i.e. cats/dogs) were present. Thus, squirrels living in close proximity to humans appear to be either more limited by food or less sensitive to predatory risk than those living in more natural areas (Bowers & Breland 1996), but on a small scale within the urban/suburban sites, squirrels responded to perceived predation risk by lower use of the most risky patches. GUDs were further used to assess the quality of urban spaces for eastern grey squirrels in Minnesota (Kay et al. 2023). Seed trays were located in campuses, residential yards and municipal parks to evaluate a possible difference among these three urban location types, but there was no difference in mean GUD among the three types (Kay et al. 2023). However, GUDs varied within location type depending upon proximity to roads; much more seeds were removed in sites away from roads than in sites near roads, suggesting that urban traffic/road density should be considered to improve the quality of urban green areas (Kay et al. 2023).

A space-use and food choice study on a red squirrel population in a semi-urban environment revealed relatively small home ranges, year-round availability of natural food resources and no seasonal changes in body mass, suggesting that these types of environments could be considered high-quality habitats (Reher et al. 2016). Although the home ranges of squirrels encompassed areas with year-round natural food resources, animals did shift the core areas of their home ranges seasonally, towards areas closer to sources of food provided by humans; consequently, human activity (i.e. supplemental food) had a direct, measurable effect on squirrels' feeding habits and movement patterns (Reher et al. 2016).

Space and habitat use

The presence of a squirrel species in urban areas is related to several factors. Different studies investigated the presence of species (in their both native and non-native locations) based on landscape features to understand which

are the major drivers associated with squirrels' occurrence in cities (Table 3). In Finland, a survey method based on mapping faecal pellets was used to determine presence/absence of Siberian flying squirrel (*Pteromys volans*). Individuals occurred principally on forest edges but also in urbanised areas, which do not seem to have a negative effect on squirrels' presence (Mäkeläinen et al. 2015). Conversely, Japanese squirrel (*Sciurus lis*) was more likely to be detected by camera traps in deep forest survey grids than in less forested sites in Japan, with no occurrence in urban areas (Saito & Koike 2013).

Other studies focused on occurrences only within the urban environment (Table 3). In general, individuals showed a negative selection for residential areas, even if they can cross them moving from one small green patch to another; or they occurred in urban areas but showed a preference for locations with denser tree cover (Bonnington et al. 2014, Jessen et al. 2018, Seki & Sato 2022). Other factors that should be considered are the type of vegetation (habitat quality, e.g. size and density of overstory trees and/or the type of ground cover) present in the urban area and the species studied (see Table 3, Weckel & Giuliano 2001, Keefe & Giuliano 2004). In fact, squirrel species can coexist in a city using different areas. For instance, in a study in Chicago metropolitan areas, using a citizen science approach, emerged that grey squirrels were more likely to be observed in densely populated areas, parks and campuses than fox squirrels, which were associated with suburban areas (Van Der Merwe et al. 2005).

Space use of arboreal squirrels, flying squirrels and chipmunks is usually of a scale that allows to clearly distinguish individuals that exclusively live in urban areas from those who live in suburban and rural areas. Hence, it makes them excellent model species for studying differences in space use along the rural–urban gradient, comparing individuals in small and fragmented urban parks with individuals in forests.

Surprisingly, only a few studies used radio telemetry to compare space use and movements between urban and rural individuals. Mäkeläinen et al. (2016) tracked the movements of *P. volans* observing an increased movement speed in the urban matrix besides a longer distance travelled in this environment, at least for females. Within the urban habitat, consisting of a fragmented set of areas with trees interspersed with buildings, flying squirrels responded to this increased amount of hostile urban matrix along their movement paths by moving faster and over longer distances to reach the desired good-quality patches (Mäkeläinen et al. 2016). In a different study, a total of 10 Eurasian red squirrels were radio-collared in Fota Island, and from the data emerged that individuals avoided human encounters. Animals were found more often in

non-public than public areas and the majority of fixes in public areas were obtained during closing hours (Haigh et al. 2017). Also, a 20-year study (1997–2017) on habitat use of red squirrels and invasive chipmunks in an Italian urban garden found that red squirrels significantly avoided human settlements within the park for the entire period of the study, while the invasive species avoided that area only for the second decade of the study (Mori et al. 2018). These studies suggested that urbanisation or its effects (human disturbance) are hostile for these species, causing individuals to avoid highly disturbed areas or change their movement patterns.

Consequently, the degree of urbanisation should also affect home ranges of squirrels and chipmunks. Indeed, urban red squirrels in Poland had significantly smaller home ranges (estimated with the minimum 100% convex polygons, MCP) compared to forest squirrels. The minimum value in the forest was approximately three times the minimum value of the urban park, and the maximum home range in the forest was around 5.5 times the maximum urban home range (Krauze-Gryz et al. 2021). In addition, the same pattern was found for core-area size (Krauze-Gryz et al. 2021). However, a different result was obtained for red squirrels studied in Germany, where neither MCP home range nor home range overlaps significantly differed between an urban and a semi-natural area (Thomas et al. 2018). This study used a small sample size (three urban and four semi-urban individuals) which could affect the significance of the results, in fact, home range tended to be smaller in the city and the overlap greater, even if it was not significant (Thomas et al. 2018). In contrast, a large number of *Sciurus niger* individuals were radio-tagged and monitored for seven seasons in Texas, showing that both seasonal core-area size and overlap were smaller in an urban than in a rural study site (McCleery & Parker 2011).

Host–parasite interactions

The selection of a more urbanised habitat rather than natural areas could also affect the relationship between hosts and parasites. In fact, mammals are host for a wide variety of ecto- and endoparasites, some of which can be transmitted to humans (zoonosis). Therefore, studies comparing host–parasite interactions and parasite communities between hosts occurring in urban vs. rural areas are necessary to investigate risks of Emerging Infectious Diseases (EID; Daszak et al. 2000) associated with mammals living in urban environments. Despite this importance, we found only one comparative study on a tree squirrel.

A host's ectoparasite fauna is expected to be poorer in parklands (lacking rich ground cover vegetation) than natural woodlands. A study in Georgia, USA, showed that

Table 3. Comparative studies which explored occurrence of arboreal squirrels, flying squirrels and chipmunks, ordered by year of publication. For each study details on species, author(s), year of publication, detection method and urban setting (G, gradient rural–urban; GU, gradient inside urban)

Species	Author(s), year	Methods of detection	Urban setting	Occurrence
<i>Tamias striatus</i>	Weckel and Giuliano (2001)	Live trapping	GU	Preference for areas with larger trees, an open shrub layer, few stems and snags and abundant herbaceous ground vegetation
<i>Glaucomys volans</i>	Keefe and Giuliano (2004)	Live trapping	GU	Occurrence in parks with larger overstory trees at lower densities and lower deciduous canopy cover; abundant herbaceous ground cover and less deciduous and dead woody ground cover
<i>Sciurus carolinensis</i>	Van Der Merwe et al. (2005)	Citizen science	GU	Association with densely populated areas, parks and campuses
<i>Sciurus niger</i> <i>Sciurus niger</i>	McCleery et al. (2007)	Radio telemetry	GU	Association with suburban areas Use of buildings as a substrate and refugia during winter and spring; avoided in the core area during spring, summer and autumn. Pavement avoided as a substrate, but included in their core areas. Grassy areas included in core areas during activity periods in spring and excluded in winter and summer
<i>Sciurus lis</i>	Saito and Koike (2013)	Camera trapping	G	Preference for the interior forest landscape
<i>Sciurus carolinensis</i>	Bonnington et al. (2014)	Visual surveys and drey counts	GU	Negative response to urbanisation. Supplementary feeders positively influenced the occurrence in winter. Canopy cover positively influenced the occurrence in winter, spring and summer. Mean tree height positively influenced the occurrence in summer
<i>Pteromys volans</i>	Mäkeläinen et al. (2015)	Faecal pellets mapping	G	Animals do not avoid living near urban areas. Present mainly in the edge areas of larger forests
<i>Sciurus carolinensis</i> and <i>Sciurus griseus</i>	Jessen et al. (2018)	Direct observation and hair snare tube surveys	GU	Occurrence in highly developed urban areas. No significant effect of tree canopy cover or development cover on squirrel observations.
<i>Callosciurus erythraeus</i>	Seki and Sato (2022)	Visual or auditory identification	GU	Selection for sites in urban areas with relatively higher tree density Negative selection for residential areas. Use of small green fragments in urban areas

grey squirrels in parkland ($n=53$ animals) had only six ectoparasite species against 17 species in a woodland population ($n=67$ animals; Durden et al. 2004). In particular, five species of ticks and three species of chiggers (arachnids of the family Trombiculidae) parasitized the woodland

squirrels compared with no ticks or chiggers on the parkland squirrels. Of the species present in both areas, intensity of infection by the flea *Orchopeas howardi* was significantly higher on woodland than on parkland squirrels. Some of the fleas and lice tested positive for *Bartonella* sp.

suggesting they might be vectors for transmitting the *Bartonella* bacteria; so far it is not known whether these ectoparasites could transmit *Bartonella* sp. to humans (Durden et al. 2004).

Population demography and occupancy

Several studies on mammals that persist in urban areas suggest that lower predation risk and higher (in part supplemental) food availability positively affect population processes such as survival and reproductive success (McCleery 2010, Santini et al. 2019). However, higher degrees of isolation and more hostile matrix surrounding the green areas inside cities may alter the advantages of living in urban parks and woodlots. Therefore, population densities in urban sites can be higher or lower than in rural sites, with different site-specific effects of dispersal rates, survival rates or reproductive rates on fluctuations in density.

FITNESS

Fitness parameters (reproductive success and survival) were investigated using different methods and measures, informing about the adaptation status of the species. Radio-tracking fox squirrels (*Sciurus niger*) during approximately two years in an urban and a rural site in Texas (USA) allowed precise estimates of survival rates (McCleery et al. 2008). Monthly survival rates were lower in rural than urban sites (0.936 vs. 0.976) over the same 12-month period, and sex and season seemed to influence survival of urban but not that of rural squirrels. More importantly, the causes of mortality differed: >60% of deaths in rural site were caused by predation against <5% in the urban site where most fatalities were caused by motor vehicle collisions (McCleery et al. 2008). This study suggests that road density, traffic intensity and other characteristics of the urban matrix may be at least as important as the park/woodland structure itself in determining the costs and benefits of occupying urban green areas (see also Hayes Hursh et al. 2023). For example, a 4.5 times more likely presence of healed fractures in urban compared to rural areas suggested a higher rate of injury and/or higher survival rates after injury in urban than in rural grey squirrels (Moncrief et al. 2022).

Mean litter size of fox squirrels in the Texas urban population was similar to values reported in rural populations (McCleery 2009). However, the proportion of reproducing females/year tended to be higher in this urban site than in rural sites. Comparing reproductive success (proportion breeding females, proportion young trapped or observed) on Eurasian red squirrels between urban park and urban forest in Warsaw (Poland), Beliniak et al. (2022)

documented a positive effect of body condition on the probability to produce offspring in both study sites. In the urban park, there was a more extended breeding season, and again, more reproducing females and higher density than in the urban forest (Beliniak et al. 2022).

A comparative study quantified survival of radio-marked Western grey squirrels (*Sciurus griseus*) using known-fate models, and annual reproductive success by following females through the breeding season and counting young at natal nests (Vander Haegen et al. 2018). Adult survival did not differ between populations from a strongly fragmented urbanised and an extensive forested landscape (Washington, USA). However, litter size was marginally smaller, and reproductive success was significantly lower in the urbanised County (Vander Haegen et al. 2018). Models suggested that the smaller urbanised population is at risk because of its small size, low fecundity and, possibly, severity of epizootic diseases such as Tularemia (Vander Haegen et al. 2018). That Western grey squirrels are sensitive to human disturbance was confirmed by spatial distribution modelling using occurrence data of the native Western grey squirrel and two non-native squirrel species that thrive in urbanised landscapes (Eastern grey and fox squirrels) in the western United States (Tran et al. 2022). Models suggested that the greatest potential conflict between non-native and native squirrels is, currently, in sites adjacent to regions of high human footprint.

DENSITY AND OCCUPANCY

Using a habitat gradient within the city (Springfield, MA, USA), grey squirrel density ranged from only 0.15 ha⁻¹ in areas of dense urbanisation to 1.08 ha⁻¹ in college campuses, cemeteries and parks (Williamson 1983). Tree basal area and density and number of oaks per ha positively affected squirrel numbers, while pavement, building cover and distance to woodlots negatively influenced squirrel activity (Williamson 1983). These results differed from those reported in Baltimore, USA. In this city, with 347 municipal parks that cover about 10% of the city's surface, grey squirrel abundance was estimated in six parks (2–7 ha in size, isolated from other parks) using time quadrant counts (Parker & Nilon 2012). Differences in squirrel densities (average 6.15 ha⁻¹, seasonal variation and differences between parks in Table 2, Parker & Nilon 2012) were best explained by park size (–), tree cover (–) with a positive effect of building cover in the surrounding city matrix. Similar results were obtained in a study across urban habitats (17 study sites) in St. Louis (Missouri, USA). Grey squirrels counted along transects were more abundant in urban parks, forest and neighbourhood areas, but occurred at low densities or were nearly absent in cemeteries and golf courses (Engel et al. 2020). Density

increased with man-induced habitat changes (more people, impervious surface cover, roads and high intensity of developed land use) and with lower tree (canopy) cover (Engel et al. 2020).

Salsbury (2008), studying the density and placement of fox squirrel dreys in 20 woodlots in the Indianapolis metropolitan area (USA), found no effect of woodlot size, shape or degree of isolation on drey density. Contrary, the occupancy of nest boxes by red squirrels was much higher in urban park than in rural areas, probably related to the higher density in the park which could result in good nesting sites becoming a limited resource (Gryz et al. 2021). Similar differences in squirrel density were reported in another city in Poland, Wrocław. Counting Eurasian red squirrels both directly and their nests (dreys), Kopij (2014) argued that squirrel density was much lower in 12 forests than in 21 parks in the city of Wrocław, and that squirrels were most common in the larger parks that were 2–7 km from city centre.

In a comparative approach of alien grey squirrel densities (visual counts along transects) between an urban park and a semi-rural woodland in Glasgow (Scotland), grey squirrels were on average more abundant in the semi-rural woodland (morning densities: rural area 2.70 ± 0.29 animals ha^{-1} , against 1.49 ± 0.21 ha^{-1} in urban park), where human numbers were lower (Kyle 2009). There was also evidence that the foraging behaviour of grey squirrels was influenced by human presence in the city centre park (Kyle 2009). In contrast, visual transect counts of Eurasian red squirrels in 11 parks and suburban forests in Warsaw (Poland) found the highest densities in relatively small parks near the city centre and lower numbers in the larger suburban forested areas (Babinska-Werka & Zolw 2008).

Another method (detection rates from camera trapping) applied in residential yards (urban) in Raleigh, North Carolina, USA, and in nearby suburban and rural sites, revealed a strong attraction of artificial feeding in yards (32.3 grey squirrels day^{-1} ; Hansen et al. 2020). Urban control (no feeder) sites had higher detection (0.55) than suburban (0.29) and rural forest (0.10). These authors also documented a positive association between prey and predator relative abundances (Hansen et al. 2020).

A 20-year multi-species approach with two native (Douglas squirrel and Northern flying squirrel) and one non-native species (Eastern grey squirrel) using data from submissions to wildlife shelters underlined that native squirrel numbers varied negatively with the amount of urban development, suggesting that regional declines in native squirrels are mainly predicted by man-induced habitat alterations of the original conifer forests (Gonzales et al. 2008).

In Finland, citizen science data from volunteer bird watchers along a 950-km south–north gradient were used

to collect data of Eurasian red squirrel. Relative squirrel abundance was ca. twice as high in urban habitats than in forests, and it increased with human population density, number of feeding sites and spruce cone crop, and decreased with latitude and season (Jokimäki et al. 2017). While there was no effect on goshawks, feral cat abundance was weakly negatively associated with squirrel abundance. They concluded that artificial feeding was a more important factor in attracting squirrels to urbanised areas than low predator presence. To what extent are these rural–urban differences due to variation in dispersal distances? Radio-tracking juvenile red squirrels revealed extremely long dispersal distances (up to 16 km) in a rural site, and much shorter distances (on average only 500 m) in an urban site (Hämäläinen et al. 2019). Dispersal paths were affected by landscape structure, and in the urban matrix disperser steps (distance between two consecutive observations) were longer than in forested areas and squirrels preferred areas with deciduous or coniferous trees. Consequently, individuals moved longer distances and were likely to circumvent barriers in their path in the rural landscape, but this did not affect how far they settled from their natal home (Hämäläinen et al. 2019). Hence, although landscape structure influences dispersal paths, it may have only a small effect on other aspects of the red squirrel populations such as gene flow. During dispersal movements, juvenile squirrels showed revisiting behaviour during dispersal to select the better site for settlement. In the urban area, all the examined juveniles performed revisits during dispersal (62% of visits), while rural individuals used a different strategy and only some of them revisited sites (23% of all visits) (Hämäläinen et al. 2020). The frequency of revisits was also affected by dispersal distance (fewer revisits with longer distances) and sex (more revisits for males), while the landscape structure had no significant effect (Hämäläinen et al. 2020). However, rural juveniles preferably choose a settlement site near built areas suggesting that squirrels thrive near the urban environment. In the same urban population, the effects of roads were different for non-dispersers vs. dispersing juveniles (Fey et al. 2016). During movements within their home range, squirrels were located further from roads and crossed them less frequently than simulated by random walk paths. In contrast, during explorative and dispersal movements, juveniles did not avoid roads and regularly crossed both big and small roads (Fey et al. 2016).

Another approach, using track tubes, looked at occupancy of small mammals (Northern flying squirrel, American red squirrel, Eastern grey squirrel and Eastern chipmunk) along a gradient from wilderness, overmanaged forest to residential areas in northern New York (USA) (Glennon & Porter 2007). Total abundance of all sampled species was highest in old-growth forest and declined along

the gradient, with lowest values in the residential sites. Detections of two sciurid species (Northern flying squirrel and Eastern grey squirrel) were too few to analyse, but chipmunks had highest abundance in old-growth forest and lowest in managed forest. In contrast, American red squirrel abundance was lowest in old-growth and highest in residential sites (Glennon & Porter 2007). Hence, responses to urbanisation were species specific. This was further confirmed by a large-scale multi-city (10 North American cities) camera trap study of eight widespread mammals (Fidino et al. 2021). The magnitude and direction of most species' responses to urbanisation within a city were associated with landscape-scale differences among the cities. Responses of two squirrel species, Eastern grey squirrel and fox squirrel, changed from negative to positive once the proportion of green space within a city was $> \sim 20\%$. Similarly, a low-intensity, mixed-detector survey (different trap models to target different-sized species, from shrews to squirrels) across 53 fragmented forests preserved in the highly urbanised Chicago metropolitan area, showed that occupancy of Eastern chipmunks and Eastern grey squirrels was highest in closed-canopy habitat (Cassel et al. 2020). Authors argued that small mammal communities can be used as bioindicators for urban-reserve networks.

Thaweepradej and Evans (2022) quantified the distribution of squirrels along an urbanisation gradient in a rapidly urbanising tropical mega-city (Bangkok, Thailand). *Callosciurus caniceps* was extremely rare in the study area, while *C. erythraeus* and *C. finlaysonii* were widespread, but only the latter had a higher abundance in more urban study sites. Moreover, urban infrastructure seemed to have increased hybridisation rates between *C. erythraeus* and *C. finlaysonii*. Overall, in this study area, urbanisation resulted in reduced squirrel diversity and abundance, in contrast with many studies in temperate regions (Thaweepradej & Evans 2022). Hence, it is possible to find squirrels and chipmunks also in megacities, settlements with more than 10 million inhabitants nowadays concentrated in the Global South, such as Bangkok, Thailand (e.g. *C. finlaysonii*, *C. erythraeus*, Thaweepradej & Evans 2022), or Dhaka, Bangladesh (*C. pygerythrus*, *Funambulus pennantii*, Jaman et al. 2021), but expected to emerge worldwide (United Nations 2019), a process that will make careful green urban planning even more important.

Finally, different modelling approaches were used to predict occurrence and persistence in urbanised landscapes. A study in the Brussels region (Belgium) used presence/absence data of Eurasian red squirrels in a fragmented and partly urbanised landscape (163 km²), considering not only the size, degree of isolation and quality of 354 habitat (wooded) patches but also several characteristics of the landscape matrix (Verbeylen et al. 2003). Patches ranged

from 0.01 to 1915 ha (mean $\pm$ SD = 7.65 ± 101.72 ha). All patch variables, size, quality and isolation, significantly affected squirrel presence and the landscape structure models using the effective distances between patches gave the best results.

A different approach with a different set of very detailed environmental variables (see table 1 in Grabow et al. 2022) was used in a recent study on the presence/absence of red squirrels in the larger Berlin area, Germany.

SPECIES DISTRIBUTION MODELLING

Grabow et al. (2022) used Species Distribution Models (SDMs) and recent data integrating techniques on two sets of citizen science data (structured camera trap data and unstructured wildlife observation data). Their modelling approach showed that using multiple data sets can improve the predictive performance of SDMs and they used the most robust SDM to reveal the suitable movement corridors for red squirrels in the urban matrix, which can be used as a basis to plan mitigation measures aimed to reduce road mortality (considered one of the major mortality risks for urban red squirrels) (Grabow et al. 2022). The authors also suggest that in Berlin, and probably in many urban settings in Europe, suitable 'green' habitats are often small and partially lack connectivity along natural corridors, a situation that will be exacerbated if additional fragmentation should occur. The approach and results presented in this study could act as a kind of template for management implications (Grabow et al. 2022).

A step further was taken by two studies that used a quantitative approach of predicted landscape change, based on different proposals of key ideas for organising space, often referred to as 'design concepts' or 'concept plans'. These concept plans that link landscape ecology theory to landscape planning are typically used by landscape architects and planners, to develop spatial concepts useful for the creation of open spaces in areas with rapid urbanisation (Penteado 2013, 2021). These studies focused on the predicted urban expansion of the city of Damascus, Oregon, USA. Alternative future scenarios of urban development were applied to test the effects of three open space spatial concepts (patches, corridors and networks), which contrasted with compact and dispersed urban development patterns, on the quantity and quality of suitable habitat for three target species within the predicted urbanised area over 50 years. Trade-offs between urban development and conservation of the three focal wildlife species, one of which is the Douglas squirrel (*Tamiasciurus douglasii*) (Penteado 2013), were analysed. The type of open space spatial concept highly influenced habitat quantity and quality differences among scenarios. For the Douglas squirrel, but not for the other target species, park system

(patches) scenarios presented an increase in the amount of high-quality habitats, while network scenarios presented the best combination of total amount of suitable habitats and increase of high-quality sites (Penteado 2013).

Somewhat similar results were found in another study that investigated how open space and urban development patterns will affect the viability of wildlife populations in urbanising landscapes, taking into account animal movement patterns in the urban matrix (Penteado 2021). Here, simulations were applied using eight scenarios for 2060 for an urbanising area near Portland, Oregon, USA. The combinations of four open space (none, corridors, parks and network) with two urban development patterns (compact and dispersed) were modelled, using the same three target species as in the previous study, predicting how the different scenarios would affect movements and, consequently, population size. For Douglas squirrels, the greenway scenarios showed the largest populations and the compact development scenarios performed best for most indicators (Penteado 2021). However, considering all three target species, networks presented the solution with more diverse habitats, sustaining higher species diversity (Penteado 2021).

A completely different kind of modelling approach, based on large-scale occupancy models, was used to explore potential effects of predator-mediated competition between native red and invasive alien grey squirrels in relation to habitat type (Twining et al. 2021). In Britain and Ireland, the recovery of a native predator, the pine marten (*Martes*

martes), influences the outcome of interspecific competition between red and grey squirrels, and in some landscapes can even reverse it in favour of the native species (reviewed in Wauters et al. 2023). Using single-species and multi-species occupancy models on 332 sites in Northern Ireland (14130 km²) at a 1 km² resolution, based on camera trap data collected by citizen scientists, Twining et al. (2021) showed that, on a regional basis, red squirrel occupancy was positively affected by exposure to pine marten, while grey squirrels had a marked negative response to the presence of this predator. However, incorporating habitat suitability models for the three species, the grey squirrels are likely to persist in urban areas, that, being inaccessible or avoided by the pine marten, can act as refugia for the IAS. Hence, despite the ongoing recovery of the pine marten and decline of grey squirrels in natural woodlands and forests (Wauters et al. 2023), isolated populations of the alien species are likely to persist in urban areas, making control of these populations a management priority (Twining et al. 2021).

SYNTHESIS

The studies included in the present systematic review are narrowly focused on 13 arboreal squirrel, 3 flying squirrel and 2 chipmunk species, a small proportion of the total number of potential species (141 tree squirrels, 44 flying squirrels and 25 chipmunks, Fig. 4, Appendix S1), with the majority of papers on two species, *Sciurus carolinensis*

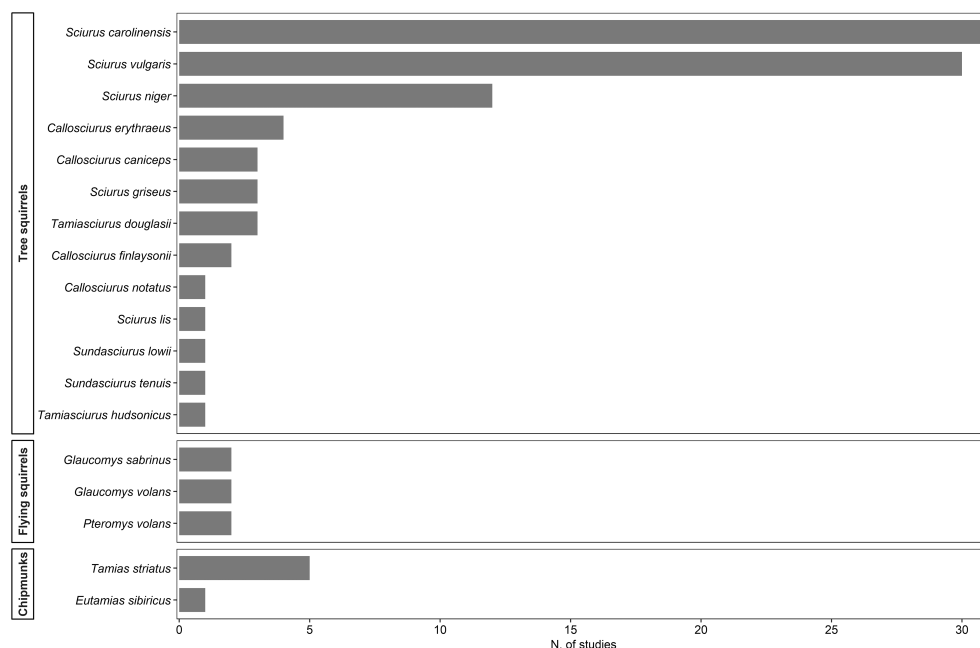


Fig. 4. Number of included studies per species of chipmunks, arboreal and flying squirrels based on the list of discussed articles. Each article may consider more than one species.

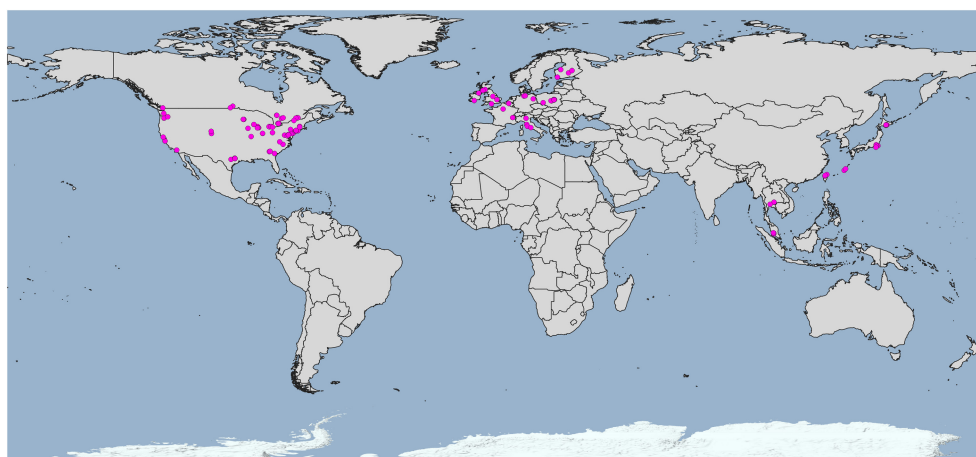


Fig. 5. Geographic locations of the study sites of the included articles on chipmunks, arboreal and flying squirrels based on the list of discussed articles; points represent the study sites (see also Appendices S4 and S5).

(38%) and *S. vulgaris* (37%). Included articles described studies conducted in three regions (North America, Asia and Europe) for a total of 13 countries. It is evident there is a big gap of information concerning Africa, where 31 arboreal squirrel species are present (Appendix S1), and Central and South America, which include the distribution of 22 arboreal and 1 flying squirrels (Thorington et al. 2012). Moreover, the majority of studies were conducted in highly developed countries (Fig. 5, Appendix S5), whereas the greatest diversity and endemism of arboreal and flying squirrels are located in tropical forests in Africa, Asia, Central and South America (Koprowski & Nandini 2008). Furthermore, Asia and Africa are the continents with the world's most fast-growing cities, and many megacities are located in the Global South (United Nations 2019), indicating a gap in knowledge in areas where it should be of significant relevance. In fact, understanding adaptation mechanisms of the species that live in countries where the urbanisation growth rate is high would allow us to apply the research results to urban planning during city development.

Despite these biases, the systematic review we conducted reveals that, even using information from urban areas situated all over the world, the definition of site types (urban, rural, semi-urban, etc.) can be considered consistent. Indeed, using only the average built-up fraction (Buchhorn et al. 2020) surrounding georeferenced sites in a radius of 200m belonging to studies included in the present systematic review (12ha area), we tried to disentangle the inconsistency around the terminology to define 'urban' (but see Padilla & Sutherland 2019 for a more comprehensive framework). Here, we highlight that not only the extreme of the scale (urban–natural) are well divided but also that site types along the gradient are consistent (urban–semi-urban–urban park–semi-rural–rural–natural;

Fig. 6). Therefore, although we considered only one type of landscape metric which defines what is 'urban' (Padilla & Sutherland 2019), the main findings we synthesised here can be generalised across included studies.

Among the mammal taxa considered in this review, there is no unidirectional pattern of changes in genetic diversity or in body size and body mass over the rural–urban gradient. It must be underlined that the studies are few and that they used different types of urban areas (parks, urban woodlands; areas with/without supplemental food). The only two studies that focused on genetics, both on Eurasian red squirrels (Rézouki et al. 2014, Selonen et al. 2018), suggest some degree of genetic connectivity (and thus gene flow) between urban populations and nearby rural ones, which should improve viability of small (sub)populations that live in urban green spaces. Clearly, more comparative studies on different species of Sciuridae along rural–urban gradients are needed to investigate whether, for example, species that occur at higher densities (e.g. grey squirrels) and/or have different dispersal patterns (e.g. short-distance dispersing chipmunks, long-distance dispersing flying squirrels) will show differences in genetic diversity between urban and rural populations.

The few morphological studies are concentrated on only three out of more than 200 species (Appendix S1). Animals in urban sites are not always larger or heavier than those in rural ones, and there is clear evidence that the habitat quality within the urban matrix is an important determinant of body mass. Moreover, some species are more prone to take supplemental food from humans than others; hence, the degree to which supplemental food is used by the squirrels can affect their body mass. Finally, the type of supplemental food items is important; those produced by man (e.g. biscuits, bread) can have negative effects on digestion and metabolism,

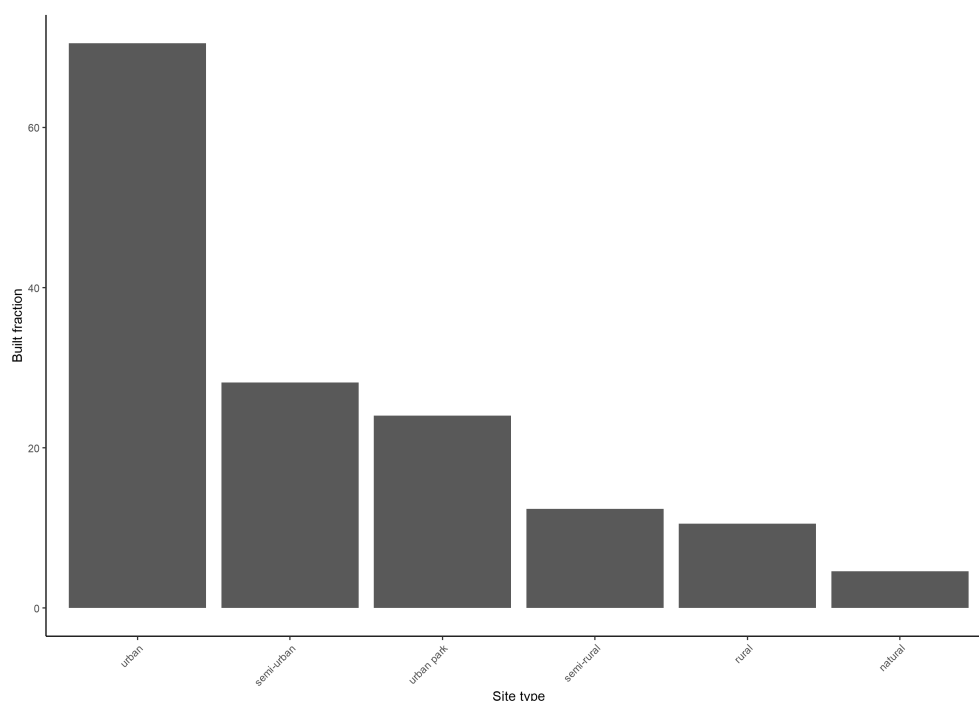


Fig. 6. Average built-up fraction in a circle of 200 m radius for each site type (217 georeferenced study sites). Site types were defined unifying sites with clearly similar terminology (used by articles' authors to describe their study sites) into six main types (urban, semi-urban, urban park, semi-rural, rural, natural; see Appendix S4).

while 'natural' energy-rich food items (e.g. hazelnuts, walnuts) are both consumed and cached for later use and can have positive effects on the squirrels' body mass. In fact, the quantity and quality of supplemental food can strongly affect space use, perceived costs/benefits of foraging on non-natural food in patches with diverse human disturbance (measured using GUDs), and diet, including changes in the use of natural food resources. These changes can produce differences not only in body mass but also in blood chemistry (in particular glucose levels), due to digestive and physiological costs in animals living in urban areas, which ultimately may reduce the health or even the fitness of squirrels living in urban areas.

Similarly to morphological changes, the different sciurid species exhibit contrasting physiological responses to the challenges posed by the urban environment. Consequently, no uniform clear pattern of physiological response to life in urbanised areas can be identified. As far as FGMs are concerned, the current review is in contrast with a meta-analysis by Dantzer *et al.* (2014) on vertebrates, where they suggested that an increase in faecal glucocorticoid metabolites levels is generally associated with human disturbance. However, our interpretation is limited by the small number of studies we found, and thus we advocate an increase in research on sciurids' physiological responses

to urban environments in order to draw more robust conclusions. Furthermore, as discussed by Shimamoto *et al.* (2020), selection in urban areas should favour endocrine phenotypes that support individual reproduction and survival in cities (but see Bonier 2012, Dantzer *et al.* 2014). In particular, some physiological stress response mechanisms might help prevent deleterious effects of high stress levels, such as down-regulation of the HPA axis (e.g. desensitisation: discussed in Lyons *et al.* 2017; habituation: Santicchia *et al.* 2022b), which ultimately could enhance fitness. However, none of the studies reported here is informative about the adaptation of individuals, since they did not explore whether changes in the physiological stress response affected fitness parameters of individual squirrels with respect to urbanisation and/or human disturbance. Hence, multi-year comparative studies, with a replicated study design of multiple sites along the rural–urban gradient, are needed to explore to what extent physiological responses favour the animal's adaptation under environmental disturbance typical for the populations in urbanised areas.

Many studies investigated behavioural changes from rural to urban sites or compared behaviour of squirrels in urban sites with more or less human disturbance. Many disturbance-related variables (man vs. predator, human behaviour, distance between squirrel and source of

disturbance), habitat characteristics (tree cover, tree height, etc.), structure (park, woodland) and even size of the green area can affect changes in behaviour. Anti-predator behaviours (FID and VED) are the most common behaviours observed to vary along the gradient, though differences in behavioural responses were also detected using other measures such as OFT and MIS tests and radio-tracking data. However, again no uniform clear pattern of behavioural changes in response to anthropic disturbance emerges from the studies reviewed here (Table 2). Behavioural responses to cope with the challenges animals need to face in urbanised areas seem to occur and might lead to adaptation to these new conditions, for example, the reduction in perceived predation risks and/or increased abilities to access food resources might enhance survival and reproductive success (Tuomainen & Candolin 2011, Lowry et al. 2013, Sol et al. 2013). However, changes in behaviour observed in urban areas could also have costly outcomes, reflected in higher vulnerability to predators where these are present in urban areas (Lowry et al. 2013; but see Kittendorf & Dantzer 2021). Although a previous review described that behavioural changes led to adaptation to urban pressures in many mammals (see Ritzel & Gallo 2020), the papers on sciurid species reviewed here show an exponential increase in studies investigating this topic during the last few years, adding knowledge, but also complexity, to the potential role of behaviour in the adaptation processes to life in the city.

Although space and habitat use were considered in several studies, only few of them assessed the habitat preferences of squirrels along the rural–urban gradient, while the others considered the animals' movement and occurrence only within the urban environment. From this, review emerges that there are several factors (see Table 3) that could affect the animal's response to the urban environment; first of all the vegetation, followed by the studied species (see also Zozzoli et al. 2018). In particular, the structure of urban green areas as well as the presence and the characteristics of the vegetation within cities are essential for the occurrence of squirrels and chipmunks within the urban environment, which would otherwise avoid residential and highly disturbed areas. In fact, the percentage of green areas with tree cover in the city is an important parameter because it relates not only to how much potential habitat there is but also to the distribution (connectivity) of parks, woodlands and potential green corridors. Concerning the home-range and core-area sizes, the pattern is not consistent among species; however, this review indicates that squirrels are able to change their space use based on the environment, altering home-range size in the urban context.

At population level (occupancy, density, estimates of demographic processes), studies on different species show

varying response patterns to urbanisation. Population demographic parameters for Eastern grey and fox squirrels, in their both native and non-native ranges, tend to be higher in urban or suburban areas than in rural ones, with the exception of one study of Eastern grey squirrels in Scotland (Kyle 2009). Also, the majority of studies on Eurasian red squirrels documented higher densities in (relatively small) urban parks than in urban forest or rural habitats, but this may depend on the amount (and quality) of supplemental feeding. In contrast, studies on native Western grey squirrels, Douglas squirrels and Northern flying squirrels revealed opposite trends, with smaller or less numerous populations in urbanised than in (semi) natural habitats. These species behave more as natural/rural habitat specialists and tend to avoid urbanised sites. For the species that thrive in urbanised areas, the matrix composition and density of impervious areas around the green parks/woodlands can be as, or even more, important than the tree cover or tree species characteristics inside suitable habitats, and impact survival (e.g. road kills) as well as dispersal distances and success. Fitness outcomes were investigated in four species (*S. carolinensis*, *S. griseus*, *S. niger* and *S. vulgaris*); three of them exhibit a fitness advantage in the urban environment showing they are adapted to live in cities. In contrast, there was a negative effect of urbanisation on some fitness components in *S. griseus*. Hence, there is no single demographic response of arboreal and flying squirrels to urbanisation, and species-specific dispersal and social behaviour seem to be key parameters that influence to what degree species are adapted to persist in small and more or less isolated green areas inside or nearby cities.

The present systematic review is focused on a limited number of sciurid species, which frequently occur in urbanised environments, with the ultimate goal of highlighting a general pattern in their responses to urbanisation and unveiling whether they have adapted to life in urban areas.

First, this review indicates that arboreal squirrels, flying squirrels and chipmunks can adopt different response strategies when they occur in the urban environment. However, our main findings suggest that different species or individuals of the same species studied in different areas may exhibit contrasting patterns. Moreover, this systematic review reveals that knowledge of some trait variation is still lacking (e.g. only two studies explored the genetic aspect, which would give essential information about the viability of populations) besides the general lack of data for several sciurid species (most of the studies focused on *S. carolinensis*, *S. vulgaris* and *S. niger*, Fig. 4). Second, few studies (only five) specifically explored differences in fitness along the rural–urban gradient informing about the adaptation to urbanisation.

Overall, this systematic review not only confirms that urbanisation can be an important driver for adaptation in small mammals but also highlights that patterns are complex and differentiated. More and detailed studies on the relationships between phenotypic traits and animals' fitness along a rural–urban gradient will be necessary to reveal to what extent these mammal species adapt to the urban environment. Combining this knowledge with monitoring and modelling studies that use a landscape and urban structure/composition approach will be necessary to produce indications for an urban planning that aims to conserve biodiversity in and around cities.

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DATA AVAILABILITY STATEMENT

Data have been included in Appendices S1–S5 submitted with the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Taxa used in this systematic review, divided into arboreal squirrels, flying squirrels and chipmunks.

Appendix S2. List of the articles on chipmunks, arboreal and flying squirrels in the urban setting without comparison.

Appendix S3. List of the included articles on chipmunks, arboreal and flying squirrels belonging to 'gradient rural–urban'

and 'gradient inside urban' classifications (see Methods for details).

Appendix S4. Geographic locations of the study sites of the included articles on chipmunks, arboreal and flying squirrels based on the list of discussed articles.

Appendix S5. Close-up of the three main areas where the study sites of the included articles on chipmunks, arboreal and flying squirrels based on the list of discussed articles falls; points represent the study sites.