


# Legacy effects of religion, politics and war on urban evolutionary biology

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Urbanization has been a defining feature of the past four centuries, with most of the global population now living in highly modified environments shared with wildlife. Traditionally, biological urban evolutionary research has focused on physical factors such as habitat fragmentation, pollution and resource availability, often overlooking the social and political forces shaping urban environments. This Review explores how religion, politics and war drive urban wildlife evolution by shaping environmental conditions and selective pressures. We synthesize existing knowledge on these influences and propose testable hypotheses to advance the field. Understanding these dynamics is essential for explaining the variability in urban evolutionary processes and predicting the future development of urban systems. By integrating social and political dimensions, we can gain deeper insights into how cities shape the evolution of the organisms that inhabit them.

Religion, politics and war are interconnected in complex ways, especially in cities where human decisions dramatically affect the environment. While religious practices can shape moral frameworks<sup>1</sup>, both religion and politics shape societal values, legitimize power<sup>2</sup> and shape public institutions<sup>3</sup>, all of which have downstream influence on the environment<sup>4</sup>. Over time, power struggles among political and religious leaders<sup>5</sup>, desire for economic gains, and political ambition can lead to war<sup>6</sup>. Thus, throughout history, these three forces have shaped societies, and the urban environment in particular. While typically viewed from a sociological perspective, the implications of religion, politics and war are rarely discussed in the field of urban evolutionary biology. Des Roches et al.<sup>7</sup> highlighted the need to study urban eco-evolutionary dynamics in the context of humans, precisely because cities

are regularly undergoing social and economic transformations that are likely to influence urban evolutionary processes. So far, however, human decisions, and specifically those guided by religion, politics and war, are poorly understood and little addressed in terms of their effect on evolutionary processes in urban organisms. This contrasts with the legacy of these cultural forces visible in the urban landscape. In this Review, we show that the downstream consequences of religion, politics and war can have far-reaching effects on the environment and on the evolutionary processes affecting urban organisms. By systematically exploring the respective effects of religion, politics and war on urban evolutionary biology, we emphasize the need to consider these drivers of human culture in understanding unexplained variation in urban evolutionary processes. Importantly, understanding these processes

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## BOX 1

## Glossary of common evolutionary biology terms

**Evolutionary potential.** The ability of a population to evolve following environmental change<sup>98</sup>.

**Gene flow.** The movement of alleles (for example, genetic variants) from one population to another, synonymous to the dispersal of animals, pollen or seeds. Gene flow adds genetic diversity to populations, which can be evolutionarily beneficial if it leads to the recovery of lost genetic variation or the spread of advantageous variants, but it can also reduce mean fitness in the population by spreading variants among populations adapted to different environments.

**Genetic drift.** Variation in the frequency of genes in a population due to random sampling that leads to random loss of genetic variability from one generation to the next. The smaller the population, the quicker it loses genetic variation. This can be problematic because genetic variation is necessary for adaptive change and its loss puts populations at risk of inbreeding<sup>99</sup>.

**Genetic variation.** Differences in DNA sequence among individuals in a population.

**Mutation.** Nucleotide base change in DNA. Mutations provide the raw material for evolution and are random with respect to function<sup>100</sup>.

**Nature-based solutions.** Services provided by nature that benefit humans.

**Phenotype.** The set of observable traits of an individual.

**Plasticity.** The ability of an organism to produce different phenotypes based on environmental variation.

**Selection.** The differential survival and reproduction of individuals with different phenotypes.

can enhance our ability to design and remodel cities to make them better for people while supporting the environment and evolutionary potential within the city.

Throughout, we use the biological definition of evolution, which is the change in inherited traits over successive generations<sup>8</sup>. Biological evolution is a population-level process whereby genotype and phenotype frequencies change across generations due to adaptive and non-adaptive processes (Box 1).

Although evolutionary thinking is not yet well integrated into urban decision-making, case studies are accumulating where sustainable design facilitates evolutionary processes. For example, Singapore—a city state where one urban environment serves as the hub of political and cultural life—has ensured that park planning is central to its culture. Park planning, offering scope for easier gene flow and the maintenance of genetic variation (Box 1), is embedded in the political framework of Singapore's national goal to be a 'city in nature'. This political planning is now essential to the identity of Singapore, providing residents with economic benefits and a sustainable urban mosaic<sup>9</sup>. Thus, almost 50% of the city is covered by green space, including mangrove habitat along the urban shoreline and a 24-km wildlife corridor that allows for genetic connectivity<sup>10</sup>. Although Singapore decision-makers may not have intentionally designed these spaces with the evolutionary consequences of urbanization in mind, their actions facilitate the evolutionary potential of the city's urban green spaces.



**Fig. 1 | Religious sites and practices can affect the evolutionary potential of urban wildlife. a–i,** Religious sites provide wildlife habitat in cities. **a,b,** They include the Brompton Cemetery in London, UK where red foxes (*Vulpes vulpes*) are common (**a**) and the Jewish Cemetery of Warsaw, Poland, where great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) are breeding in nest boxes (**b**). **c,d,** Some religious sites are specifically dedicated to the preservation of biodiversity, including the sacred groves and biodiversity park in Visakhapatnam, India (**c**) and the Tian Tan Buddha surrounded by forest in Hong Kong (**d**). **e–g,** Many religions honor or hold specific species sacred: for example, the Karni Mata temple in Deshnoke, India is home to a large number of black rats (*R. rattus*) which are fed by devotees (**e**), sika deer (*Cervus nippon*) in Japanese temples are revered and, as a result, reach unusually high population sizes (**f**) and the Shinto Otoyō Shrine in Kyoto, Japan is guarded by rodent statues (**g**). **h,i,** Religious activities can also directly influence urban wildlife such as prayer animal releases, a Buddhist ceremony, pictured here as the release of fish by a monk in Hong Kong to 'free the spirit of tsunami victims' following the 2004 tsunami (**h**), or indirectly influence urban pathogens such as during mass pilgrimages like the Hajj at Al-Haram Mosque in Saudi Arabia (**i**). Credits: **c,** Exotica/Alamy Stock Photo; **d,** Buddy Mays/Contributor/Corbis Historical/Getty; **e,** Roberto Fumagalli/Alamy Stock Photo; **f,** Planet One Images/Contributor/Universal images group/Getty; **g,** VW Pics/Contributor/Universal Images Group/Getty; **h,** SAMANTHA SIN/Stranger/AFP/Getty; **i,** Abid Katib/Staff/Getty Images News/Getty.

It is important to note that biological evolutionary change can occur rapidly, over just a few generations; thus, we can shape evolutionary processes within human lifetimes<sup>11</sup>. This is important because, when accounting for evolutionary processes in urban planning, humans can create long-term, beneficial environmental change in their cities. These changes may align with cultural and political goals while also supporting natural processes that address social and environmental issues. In this Review, we provide key examples of existing knowledge about how religion, politics and war influence the landscape of cities and explore the possible evolutionary consequences of these landscape changes.



We also propose testable hypotheses to advance our understanding of the effect of religion, politics and war on urban evolutionary biology in future research.

Religion’s effect on urban evolutionary biology

Religion’s influence is inextricably linked to history, culture and politics. Eluding simple definition, religion comprises beliefs related to supernatural phenomena (for example, deities) that are believed to influence the world in diverse ways including communal practices such as ritual, narrative and evidential testimony as well as myths that support systems of belief and practice. Social sciences have moved away from a fixed conception of religion toward studying the ways in which beliefs become embedded in a wide variety of political and social institutions, power relations, daily rituals, migrations and moral practices<sup>1</sup>. The goals of addressing the effects of religion on urban evolutionary processes include studying the environmental impact of sacred sites<sup>12</sup>, and looking at the variety of ways religion influences urban wildlife and their associated ecologies.

Globally, 77% of people follow 1 of 4 major traditions (Christianity, Islam, Hinduism or Buddhism), with another 16% classified as religious but unaffiliated with the 4 major religions<sup>13</sup>. One commonality of nearly all religions is outdoor sites of sanctuary and worship, such as shrines, temples, sacred groves or churchyards (Fig. 1). These sites may be important green spaces in cities otherwise lacking them, and are often purposefully maintained to serve dense human communities<sup>14</sup>. For example, *Candomblé*, a polytheistic religion brought to Brazil by enslaved Africans, sacralizes nature, which leads to environmental activism among its practitioners, who work to protect nature in urban settings<sup>15</sup>. Similarly, sacred urban sites in Zimbabwe<sup>16</sup>, South Africa<sup>17</sup>, India<sup>18</sup> and various cemeteries around the world<sup>19</sup> could contribute to biodiversity conservation and rehabilitation. Sacred status often enhances species protection<sup>20</sup> and reduces genetic drift<sup>21</sup>, promoting evolutionary change, as reported in Table 1.

Religious cultures can, thus, promote interactions between humans and urban wildlife, leading to evolutionary change in the latter: signatures of artificial selection in domestic chickens (*Gallus gallus*) reflect increasing urbanization and interest in alternative protein sources that could be eaten during religious fasting<sup>22</sup>. Domestic cattle (*Bos taurus*) and wild Hanuman langurs (*Semnopithecus entellus*) are common in some Indian cities, where their populations may be buffered against drought or starvation by religiously motivated stewardship<sup>23</sup>. Urban sacred sites may be dedicated to certain species, such as the Ootoy Shrine in Kyoto, Japan, famous for its guardian rodents (Fig. 1g), or the Karni Mata temple in Deshnok, India (Fig. 1e). Karni Mata houses thousands of black rats (*Rattus rattus*) that are fed daily by priests and devotees, allowing for population growth of this species beyond what the natural environment could sustain<sup>24</sup>. All of these examples of demographic changes in population size and structure can shape the evolutionary processes of genetic drift, gene flow and natural selection in urban populations, as detailed in Table 1.

If species are attracted by religious sites or practices, then it is also possible that unpredictable interactions among organisms arise and lead to evolutionary changes that are difficult to predict. Of particular concern are evolutionary changes that could pose threats to humans and urban environments. Mass religious pilgrimages (Fig. 1i) or other activities that cause humans to gather in large numbers may affect population size and gene flow of pathogens and/or invasive species (Table 1). For example, coordinated ‘prayer animal release’ of American bullfrogs (*Rana catesbeianus*) among some Buddhist communities in Asia has led to widespread decline of native species in urban aquatic environments<sup>25</sup>. This decline can lead to small, fragmented populations, increasing the potential of genetic drift of native populations. Respectful engagement and collaboration with religious communities hold promise for modifying these practices to be ecologically positive<sup>26</sup>.

Table 1 | Evolutionary processes associated with religious practices

Mutation	• High population densities and close human contact, which often occur at religious pilgrimage sites, lead to pathogens having increased transmission rates <sup>67</sup> and novel mutations <sup>68</sup> .
Gene flow	• Urban cemeteries, which often have a religious association, act as refugia and ecological corridors allowing gene flow <sup>19,21</sup> . • Prayer animal releases in cities often involve the capture and release of wild animals; this release may occur far from where the animal was captured leading to human-facilitated gene flow <sup>69</sup> . In addition, prayer animal releases that involve non-native animals such as red-eared sliders ( <i>Trachemys scripta</i> ) can lead to hybridization with local native species and the introduction of new alleles in the population <sup>70</sup> .
Selection	• Over 90% of wine-associated yeast strains belong to the same genetic cluster suggesting an initial domestication of yeast <sup>71</sup> . Because wine is associated with many religious events, religious wine-making that took place in monasteries probably influenced selection on <i>Saccharomyces cerevisiae</i> <sup>72</sup> . • European rabbits ( <i>Oryctolagus cuniculus</i> ) were domesticated relatively recently in French monasteries due to a papal edict stating that newborn rabbits could be eaten during the fasting period of Lent. During this time, monasteries selectively bred rabbits for docility <sup>73</sup> .
Genetic drift	• Walls were constructed around religious buildings in the city of Oviedo, Spain, leading to population differences among fire salamanders ( <i>Salamandra salamandra</i> ) within and outside the walled areas <sup>74</sup> . • Monasteries and shrines in Japan created conservation areas within cities for sacred sika deer ( <i>C. nippon</i> ) that were otherwise heavily hunted outside of these protected environments. Genetic structure suggests that protection within the religious sanctuary of Kasuga Taisha Shrine in Nara city isolated one population in particular <sup>75</sup> .

In addition, one of the most profound periods of environmental change in the Americas was the period of European colonialism that began in 1492 with Columbus’s accidental arrival in the Caribbean. Columbus’s voyages were partially dedicated to raising funds for religious crusades, and this religious-driven colonialism brought about environmental damage due to invasive species from Europe and its overseas colonies<sup>27</sup>. Colonization and the destruction of pre-Columbian urban habitats, resulted in a probably human-driven period of global cooling and probably changed the evolutionary trajectory of a wide range of taxa<sup>28</sup>. Modern colonization persists, driven by religion and politics, often sparking wars, as evident in present-day worldwide conflicts.

Politics’ effect on urban evolutionary biology

The environment across the planet is shaped by human synergies and tensions, including religious and political conflicts. Politics emerges wherever people interact with one another to make decisions that collectively affect society. Political decisions are based on the interactions between rules (for example, constitutions), realities (for example, facts of the situations) and choices.

While political decisions are often made by elected representatives or legislative bodies (such as parliament or congress), a large number of cities around the world have been deeply shaped by a history of political colonization over the past five centuries. In South America and Africa, this historical legacy of colonization is currently compounded by the fastest rate of urban growth in the world<sup>29</sup>. Although the urbanization process in Latin America began in the pre-Columbian period and was driven by an agricultural technological revolution, the European conquest put an end to Indigenous urbanism<sup>30</sup>. In South America and Africa, urban centers were used for political consolidation and

**Table 2 | Evolutionary processes associated with political ideologies**

<b>Mutation</b>	<ul style="list-style-type: none"> <li>In the USA, lower-income neighborhoods with a higher non-white population are more likely to be exposed to mutagens<sup>76</sup>.</li> <li>Paternal diets high in cured meats and sweets, which are often the main type of food available in urban food deserts<sup>77</sup>, increase the likelihood of novel germline cancerous retinoblastoma gene mutations<sup>78</sup>.</li> </ul>
<b>Gene flow</b>	<ul style="list-style-type: none"> <li>The European Green Belt is an initiative that started in 1989 with the dismantling of the Soviet Union. This corridor runs along the same path as the Iron Curtain, including multiple cities, providing over 12,000 km of protected land in which wildlife can move, thereby facilitating gene flow<sup>79</sup>.</li> </ul>
<b>Selection</b>	<ul style="list-style-type: none"> <li>Research has shown Atlantic killifish (<i>Fundulus heteroclitus</i>) repeatedly experience selection from industrial pollutants<sup>80</sup>. The polluted areas in which these fish come from were predominantly in cities with high populations of people of color, while the non-polluted waterways used as a comparison were in predominantly white cities (<a href="https://www.census.gov/quickfacts/fact/table/US/PST045221">https://www.census.gov/quickfacts/fact/table/US/PST045221</a>).</li> </ul>
<b>Genetic drift</b>	<ul style="list-style-type: none"> <li>Urban highways across the USA have been placed in particular neighborhoods based on political agendas<sup>81</sup>, leading to genetic drift in urban animals, including bobcats and coyotes<sup>82</sup>.</li> <li>In the USA, genetic drift has increased in urban wildlife populations inhabiting minority neighborhoods, probably due to lack of green spaces that would facilitate gene flow and due to increased industrial development<sup>37</sup>.</li> </ul>

socioeconomic control<sup>31</sup>. This colonization had effects on biodiversity via the introduction of non-native species that often outcompeted native species, leading to the loss of local species, increased genetic drift and reduced genetic diversity<sup>32</sup>. Given that global, national and local politics are fundamental to human societies, political systems directly and indirectly shape environmental policies, urban environments and cities' potential for evolutionary change (Table 2).

Regional and local urban political decisions are also key players in urban land management. Local environmental policies that focus on green spaces, greenbelts and waste management are all driven by political decisions<sup>33</sup>. For instance, in the UK and New York City, USA, early proponents of greenbelts (that is, contiguous areas of land around cities where development is not permitted) viewed these areas as a way for the urban working class to readily access nature<sup>34</sup>. In some cities, greenbelts provide useful refugia for species that otherwise would not survive in cities<sup>35</sup>. In parallel, the rise of urban allotment gardens was promoted as social welfare policy for the very same aim across much of Eastern and Western Europe after the Second World War.

Urban policies have also shaped the availability of green habitats in different neighborhoods, with Schell et al.<sup>36</sup> highlighting that race-driven practices can act as an important driver of urban landscape heterogeneity in terms of flora and fauna. This hypothesis was further confirmed at a genetic level: Schmidt and Garroway<sup>37</sup> demonstrated that these political changes implemented in the urban space have evolutionary consequences, leading to a reduction in genetic diversity and connectivity of wildlife populations inhabiting minority neighborhoods. Research consistently shows that poorer urban areas tend to have less access to green spaces than wealthier neighborhoods, as demonstrated in Germany<sup>38</sup> and in The Netherlands<sup>39</sup>. In England, Black people are nearly four times less likely to have outdoor space at home, compared with white people (<https://www.ons.gov.uk/economy/environmentalaccounts/articles/oneineighbritishhouseholdshasnogarden/2020-05-14>). These examples highlight repeatable covariation between the urban environment and ethnic and economic make-up, and may result in reduced gene flow and increased drift in urban wildlife from these areas. In the twentieth-century USA, politics influenced residential racial segregation in US cities via racial covenants (that is,

contractual agreements that prevent the sale of a house from one race to another) and redlining (a practice in which services were withheld from minority neighborhoods that were deemed 'hazardous'; Fig. 2). Although racial covenants and redlining are not the only causes of segregation in the USA, they can act as a proxy for understanding the effect of segregation on the urban landscape because specific locations are included, providing historical and geographical data<sup>40</sup>. These historical policies have influenced the resources and management of parks in the USA; for example, parks in poorer, Black neighborhoods tend to have fewer trees and bushes and more open spaces allowing law enforcement to monitor these areas more easily, a process known as 'crime prevention through environmental design'<sup>41</sup>. Given that urban parks globally harbor much of the wildlife within cities<sup>42</sup> and amount to a large portion of urban biodiversity, park design can have far-reaching downstream consequences in terms of urban biodiversity and opportunity for gene flow. Thus, in the USA, non-white neighborhoods are likely to have a limited capacity to support large, well-connected wildlife populations, and simultaneously have reduced access to nature for their human inhabitants<sup>37</sup>.

We note that environmental damage related to political systems is present in many forms of governance. At national and global scales, transitions from communism to capitalism clearly affect urban development, and can have cascading effects on evolutionary dynamics. Specifically, the collapse of communist governments behind the Iron Curtain in Europe starting in 1989 initiated substantial changes in land development across 15 countries east of the Iron Curtain<sup>43</sup>. The shift from a planned socialist economy to a neoliberal economic system also induced vast urban transformations. A study comparing five capital cities of Europe (Warsaw, Budapest, Prague, Bucharest and Sofia) during the years 1991, 2000 and 2015 demonstrated that this change led to high and unplanned growth in the cities. The capitalism-driven value of land radically changed building practices: this often resulted in dense urban development post-1989, the development of gated communities in suburban areas, urban sprawl, gentrification phenomena, and a decrease in urban green areas<sup>43</sup>. These changes to the landscape are likely to reduce gene flow and population sizes of urban wildlife (Fig. 2). However, so far, these market-driven predictions are largely untested, and may be mitigated by governments that choose to center green development, such as Singapore<sup>9</sup>.

Increasingly contrasted takes on political agendas can lead to political tensions. These are sometimes materialized as physical barriers dividing the urban space, leading to disrupted gene flow and increased genetic drift. Recent examples include the 34 km of 'peace walls' that were built to separate Catholic and Protestant neighborhoods in Belfast, Northern Ireland<sup>44</sup>; a 155-km wall that divided communist East Berlin and capitalist West Berlin between 1961 and 1989; the 708-km-long Israeli West Bank barrier, which stands at the intersection of political and religious differences between Palestine and Israel; and the transborder agglomeration of El Paso–Juarez that has been walled off as part of the larger Mexico–US border wall. With the exception of the Berlin Wall, these concrete constructs are still standing, and are a prime example of a physical barrier possibly constricting dispersal, fragmenting populations and hampering gene flow in the long term<sup>45</sup>. Evidence on the effect of walls on wildlife population genetics is scant, and data from urban wild boar (*Sus scrofa*)<sup>46</sup> and hedgehogs<sup>47</sup> suggest that the dismantling of the Berlin Wall, and the availability of a high number of urban green patches in the city, cancel out any long-term effect of the Berlin Wall on the population genetic structure of these two species. However, even if the population structure may be restored, the effects on genetic diversity due to drift in these once fragmented populations can have long-term effects that take time to recover. Thus, calls for further research are warranted, and the availability of multiple cities with walls of different ages and geographical spans offer a powerful experimental framework for the testing of the genetic effect of urban walls on gene flow of urban wildlife.





**Fig. 2 | Political systems affect urban design, including the amount and distribution of green areas across the urban matrix.** An illustrative example from Eastern Europe (left) and North America (right), reflecting how political systems shape urban green areas in residential neighborhoods. In Warsaw, Poland, land ownership and the timing of residential area construction after the Second World War (state owned 1945–1989; privately owned post-1989) is likely to modulate the scale of wildlife gene flow in urban residential areas in large cities of the entire Eastern Bloc. Buildings built between 1945 and 1989 were erected on city-managed land, under communist regime. Residential areas built after 1989, on land with private ownership, are usually built more densely. In Detroit,

USA, segregation influences the distribution of urban green areas across the urban matrix. Starting in 1935, redlining was a common discriminatory practice in US cities, in which services were withheld from neighborhoods graded ‘D’. Neighborhoods were graded based on environmental conditions and the number of racial minorities, with predominantly white neighborhoods given an ‘A’ grade and racial minority neighborhoods given a ‘D’ grade. This resulted in more financial resources for grade ‘A’ neighborhoods. Credit: Imagery ©2025 Google, Imagery ©2025 Airbus, CNES/Airbus, MGPP Aero, Maxar Technologies, Map data ©2025 Google.

War’s effect on urban evolutionary biology

Increasing political tensions can lead to war and between the end of the Second World War in 1946 and 2014, we have seen 254 armed conflicts around the world<sup>48</sup>. War continues to have far-reaching effects on cities and the nature within them<sup>49</sup>. Despite the known harms of war on the environment<sup>50</sup>, we are only starting to understand its evolutionary implications. We acknowledge that the lack of wildlife data from war zones provides challenges in predicting how war shapes evolution. A tool that may become instrumental in bridging this knowledge gap could stem from the use of remotely sensed imagery (satellites and drones) using data generated by smartphone users and stored digitally online<sup>51</sup>. These data can be used to generate timelines of environmental change within and outside of war-torn cities. For example, social media such as blog posts, videos and photos capture interactions with wildlife during the Russian invasion of Ukraine, revealing the effect of war on nature in almost real time<sup>52</sup>. Distinct stages of war—pre-war, active war and post-war—as detailed below, may affect urban environments and the evolutionary processes of wildlife that cities harbor in different ways.

During pre-war operations, military training requires land resources for practices that include urban areas, often causing environmental disturbance<sup>53</sup>. At many training sites, contamination from radioactive waste, lead, propellants, explosives, solvents and fuels persist in soil and water for decades<sup>54</sup>. For many organisms, these initial disturbances and residual chemicals may be lethal or sublethal, creating novel selective pressures from which adaptation and/or plasticity may arise<sup>54</sup>.

In the active phase of war, substantial destruction of urban habitats occurs due to bombing, disruption of government and other military activities—all of which may affect evolutionary processes (Table 3). From the start of the full-scale Russian invasion of Ukraine in early 2022, thousands of air strikes have been carried out (<https://missilethreat.csis.org/missile-maps-infographics/>). These air strikes, along with the dispersion of vehicle fuel, lubricants, solvents, electroplating waste and placement of landmines, have led to more than 37,000 fires across Ukraine affecting approximately a quarter of a million acres of forests (<https://uncg.org.ua/en/4-months-of-war-100000-ha-of-ukraine-burnt-up/>). This is likely to alter patterns of gene flow and genetic drift in suburban forests and possibly also in cities; however, the direction of these patterns will need to be tested. Human depopulation due to

**Table 3 | Evolutionary processes associated with armed conflict and war**

<b>Mutation</b>	<ul style="list-style-type: none"><li>• Evidence of an effect of radiation from atomic bombs on mutation rate is inconsistent in humans<sup>83,84</sup> and wildlife<sup>85–87</sup>. However, there is conclusive evidence that exposure to radioactive fallout from nuclear weapons tests carried out in Kazakhstan in the late 1940s to early 1950s roughly doubled germline mutation rate in affected human populations<sup>88</sup>.</li></ul>
<b>Gene flow</b>	<ul style="list-style-type: none"><li>• The spread of horseweed (<i>Erigeron canadensis</i>), ragweed (<i>Ambrosia artemisiifolia</i>) and greater burdock (<i>Arctium lappa</i>) in urban areas of southern and eastern Ukraine are attributed to military invasions<sup>89</sup>.</li><li>• The first observation of sand dropseed (<i>Sporobolus cryptandrus</i>) was in 2014 near the city of Luhansk, Ukraine, with the closest known locations more than 150 km away in Russia. Gouz and Timoshenkova<sup>90</sup> attributed this introduction to the first wave of Russian aggression in Ukraine.</li><li>• The use of military tanks creates vernal pools that provide habitat to fairy shrimp (<i>Anostraca</i>) in Poland<sup>91</sup> and Slovenia<sup>92</sup> and may transport and create new habitat for these organisms during military invasions of cities<sup>92</sup>.</li><li>• War zones disrupt the migration of greater spotted eagles (<i>Clanga clanga</i>) as they move across cities in Eastern Europe<sup>93</sup>.</li></ul>
<b>Selection</b>	<ul style="list-style-type: none"><li>• In Mozambique, phenotypic change related to the birth of tuskless African elephants (<i>Loxodonta africana</i>) has been demonstrated to co-vary with intense poaching related to the 20-year civil war<sup>94</sup>.</li></ul>
<b>Genetic drift</b>	<ul style="list-style-type: none"><li>• Prolonged urban sieges lead to famine among humans, with documented dietary shifts. For example, during the siege of Leningrad (1941–1944), urban inhabitants were reported to eat mice, rats, pigeons and cats<sup>95</sup>, which probably reduced population sizes, increasing the possibility of genetic bottlenecks and genetic drift in these urban species.</li><li>• Famine during war in the Democratic Republic of the Congo increased the desire for bushmeat in cities and led primates to experience a fivefold increase in hunting<sup>96</sup>. Moreover, bushmeat hunting of primates is known to lead to population differentiation<sup>97</sup>.</li></ul>

war may also lead to wildlife reoccupying urban spaces. During the 2022 Russian invasion of Kharkiv, Ukraine, wildlife species including roe deer (*Capreolus capreolus*) and wild boar were reported in urban ‘Sokil’nyky-Pomirky’ Regional Landscape Park after more than a decade-long absence (Y.V., personal observation). This suggests that

Kimoka, Democratic Republic of Congo



Bakhmut, Ukraine



**Fig. 3 | War decreases tree cover in cities, which is likely to decrease gene flow and increase genetic drift.** Wareads to infrastructure instability and heating shortages, leaving urban residents to seek wood in their immediate proximity for heating. Evidence of urban tree felling for heating has been reported in major war

events during 2025 in Kimoka, Democratic Republic of Congo (left) and during 2022 in Bakhmut, Ukraine (right). Credit: left, JOSPIN MWISHA/Contributor/AFP/Getty; right, Laurent Van Der Stockt/Contributor/Getty Images News/Getty.

human depopulation of cities during wartime may alter urban wildlife activity, potentially allowing for habitat connectivity and gene flow (Table 3). Conversely, the displacement of human populations is likely to affect synanthropic animal species in cities affected by war. For example, house sparrows (*Passer domesticus*) became locally extinct in 2022–2024 in the most high-storied residential and industrial areas of the city of Kharkiv, Ukraine, following a massive (up to 40–50% of pre-war population) human exodus from the city during the early months of the full-scale Russian invasion. Only small groups of house sparrows persist in a central market where people continue to sell and buy food (Y.V., personal observation), thereby probably increasing genetic drift in these urban populations. Such a decreasing trend in wild commensals is likely to be further exacerbated in cities exposed to long-term war activities, where food waste is likely to be considerably reduced relative to pre-war conditions in the city. Wars can also produce new forms of urbanization. Such is the case of the Northern Uganda civil war (1986–2006), which displaced over 1.5 million people, and intense humanitarian involvement led to the expansion of local towns, along with long-term displacement camps becoming urban zones themselves<sup>55</sup>. This civil war reshaped depopulated rural areas where agricultural land was grown over with bush<sup>55</sup>, possibly facilitating gene flow in areas with increased vegetation, and restricting gene flow in and around displacement camps.

During war, many militaries practice urbicide (the deliberate destruction of cities, their iconic architecture and their identity). Urbicide can disrupt established evolutionary dynamics that bear some similarities to extreme weather events<sup>56</sup>. For example, the breaching of the dam at Kakhovka Hydropower Plant by the Russian military in June 2023 released the reservoir's vast contents that flooded cities, probably destroying previous evolutionary interactions. Importantly, such events may cause mass mortalities in many species, leading to population bottlenecks. Changes in urban canopy cover in wartime are another example of the long-lasting and far-reaching effect of war on urban evolutionary biology (Fig. 3). As war disrupts public services, people are often forced to seek heat, clean water and food via alternative means<sup>57</sup>. Thus, during the siege of Sarajevo (Bosnia and Herzegovina), three-quarters of all urban trees within the siege line were cut down for firewood<sup>58</sup>. Similar patterns of urban tree use can be observed across other war-torn cities, such as Kimoka in the Democratic Republic of Congo and Bakhmut in Ukraine (Fig. 3). The removal of such substantial amounts of canopy cover from the urban space probably affects wildlife relying on these trees<sup>59</sup>, resulting in disrupted corridors of gene flow and increased genetic drift.

Finally, post-war human displacement and abandonment can leave behind built environments and semi-natural green areas that attract wildlife<sup>60</sup>. These sites may become sanctuaries due to reduced human presence and limited development. For example, a demilitarized zone between North Korea and South Korea was established in 1953 at the end of the Korean War, with laws preventing either side from developing the land. This 250-km-long strip of land is heavily fortified,

with cities on either side of the border, and has become an accidental nature reserve<sup>61</sup> with damaged forests and farmland being reclaimed by wildlife<sup>62</sup>. Recently, Asiatic black bears (*Ursus thibetanus*), Amur leopards (*Panthera pardus orientalis*) and yellow-throated martens (*Martes flavigula*) have returned to the area<sup>63</sup>. However, because of the continued political tension between North Korea and South Korea, minimal wildlife research has been carried out in the demilitarized zone, and it is unknown how this post-war solution has changed the evolutionary potential of the region.

## Future directions

Human decisions are often guided by religion, politics and war—yet these are cultural and social factors that are often not considered when discussing urban evolutionary biology. It is now well established that religious practices have shaped urban biodiversity and there are some well-documented examples on how sacred sites positively co-vary with high fauna and flora diversity<sup>64</sup>. Here we argue that such practices also generate downstream evolutionary change in urban wildlife (Table 1). Protecting these sites thus allows for the maintenance of a genetic repository of urban flora and fauna in the long term, maximizing their evolutionary potential in the long term. We also have a clear demonstration of the extent to which racist urban stratifications in the USA have had major downstream evolutionary consequences on urban wildlife<sup>37</sup>, yet similar comparisons of the evolutionary effect of contrasted political regimes are so far untested. We, thus, hypothesize that the communist-to-capitalist political transition occurring after 1989 across the entire European continent east of the Iron Curtain may have had similar detrimental effects on gene flow and genetic diversity as segregation on urban wildlife in the USA<sup>36,37</sup>. Finally, there are current military conflicts in which the collection of evolutionary data is impossible. Ongoing military conflicts have progressed over the course of our writing, limiting the extent to which we could discuss evolutionary outcomes associated with these conflicts. Community science and digital data methods can facilitate data collection in war zones and these methods can complement existing approaches and provide a wide range of near-real-time digital metrics for future analyses (for example, remote sensing data reports urbicide in Gaza (<https://beiruturbanlab.com/en/Details/1977>)). In the post-war stage, including an evolutionary biology perspective to the planning of green areas in cities is essential to maximize the evolutionary potential of urban wildlife.

Our past decisions, most often made without considering evolutionary processes, have largely shaped the present state of urban biodiversity. We acknowledge that much of the research on evolution in cities has been conducted in the USA and Western Europe<sup>65</sup>. This bias needs remedy. Achieving this goal requires global efforts across diverse scientific fields working together to determine the effects of religion, politics and war on evolution and how these factors will shape the evolutionary trajectory of urban wildlife in cities worldwide over the next century. In light of current evidence, we urge urban planners



**BOX 2**

# Testable hypotheses for future research furthering our understanding of the effect of religion, politics and war on urban evolutionary biology

## Religious influence on urban evolutionary biology

Hypothesis 1: Religious differences in attitudes towards wildlife lead to distinct evolutionary dynamics in urban wildlife, with different religious orthodoxies, traditions or practices driving divergent evolutionary trajectories in species populations.

Hypothesis 2: Divergent evolutionary histories influenced by religious practices create feedback loops, where biological changes in urban wildlife populations further reinforce or alter those religious practices.

## Harnessing religious movements for evolutionary potential

Hypothesis 3: Religious movements that promote environmental stewardship can be harnessed to maximize the evolutionary potential of urban wildlife by encouraging practices that support biodiversity, habitat preservation and gene flow in urban environments.

## Political influence on urban ecosystems and evolution

Hypothesis 4: Political forces, such as policies related to urban planning (for example, redlining in the USA or the communism-to-capitalism transition) result in distinct urban ecosystems that lead to measurable differences in gene flow and genetic drift in populations of urban wildlife.

Hypothesis 5: Political history, including governance models and land-use policies, substantially affects the genetic diversity and evolutionary potential of urban species through the creation of fragmented or continuous habitats.

## Urban greenbelts and garden allotments

Hypothesis 6: Urban greenbelts and garden allotments maintain evolutionary potential in urban wildlife by providing critical habitats for species survival, gene flow and local adaptation in otherwise highly modified urban environments.

## War and extreme weather as evolutionary frameworks

Hypothesis 7: Wartime conditions, including habitat destruction from bombing or military occupation, create evolutionary pressures on urban wildlife similar to those observed during extreme weather events, leading to rapid adaptation or population bottlenecks and resulting in strong genetic drift.

## Environmental peace-building in post-war recovery

Hypothesis 8: Environmental peace-building efforts that focus on restoring ecosystems post-war can be expanded to promote the evolutionary potential of urban wildlife, leading to increased biodiversity and resilience in recovering urban environments.

## iEcology and community science in documenting war's impact

Hypothesis 9: iEcology and community-driven science projects can effectively document the effect of war on urban ecosystems and provide valuable data on habitat fragmentation, evolutionary processes and species decline caused by conflict.

## Physical political barriers and genetic differentiation

Hypothesis 10: Physical political barriers, such as walls or restricted zones, consistently lead to genetic differentiation in urban wildlife, creating isolated populations with reduced gene flow and increased genetic drift, particularly in species with limited dispersal capabilities.

## City-specific evolutionary processes

Hypothesis 11: Biological evolutionary processes differ between groups of cities based on their unique cultural legacy in terms of religious, political and historical characteristics, which contributes to the unexplained variance in urban evolutionary biology processes.

to consider evolutionary interactions, especially the scope for facilitating gene flow between patches of urban green spaces to maximize the evolutionary potential of urban wildlife when designing or remodeling cities. Moreover, we view the consideration of social-political processes that shape cities as necessary to ensure the health of people and wildlife in the long term.

Finally, the challenges of the climate crisis invoke the necessity of new collaboration between natural scientists, social scientists and humanities. As this REview has argued, urban evolutionary processes may be shaped by religious differences, political tensions and war, and further study is needed to understand the specifics of how these social-political processes shape evolutionary trajectories. Social sciences are readily exploring interspecies connections and interdependence in an ecological perspective, inferring: the formation of new ecologies around environmental degradation; intersections of Indigenous and ecological science; and how the histories of colonialism, racism, industrialism and the unlimited growth imperative of capitalism are deeply connected with ecological concerns<sup>66</sup>. Evolutionary biologists can learn from these lines of thought and research, which offer new and critical modes of engagement with evolutionary processes. Box 2 summarizes hypotheses amenable for testing in regards to how human behaviors related to religious practices, politics and war shape the urban landscape and evolutionary change in urban organisms. A greater understanding of these interactions, illustrated and ultimately quantified with case studies from across the globe, is crucial to

gain insight and predictive power into how urban systems will develop over time.

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## Author contributions

M.S. conceived the paper with input from E.J.C. and C.J.G. E.J.C. and M.S. collaboratively developed the overarching themes, and E.J.C., A.E.C., Z.J., H.K. and J.M.-S. coordinated the writing of individual sections. All authors contributed to the development of the paper, including literature reviews and writing.

## Competing interests

The authors declare no competing interests.

## Additional information

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