Reviewing the role of urbanisation in facilitating the introduction and establishment of Invasive Animal Species

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Abstract

While urbanisation is often associated to a loss of biodiversity, non-native invasive animal species are strikingly successful in urban landscapes. As biological invasions are recognised to have detrimental environmental, social and economic impacts, extensive understanding of the interactions between invasive species and the abiotic and biotic environment is necessary for effective prevention and management strategies. However, the mechanisms underlying the success of invasive animals in urban environments are still poorly understood. This literature review aims at summarising and explaining the mechanisms enhancing biological invasive potential in urban environments, by both isolating and interlinking the abiotic and biotic drivers involved. Ultimately, providing a first conceptual review of the role of urbanisation in the introduction, establishment, and potential further spread of invasive animal species through anthropogenic landscapes. Moreover, we provide a review of the current state of literature, and identify important knowledge gaps, such as the scarcity of studies investigating socio-economic spatial patterns in the presence and abundance of invasive species, or literature investigating the role of urban landscapes in adaptive evolution of invasive animal species.

1. INTRODUCTION

Invasive animal species (IAS) are non-indigenous species (NIS) that have established a large self-sustaining population, maintained over multiple generations and dispersed away from its point of introduction (Santana Marques et al., 2020; Colléony and Shwartz, 2020)). Previous studies have suggested that IAS can be strikingly successful in urban areas (Santana Marques et al., 2020; Hima et al., 2019). On one hand, cities can supply constant resource availability throughout the year and predation is often relaxed in urban areas (Carthey and Banks, 2018; Santana Marques et al., 2020; García-Arroyo et al., 2020). On the other hand, cities are also associated with a range of pollutants, such as light at night, noise, chemicals, heavy-metals, increased ambient temperatures, habitat loss and fragmentation, and novel impervious surfaces and structures (Buchholz and Kowarik, 2019; Santana Marques et al., 2020; McMahon et al., 2017; Harrison and Winfree, 2015). Whilst native species are consequentially negatively associated with urban land cover (Botham et al., 2009), both IAS richness and abundance are positively correlated to increasing urbanisation, especially in invertebrates (Cadotte et al., 2017). In fact, many of the most common urban species are invasive (Shochat et al., 2010).

IAS alter ecosystem function and native community structure, promoting simplification of communities and biotic homogenisation (Barsotti et al., 2021; Hima et al., 2019). Native species are reduced or displaced through competition for resources and breeding sites, predation and hybridisation (Colléony and Shwartz, 2020; Barsotti et al., 2021; García-Arroyo et al., 2020). Additionally, IAS may carry harmful pathogens and parasites (Ficetola et al., 2007; Hernández-Brito et al., 2020; Haag-Wackernagel, 2004), and can be serious agricultural pests (Godefroid et al., 2020; García-Arroyo et al., 2020; Cesari et al., 2018). Some IAS may also cause damage to infrastructure (García-Arroyo et al., 2020) and provoke human and animal allergic reactions (Godefroid et al., 2020). Knowledge on the extent of the impacts of some of the globally most common IAS are still lacking (García-Arroyo et al., 2020).

Because of the widely reported effects of IAS, biological invasions are now internationally recognised to have detrimental environmental, social and economic impacts (Roy et al., 2014; Colléony and Shwartz, 2020; García-Arroyo et al., 2020; Padayachee et al., 2017), and are listed as the second major driver of species extinction (García-Arroyo et al., 2020), particularly for vertebrate populations (Barsotti et al., 2021). Still, biotic range shifts have been happening at unprecedented rates world-wide for some decades (Godefroid et al., 2020). Prevention is the most cost effective and environmentally desirable defence strategy against IAS (Roy et al., 2014; Wittenberg and Cock, 2001). Effective prevention relies on understanding biological invasions and the interactions between IAS and the abiotic and biotic environment (Suppo et al., 2018). Yet, the mechanisms underlying the success of IAS in urban environments are still poorly understood (Santana Marques et al., 2020). It is difficult to isolate mechanisms influencing invasion potential, as these are often confounded with different conditions influencing vulnerability to invasions (Crooks et al., 2011).

This review aims at summarising and explaining the mechanisms enhancing biological invasive potential in urban environments; and ultimately the role of urbanisation in the establishment and spread of IAS. After a systematic literature search, a total of 59 studies were selected and reviewed, building a comprehensive collection of knowledge involving the introduction pathways of IAS and urbanisation, and the abiotic and biotic urban drivers implicated in the facilitation of establishment of invasive species. Moreover, the characteristics of urban animals leading to their success in anthropogenic landscapes were taken into consideration to better understand the success of IAS in urban environments.

2. LITERATURE SEARCH AND CRITERIA FOR INCLUSION

A first literature search of the Web of Science Core Collection (WoS), Scopus and University of Glasgow (UofG) Library search engine was performed in December 2020. The search aimed to provide comprehensive literature on invasive animal species in urban environments, aiding in identifying major urbanisation mechanisms/drivers involved in the establishment and spread of IAS. We conducted this search using the keywords (KW): (1) KW=(“urban” AND “biological invasive potential”) and (2) KW=(“urban” AND “invasive species”). 22 papers were thus obtained, including comprehensive reviews on the topic as well as focused case study papers. Once mechanisms involved were identified, the research was continued (January-March 2021) on the same databases (databases time-frame covered: 1990-present): (3) KW=(“urban” AND “invasive species” AND (“introduction” OR “pathway” OR “exploiter”

OR “breeding” OR “nesting” OR “resources” OR “resource availability” OR “pollution” OR “climate” OR “homogenisation” OR “biotic resistance” OR “predation” OR “pathway” OR “vegetation” OR “water availability” OR “pollination” OR “spread”)), resulting in 1,685 results on WoS, 11,382 on scopus and 44,706 on UoG Library; and (4) KW=(“urban” AND “animal assemblages”), resulting in 402 results on WoS, 26,220 on Scopus and 56,449 on UoG Library. Further useful papers were identified from the references of papers obtained from searches (1), (2), (3) and (4). To comprehensively include literature across taxa, a further search was performed, in January-March 2021: (5) TS=(“urban” AND “invasive species” AND (“bird” OR “avian” OR “reptile” OR “amphibian” OR “invertebrate” OR “marine” OR “mammal” OR “rodent”)), producing 523 more results on WoS, 27,120 on scopus and 26,568 on UofG Library.

As the interest was in exploring the role of urbanisation in facilitating the introduction and establishment of IAS, studies were included if containing relevant and insightful information on urban drivers involved, relevant information on urban ecology and urban animals, discussions on the topic of invasive alien species in urban environments, relevant literature on biological invasions and invasion pathways, and exemplar case studies. Consequentially, a total of 59 papers were selected and reviewed. The resulting literature reviewed can be found summarised and organised by urban drivers (abiotic and biotic), with specified taxon in focus and world region where the studies were performed, in Table S1 of the Supplementary Materials. The literature reviewed spans a wide range of taxonomic groups, although avian and terrestrial invertebrate arthropod species receive more far attention (23.7% and 20.3% of reviewed literature respectively), and aquatic species and herpetofauna are understudied (see Figure 1.a.b.). Studies performed in Europe and North America composed the largest bulk of literature (30.5% and 20.3% respectively), with South America and the Middle East (both 3.4%) particularly lacking behind. Studies taking place in Panama were considered as North or South America if data-collection occurred North or South of the Panama Channel respectively.

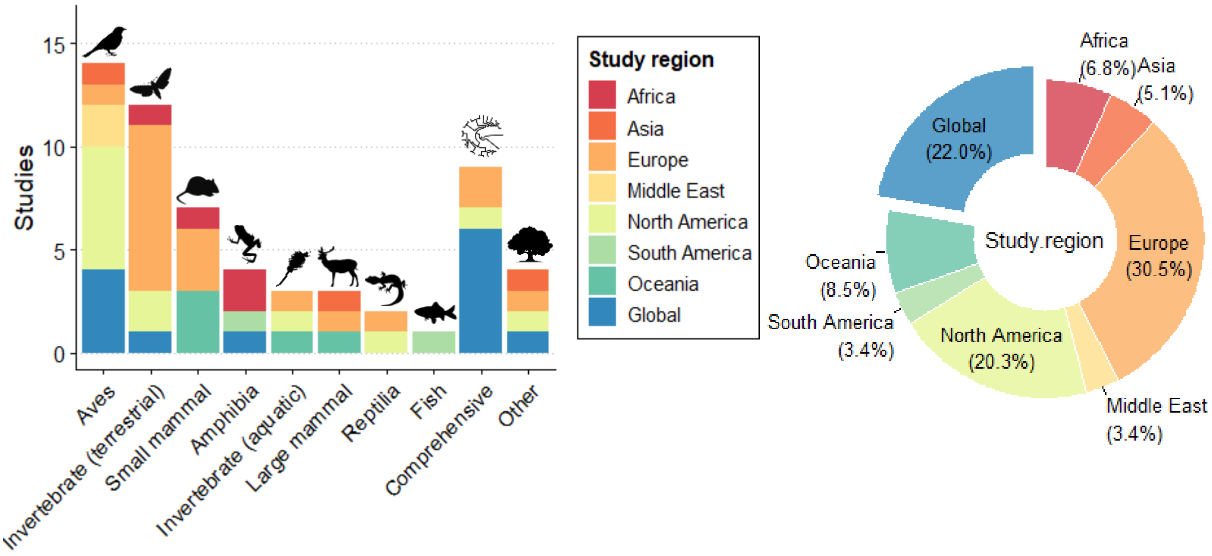

Figure1.a.b. – On right, (**a**) descriptive summary of reviewed number of studies per taxonomic groups, subdivided by world region provenance of studies. On left, (**b**) proportions of reviewed literature by world region provenance. (Image sources: Google Images).

3. THE INTRODUCTION AND DISPERSAL OF INVASIVE ALIEN SPECIES

A large proportion on alien species introduction is unintentional (Suppo et al., 2018), mostly through commercial hubs at transport networks (i.e. seaports, airports, road and river transport networks) (Hima et al., 2019; Godefroid et al., 2020). Travel and tourism are also to be accounted for (Padayachee et al., 2017). This is referred to as the “stowaway” pathway (Padayachee et al., 2017). Insects (especially social insects) are the most popular invaders world-wide; their small size easily grants them accidental transportation, and r-selection life-strategy allows for high propagule pressure (i.e. quantification of the organisms introduced into the community and number of introduction events) (Suppo et al., 2018; Banha et al., 2017). Small mammals (e.g. rodents) are also typically introduced as stowaways (Anderson, 2009). Otherwise, invertebrates are often introduced through the “contaminant” pathway (Padayachee et al., 2017), where IAS are transported unintentionally together with an intentionally transported commodity (e.g. commensal species, food, plants, etc). The contaminant pathway differs from the stowaway pathway by being predictable from knowledge of the shipped commodities and their shipping routes (Hulme et al., 2008). Non-native ornamental vegetation for urban landscaping and private gardens can often carry highly invasive and undesired species, such as the oak processionary moth (*Thaumetopoea processionea*) (Godefroid et al., 2020). Horticultural activities and transportation of timber or fresh/live comestibles transportation may also introduce exotic pests (Marzluff, 2005; Hulme et al., 2008).

Most vertebrate IAS are introduced intentionally, for landscape and fauna improvement or above all through pet trade, to pet shops and homes (Padayachee et al., 2017; Hernández-Brito et al., 2020). Spread is by escape and unaided dispersal (Padayachee et al., 2017), or release (Hulme et al., 2008). The exotic pet trade is key for avian invasions (García-Arroyo et al., 2020), and pet release is considered the most important pathway for reptiles, such as the highly invasive red-eared slider turtle (Banha et al., 2017) or Burmese python (Orzechowski et al., 2019).

Disturbance from agricultural intensification and urbanisation causes native fauna to decline (Marzluff, 2005; Colléony and Shwartz, 2020), particularly specialist and susceptible species (Colléony and Shwartz, 2020; Padayachee et al., 2017). Contrastingly, IAS propagule pressure in urban areas can be relatively high (Banha et al., 2017; Cadotte et al., 2017). With over 55% of the human population now living within urban areas (Ritchie and Roser, 2018), cities are hubs of movement of people and goods (Padayachee et al., 2017). Thus, cities are often the first and most prominent introduction point (Hernández-Brito et al., 2020; Cadotte et al., 2017; Padayachee et al., 2017). Urban settlements are interconnected by transport corridors, both aquatic (i.e. rivers and canals) and terrestrial (i.e. roads) (Botham et al., 2009), facilitating the natural and un-aided dispersal of IAS to the surrounding areas and other urban centres. IAS can easily travel through their preferred urban and peri-urban conditioned environments avoiding the more difficult and unfitting native natural conditions. For instance, the Asian tiger mosquito (*Aedes albopictus*) has successfully reached continental and global expansion by both dispersing naturally alongside roads and long-distance human-aided dispersal (Sherpa et al., 2020); as stowaway in passenger cars (Eritja et al., 2017) and through importation of goods, such as used tires. *A.albopictus* is a disease vector for dengue and dengue haemorrhagic fever (Knudsen et al., 1996).

4. WHAT MAKES AN URBAN ANIMAL: A TRAIT-BASED APPROACH

Recognition of the basic characteristic of the urban environment, and what makes a potential urban animal, is crucial to understanding invasive success on IAS in urban environments (Suppo et al., 2018; Kark et al., 2007). Acting as a filter of native biodiversity (Alberti, 2015; García-Arroyo et al., 2020), the urban environments weeds out the more specialised and susceptible fauna (Colléony and Shwartz, 2020; Padayachee et al., 2017; Marzluff, 2005). A process reminiscent of invasion biology, where a few species take over the habitat and dominate in abundance (Kark et al., 2007; Colléony and Shwartz, 2020). Urban fauna can be placed under three categories: urban avoiders, exploiters, and adapters (Kark et al., 2007). Urban avoiders are native species that cannot occur in disturbed city areas as incapable of adapting to the urban environment (Colléony and Shwartz, 2020; Kark et al., 2007). Urban adapters capitalize on urban resources (Colléony and Shwartz, 2020) and thrive at intermediate levels of urbanisation (e.g. suburbs); they can be both native and invasive (Kark et al., 2007). Where urbanisation is most intense, urban exploiters reach high densities (Gering and Blair, 1999; Colléony and Shwartz, 2020). Exploiters can benefit from urbanisation, by adapting to exploit the urban environment (Colléony and Shwartz, 2020) and forming commensal relationships with humans, frequently becoming dependent on urbanisation and ubiquitous globally (Kark et al., 2007). Urban exploiters are most often native synanthropic species or exotic (Shochat et al., 2010; Colléony and Shwartz, 2020).

Urban exploiters have advantageous life-history traits that respond positively to the “urban filter” (Gering and Blair, 1999; Santana Marques et al., 2020). Sociality improves foraging ability (improved localisation and communication of food sources) (Kark et al., 2007; Shochat et al., 2010), avoidance of predators, and eases competition. Urban species are also commonly sedentary, as sedentary avian species in a relatively stable urban environment are likely to monopolise the usually scarce nesting sites available in cities whilst migrants are away (Kark et al., 2007). In fact, an animal’s breeding ecology is in itself a key factor for urban success (Kark et al., 2007; Gering and Blair, 1999). Diet plays an important role in urban success (Kark et al., 2007). Food resources can be increased under urbanisation, but are less varied and often novel (Carthey and Banks, 2018; Colléony and Shwartz, 2020). For bird species, granivores, fructivores and especially omnivores (Jerusalem: 50% of urban-downtown avian species) are favoured, whilst invertebrate feeders decrease; ground invertebrate-feeders persist (Kark et al., 2007). Urban successful species are usually ecological generalists (Colléony and Shwartz, 2020) with affinity for feeding innovations and adapting to new foods, such as scavenging on human refuse. Behavioural flexibility (Kark et al., 2007) and dominant or aggressive interspecific behaviours allow for effective use of resources and upper-hand in competition for food and breeding patches (Shochat et al., 2010; Ficetola et al., 2007).

Urban-successful IAS are commonly urban exploiters (Shochat et al., 2010; Kark et al., 2007), and typically possess the life-history traits desired for invasive success (Gering and Blair, 1999). Human-commensal and intentionally human-introduced species may have the further advantage of pre-adaptation to human-modified environments (Kark et al., 2007). House sparrows and rats have been associated with humans for millenniums (García-Arroyo et al., 2020; Anderson, 2009). For instance, house sparrows are ecologically and physically plastic, and aggressive towards both conspecifics and heterospecifics (García-Arroyo et al., 2020). Rats are generalist omnivores that, through high evolutionary potential by high fecundity and rapid generations, have achieved immunity to poisons (Collins et al., 2000; Anderson, 2009). IAS may also act as vectors of parasites (Hernández-Brito et al., 2020) and pathogens from their native range (e.g. American bullfrog and chytridiomycosis (Ficetola et al., 2007)). Carrying disease may be advantageous towards invasive-success when natives occupying their niche are vulnerable to the same disease: for example, asymptomatic invasive American eastern grey squirrel widely displace native Eurasian red squirrel by fatal Squirrel Pox Virus infections (Chantrey et al., 2014).

5. THE URBAN HABITAT AS FACILITATOR OF IAS

Urban landscapes are uniquely altered habitats (Cadotte et al., 2017; Collins et al., 2000), where abiotic and biotic conditions are artificially maintained, contrasting to the surrounding natural environment (Alberti, 2015). Deep modifications are produced on the habitat structure, local seasonal variation and temporal variability of resources, water systems as well as climate and temperature (Alberti, 2015; Collins et al., 2000). The structural and biotic conditions also prompt changes in soil structure and nutrient dynamics of the ecosystem; whilst some nutrients are mobilised (e.g. phosphorus and nitrogen pollution nutrient pollution), others are depleted (Cadotte et al., 2017; Collins et al., 2000; US EPA, 2013). Green spaces are reduced and patchy, replaced by novel anthropogenic surfaces and structures (Colléony and Shwartz, 2020; Buchholz and Kowarik, 2019; Groffman et al., 2014). These remaining green spaces lack tree cover, increasing the amount of sun-light to the ground and thus promoting growth of weedy vegetation (Cadotte et al., 2017). Ground cover is overall largely simplified, often purposely maintained as homogenous short grass (Marzluff, 2005; Groffman et al., 2014). Native vegetation is scarce in cities (Kark et al., 2007; Marzluff, 2005), with exotic vegetation being intentionally introduced as ornamental plants or for horticulture (Godefroid et al., 2020; Groffman et al., 2014; Hulme et al., 2008). In the UK, plants introduced after the 1500 dominate urban assemblages, whilst archeophytes are no longer strongly associated to urban land-cover (Botham et al., 2009).

Such unique and novel habitat characteristics are hostile for many, but become beneficial to IAS that can tolerate the unconventional conditions and capitalise on the many offered opportunities (Cadotte et al., 2017; Collins et al., 2000). Moreover, increased forest edge effect by fragmentation of natural habitats and high-within habitat heterogeneity, combined with novel anthropogenic disturbances maintaining habitats at an early successional stage, suggests a fast generation of unique and colonisable niches (Alberti, 2015; Padayachee et al., 2017; Marzluff, 2005). Examining the interactions between the abiotic environment and IAS is important for understanding biological invasions (Suppo et al., 2018).

5.1. Climate and urban heat island effect

The most important environmental factor facilitating biological invasions is climate (Vimercati et al., 2018; Ficetola et al., 2007). Invasion potentials are often predicted based on the affinity of the regional climate and the realised niche of the targeted IAS in its native range (Ficetola et al., 2007). Urbanisation often ameliorates the local climate (Hernández-Brito et al., 2020; Collins et al., 2000), opening new niches that IAS can exploit. The most influential climatic factor is temperature, particularly for ectotherms and species with temperature-dependant sex determination (Banha et al., 2017; Javal et al., 2018; Ficetola et al., 2007). Due to decades of human activities, such as burning of fossil fuels, and the reduction of photosynthetic organisms (US EPA, 2015; Santana Marques et al., 2020; Collins et al., 2000), carbon dioxide concentrations in cities are far higher than the global average. This causes temperatures within cities to significantly exceed those of the surrounding areas, a process known as the “urban heat island” effect (Collins et al., 2000; Alberti, 2015). The heterotrophic nature of urban systems is also an important factor: a typical city is estimated to convert into heat 70 times more usable energy per square meter than its close natural surroundings (Collins et al., 2000). Precipitation, another important climatic feature (Ficetola et al., 2007), is also impacted by anthropogenic activities. Regional precipitation patterns are affected by the regular fluctuations of weekly cycles of air pollution, air carbon-monoxide and ozone levels accumulating during the working weekdays, leading to a higher probability of precipitation during weekends (Collins et al., 2000; Cerveny and Balling, 1998). The milder microclimate of cities extends growing seasons in temperate regions, while irrigation in arid tropical and subtropical regions prevents extended droughts (Alberti, 2015). These conditions favour tropical non-indigenous animal and plant species (Cadotte et al., 2017; Hernández-Brito et al., 2020; Alberti, 2015). Human utilities also become involved in ameliorating tolerance to extreme climates. For instance, rosy-faced lovebirds in Phoenix (USA) use relief-air vents on building surfaces to cool down in summer, and European starlings perch atop of chimneys in lower winter temperatures (Mills and McGraw, 2021).

5.2. Novel structures and surfaces

Urbanisation gives rise to novel structures, convenient to humans but composed of impractical, and often also rough and unpleasant materials; such as concrete, metal or plastic/glass (Gering and Blair, 1999; Groffman et al., 2014). Regardless, anthropogenic structures provide excellent breeding and roosting/nesting opportunities for many IAS (Kark et al., 2007). Dispersal and breeding of invasive mosquitos is largely dependent on anthropogenic conditions; demanding standing water-filled artificial containers (i.e. used tired, flowerpots, abandoned bottles and jars) (Sherpa et al., 2020) to deposit their eggs and mature to adulthood (Eckhoff, 2011). Moreover, the degeneracy of the habitat allows for high predictability and visibility of food for urban exploiter generalists (Anderies et al., 2007; Carthey and Banks, 2018). Increased open spaces and absence of tree cover are particularly beneficial for air mobile organisms. Urban landscapes and contained structures are increasingly similar across different human settlements, advantaging species pre-adapted to human structures in invading other regions containing humans (Kark et al., 2007; Crooks et al., 2011). This is usually the case for exotics introduced via the pet trade, as they have been adapted or exposed to anthropogenic conditions (Crooks et al., 2011).

5.3. Availability of breeding sites

The variety of breeding locations (e.g. nest/den opportunities, fish and amphibian spawning grounds) is skewed in urban environments (Cadotte et al., 2017). Native vegetation is scarce, dead trees are removed (Kark et al., 2007), and wetland or water systems are often absent or largely diminished and altered (Groffman et al., 2014). Ground nesting is also disfavoured by the vast amount if impervious surface, and the portion of ground unused by humans is threatened by predatory domestic animals (i.e. cats and dogs) (Kark et al., 2007). Hence, the ability to exploit novel breeding sites is a key factor for urban success (Kark et al., 2007; Gering and Blair, 1999). Black rats are highly flexible nesters; nesting in tree cavities, on the ground and inside buildings (Dowding and Murphy, 1994; Cox et al., 2000). Buildings translate to cliff-sides or rock, so avian cliff, cavity and rock nesters are advantaged. For instance, feral pigeons see cities as habitats rich in nesting availability as they descend from rock doves (*Columba livia*), which naturally nest at seaside cliffs. With their native predators removed, they have become one of the most successful and cosmopolitan bird species, having invaded cities in every continent (excluding Antarctica) (Goerlich-Jansson, 2020). Another highly successful invasive urban bird is the house sparrow, as their aggressive behaviour aids effective nesting when competition for resources is high (García-Arroyo et al., 2020). Monk parakeets (*Myopsitta monachus*; IAS in North America and Western Europe, Asia, Africa and some oceanic islands) instead avoid competition for nest sites altogether, by building their own nests (Hernández-Brito et al., 2020). Canopy nesters are also common in cities and suburbs (Kark et al., 2007). Furthermore, exotics make use of introduced non-native vegetation they may be pre-adapted to for roosting and breeding (Gering and Blair, 1999; Shochat et al., 2010; Godefroid et al., 2020).

5.4. Habitat homogenisation, aquatic features and water availability

Urban habitats are designed to best fit human activities (Alberti, 2015). Regardless of within-habitat heterogeneity relying partly on the choice of individual home owners (Colléony and Shwartz, 2020), different anthropogenic habitats across the globe are still highly similar. More similar to each other than their respective natural environment (Alberti, 2015). Recurring structural patterns such as altered plant ecology by replacement of natural vegetation assemblages by turfgrass, popular and horticultural plant species, as well as the addition of impervious surfaces (e.g. asphalt) alter the local soil ecology via changes in soil moisture and organic matter. In naturally arid environments soil organic matter is greatly increased and in humid environments it is slightly decreased. Other structural aspects of the urban environment that can have ecological impacts are roads and residential landscape planning (Groffman et al., 2014). Continental and global homogenisation reduces extreme and unfavourable environments, improving net ecosystem compatibility for IAS (Ficetola et al., 2007; Vimercati et al., 2018; Barsotti et al., 2021).

Water availability and aquatic features of an ecosystem are limiting factors for many species (Barsotti et al., 2021), particularly for aquatic or semi-aquatic organisms needing permanent surface water arrangements for breeding or foraging purposes (Ficetola et al., 2007). Urbanisation deeply modifies the structure, distribution and character of the hydrography of natural landscapes. Introduction of new aquatic systems and/or removal or alteration of locally abundant systems leads to a homogenisation of habitats towards an intermediate ideal between wet and dry (Figure2) (Groffman et al., 2014; Collins et al., 2000). In temperate or humid zones there is usually a loss of natural channel networks, reduction of lakes and wetlands and redirection of rivers/streams, with simultaneous creation of artificial canals, ponds and reservoirs for flood control, drainage and fill, water supply or recreation. In arid areas surface water systems are introduced for more productive (and aesthetic) land (Groffman et al., 2014). Moreover, water in naturally arid biomes is made available by artificial ponds and irrigation in gardens, suburban area lawns and agricultural grounds (Vimercati et al., 2018; Alberti, 2015); in the USA suburban private lawns were found to make the largest part of all urban land cover (Groffman et al., 2014). The guttural toad (*Amietophrynus gutturalis*), endemic to more humid regions of southern Africa, have spread to drier African areas. Though they still show physiological responses to the abiotic stressor and dryness, sheltering by human-created water sources (e.g. artificial ponds) and irrigation allows survival and selection to conquer the new environment (Barsotti et al., 2021).

5.5. Anthropogenic resources

IAS are welcomed into cities by an abundance of resources provided by humans (Hernández-Brito et al., 2020; Carthey and Banks, 2018); which they can forage for efficiently given the lowered predation pressure (Shochat et al., 2010). Resource availability in urban forests can be 2-3 times higher than in rural forests for generalist avian species, and in city habitats possibly 4 times higher (Shochat et al., 2010). This surplus is credited to both intentionally (e.g. bird feed) and unintentionally (garbage, ornamental and agricultural vegetation) human-provided resources (Colléony and Shwartz, 2020). Species in downtown areas rely particularly on human refuse. Diet is a limitation, as certain types of resources are reduced by urbanisation. Herbivores, granivores and fructivores prevail over carnivores and insectivores, and generic omnivores are most favoured (Kark et al., 2007). IAS quickly grow bold and efficient when foraging on urban resources, with little fear of humans, but retaining neophobic behaviour towards unfamiliar stimuli, thus limiting risk from unknown toxins, while maintaining the need to expend energy exploring new areas and food sources (Carthey and Banks, 2018).

The introduction of non-native vegetation is greatly beneficial to IAS feeding (Gering and Blair, 1999; Colléony and Shwartz, 2020). Invasive pollinators exploit ornamental flowering plants similar to those of its native range, if not from its native range (Cadotte et al., 2017). Some natural ecosystems are not characterised by abundance of fleshy fruit, but fructivorous IAS can rely on introduced non-native fruit bearing vegetation (Collins et al., 2000; Cesari et al., 2018). Urbanisation can also increase food supply indirectly. Organic pollution as a result of contamination from sewage in urban streams increases abundance of highly nutritious chironomid larvae, a great source of food for invasive fish species. In Rio de Janeiro, Brazil, invasive guppy fish (*P. reticulata*) reached 26 times higher densities and larger body sizes in disturbed urban streams than undisturbed rural streams. Physical condition and fecundity were also higher. Resource availability was high enough to negate predation pressure when other fish were present in the stream (Santana Marques et al., 2020).

5.6. Chemical and heavy metal pollution

In marine systems, urban harbours bays and estuaries (Crooks et al., 2011) usually suffer from aquatic heavy-metal and chemical pollution, manly from urban/industrial/agricultural runoff, sewage and industrial waste discharge, antifouling and preservative products (Varó et al., 2015; Crooks et al., 2011). Yet these very systems are prone to biological invasions (McKenzie et al., 2011), more than open coastal areas (Crooks et al., 2011). Propagule pressure is complicit, as urban estuaries/harbours/bays are often introduction sites of IAS (e.g. stowaway pathway through shipping trade) (McKenzie et al., 2011; Crooks et al., 2011). But aquatic pollution has also been positively associated with a range of marine IAS (McKenzie et al., 2011). Copper is a common polluting heavy metal, lethal to marine invertebrates in high concentrations (Crooks et al., 2011). Copper exposure causes declines in abundance and diversity (>40%; Crooks et al., 2011) of natives, but IAS either show no change or even increase in abundance, which suggests increased tolerance to heavy-metal pollution (Crooks et al., 2011; McKenzie et al., 2011). For instance *Watersipora subtorquata*, an invasive Bryzoan typically introduced via hull fouling, was found to possess copper tolerance as a genetically heritable trait (McKenzie et al., 2011). Higher levels of heavy-metal pollution induced production of larger, more pollution-tolerant larvae. Larger larvae can also swim longer, grow faster and reach reproductive maturation earlier, all of which confer advantages in a polluted environment. But large larvae are also energetically expensive to produce, leading to lower fecundity. The inconsistent and fluctuating levels of heavy metal pollution exposure of urban systems selects for plasticity in variability of larvae size production, which has been suggested as an underlying mechanism of increased copper tolerance (McKenzie et al., 2011). Such findings may reflect an anthropogenically-induced selective process that occurs in urban settings. Alternatively, selection of individuals with pre-adaptation to high copper concentration may occur during the transport phase (Crooks et al., 2011).

Tolerance to anthropogenic contaminants has also evolved in terrestrial IAS resisting pesticides and herbicides (McKenzie et al., 2011). Invasive *Artemia franciscana* was found to be more tolerant to chlorpyrifos (an organophosphate pesticide) than its native sibling species *A. parthenogenetica*. Both species showed tolerance to higher ranges of the toxicant, but the fecundity of *A. franciscana* was less affected. Fecundity is an out-competitive advantage leading to colonisation and establishment (Varó et al., 2015).

6. INTERSPECIFIC INTERACTIONS AND IAS IN URBAN HABITATS

6.1. Community structure and biotic homogenisation

A key theme in urban ecology is ecosystem health. Cities are islands of highly simplified and weakly integrated biological communities that are often poor in native (including endemic) species. These factors facilitate biological invasions by opening niche space while relaxing or removing biotic resistance (predation and competitive interactions) (Cadotte et al., 2017; Shochat et al., 2010; García-Arroyo et al., 2020; Alberti, 2015). Anthropogenic disturbances weed out sensitive species, and altered and degraded habitat and abiotic conditions filter local assemblages to a selected few (Padayachee et al., 2017; Alberti, 2015; Cadotte et al., 2017). Native bird diversity is generally negatively associated with urbanisation, albeit multiple urban bird diversity studies have found overall bird biodiversity (natives and non-natives) to peak at intermediate urban levels (Marzluff, 2005; Batáry et al., 2018). On the greater urbanised gradient, loss of green spaces, reduction of native vegetation and overall habitat simplification removes niches, skew breeding opportunities and variety of resources, and compromises life-history strategies; disfavouring specialised and susceptible species (Colléony and Shwartz, 2020; Marzluff, 2005; Cadotte et al., 2017; Kark et al., 2007). Contrastingly, intermediate urbanisation may provide favourable conditions of resource abundance and relaxed predation, whilst retaining reasonable green spaces and native vegetation cover (Batáry et al., 2018) and increasing forest edge effect through within-habitat heterogeneity (Alberti, 2015; Marzluff, 2005; Padayachee et al., 2017).

Nonetheless, loss of native habitat land-cover (e.g. forest) is strongly associated with local extinctions (Marzluff, 2005); coming with a dispossession of a variety of resources and breeding sites (García-Arroyo et al., 2020). Anthropogenic settlements and commodities (e.g. transportation channels; roads) and agricultural/horticultural lands cleave and perforate natural habitats; creating a patchy and fragmented habitat (Marzluff, 2005; Groffman et al., 2014). This severing of connections complicates dispersal, particularly penalising less mobile organisms (Alberti, 2015). Habitat loss and fragmentation also poses a problem for high trophic level predators, which typically require large territories, with sustained prey populations. Moreover, humans have tampered extensively with the trophic ecology of human-inhabited regions, removing predators or sequestering land from herbivores for pastures (Jiang et al., 2016; Nilsen et al., 2007). Urbanisation also comes with new threats (e.g. window collisions, cat predation, moving cars) (García-Arroyo et al., 2020) and . The resulting depauperate assemblages are dominated by few dominant urban exploiters, usually synanthropic natives or IAS (Shochat et al., 2010; García-Arroyo et al., 2020).

As a result of urban selective pressures and the expansion of invasive NIS, biotic homogenisation is occurring globally (Kark et al., 2007). Congruent with large-scale habitat homogenisation, this results in increased opportunity of conditions fitting for biological invasions. When the biota of different urban ecosystems become nearly interchangeable, this complicates the conservation of native species (Groffman et al., 2014; Wang et al., 2021; Collins et al., 2000; Simberloff and Holle, 1999).

6.2. Biotic interactions: established IAS and exotic vegetation

Biotic interactions between IAS are an important aspect of the colonisation process, as they may facilitate invasions predominantly through indirect effects, but also via direct trophic (mutualistic, commensal) effects (Simberloff and Holle, 1999; Alberti, 2015; Cadotte et al., 2017). IAS act towards impoverished and simplified communities of low biodiversity, by displacing and/or removing natives and altering ecosystems and their functions which, simultaneously with the direct effects of urbanisation on biodiversity (García-Arroyo et al., 2020), may create conditions exploitable by other IAS (Cadotte et al., 2017). Direct competitive interactions of established IAS with natives are widely reported (Simberloff and Holle, 1999). For instance, population density of invasive house sparrow was negatively associated with native avian species richness across four urban settlements in western Mexico. House sparrows compete for nesting opportunities and food resources by superior aggressiveness, and can be sources of pathogens such as avian pox and malaria (García-Arroyo et al., 2020). The tadpoles of American bullfrogs can outcompete native tadpoles, forcing skewed realised niche and alterations of their microhabitat that render them more susceptible to predators, whilst the adults are generalist that can predate also on other native amphibians (Ficetola et al., 2007).

Habitat modification by IAS that are ecosystem-engineers may directly render the habitat unfavourable for natives, or ignite a cascade of changes leading to a similar outcome and consequently creating opportunity for invasive species (Simberloff and Holle, 1999). Asian water buffalo introduced to northern Australia in the 1800s (Skeat et al., 1996) as life-stock and beasts of burden, quickly became feral and dispersed. Altering habitat hydrology and plant communities of forests and flood plains, and compacting soil, promoted domination by an already invasive Central American shrubby legume *Mimosa pigra*, ultimately damaging local fauna dependent on the native sedgelands habitat. Another example is the zebra mussel *Dreissena polymorpha*, invasive to the Great Lakes region of the USA since the 1980s. Being a highly efficient filter-feeder, *Dreissena* cause a decline in phytoplankton biomass whilst achieving deposition of rich excreted organic material. The new soft and deposit-feeder-friendly benthic substrate is improper to some native inhabiting invertebrates, but beneficial to others, such as the invasive Eurasian faucet snail *Bithynia tentaculata* (Simberloff and Holle, 1999).

IAS profit from exotic vegetation for familiar food and shelter (Gering and Blair, 1999). For instance, invasive fructivores in ranges lacking native fleshy fruit-bearing vegetation may feed from exotic horticultural plants (Collins et al., 2000; Cesari et al., 2018). Florida invasive red-whiskered bulbuls utilise the same nesting and feeding resources that they would in their native range of tropical Asia, thanks to the extensive anthropogenic modification of urban flora (Simberloff and Holle, 1999). The popularity of highly attractive exotic ornamental plants attracts exotic pollinator species with shared eco-evolutionary history, whilst afflicting native pollinator populations. Although the plant species tend to be most alluring to both native and invasive pollinator species, accessibility of flowers and quality of the nectar or pollen are often incompatible with native pollinators, inducing them to only hover around but not enter and pollinate flowers. This negative impact on pollination network is particularly meaningful in highly urbanised settings, where density of both plant and pollinator species is already low(Buchholz and Kowarik, 2019).

6.3. Biotic resistance and relaxation of predation pressure

Overcoming biotic resistance (the suppression or prevention of IAS by predation and competition from natives) is key for successful establishment of IAS (Santana Marques et al., 2020; Carthey and Banks, 2018). Though IAS may no longer need to deal with their native-range predators, they will have to respond to predation pressure from unfamiliar local predators. IAS will not have shared evolutionary history with native predators making them vulnerable due to naiveté and lack of anti-predator behaviour (Carthey and Banks, 2018; Twining et al., 2020). Biotic resistance controls the spread of IAS in natural areas, but in cities the diversity and abundance of native competitors and predators is usually low (Hernández-Brito et al., 2020; Santana Marques et al., 2020). Despite the presence of invasive non-native predators (e.g. cats) (Carthey and Banks, 2018; Shochat et al., 2010), predation pressure generally relaxes with increasing urbanisation (Friesen et al. 2013). Studies such as Gering and Blair (1999) or Roshnath et al. (2019) indicate that predation pressure on avian nests is lower in urban environments than in semi-natural or natural areas. This can explain the high abundance of prey avian IAS (e.g. European starling, house sparrow, feral pigeon) in cities (Gering and Blair, 1999). Urban birds and mammals (e.g. squirrels) also forage more freely and efficiently, rather than only foraging close to shelter suggesting perceived safety from predation (Shochat et al., 2010). The urban landscape can also be heterogeneous, there is often variability in predation pressure within the same city (Gering and Blair, 1999), which might offer refuge from predators (Hernández-Brito et al., 2020).

Predator release profusely aids biological invasions (Hernández-Brito et al., 2020). In guppies (*Poecilia reticulata*), absence of predators has resulted in larger body size, enabling specimen to travel longer distances and thus facilitating dispersal. Larger body size also allows better persistence in difficult urban streams, and for females it is associated with higher fecundity and more offspring (Santana Marques et al., 2020). Predation relaxation allows IAS to develop facilitative interactions with native species, granting safety from predation also in areas with biotic resistance. Invasive alien monk parakeet in central Spain have begun nesting close to active nests of large native white stork, reducing predation risk from raptors, and enabling spread into rural areas (Hernández-Brito et al., 2020).

Despite the evidence we presented, the extent of the relevance of biotic resistance in urban settings is debated. In some systems the native predators mostly ignore invaders, while in other scenarios predation by natives has little influence on invader success (Hernández-Brito et al., 2020; Santana Marques et al., 2020). For example, the presence of other fish species in urban streams showed negative but insignificant effects on guppy traits and density. This is explained by compensatory life-history traits and high food availability (Santana Marques et al., 2020). Moreover, in some IAS a high marginal value of food in urban landscapes may induce bold behavioural syndrome, where anti-predator responses become weakened or absent even if the predator is recognised. For example, Carthey and Banks (2018) found invasive peri-urban black rats to be naïve of unfamiliar native predators but also unresponsive to recognised exotic predators, when rushing for valuable urban food (i.e. peanuts) (Carthey and Banks, 2018). Furthermore, as noted earlier, habitat heterogeneity and variability in predation pressure amongst sites (Gering and Blair, 1999) can create refuge from predation (Hernández-Brito et al., 2020).

8. CONCLUSIONS AND FUTURE OUTLOOKS

Biotic and abiotic characteristics of the urban landscape facilitate biological invasions through an interacting and complex set of mechanisms. Starting with increased NIS propagule pressure by high rates of intentional and unintentional introductions (Banha et al., 2017; Hulme et al., 2008), trait-selected non-indigenous animal species take advantage of increased resources, interspecies mismatches and often absent or weak biotic resistance (Kark et al., 2007; Hernández-Brito et al., 2020; García-Arroyo et al., 2020) due to the removal of native predators and competitors in urban areas (Groffman et al., 2014). Furthermore, the milder urban climate, the presence of artificial structures and exotic flora may facilitate the establishment and spread of IAS (Collins et al., 2000; Groffman et al., 2014; Barsotti et al., 2021; Simberloff and Holle, 1999). This is further aided by interspecific interactions between IAS and between habitat and ecosystem-engineer IAS (Simberloff and Holle, 1999). Meanwhile, urban expansion and global homogenisation broaden invasive potential of IAS to a wider range of locations (Groffman et al., 2014; Barsotti et al., 2021). Inter-cities connections aid dispersal of established IAS populations (Sherpa et al., 2020; Botham et al., 2009). Simultaneously, urban refuge conditions allow for development of adaptations that may also spread to the natural non-native environment (Hernández-Brito et al., 2020).

With rising urban expansion and globalisation, biological range shifts and their destructive natural, economic and health impacts are a growing concern (Padayachee et al., 2017; Godefroid et al., 2020; Hima et al., 2019). Understanding of IAS and their interactions with the abiotic and biotic environment is crucial to developing strategies to minimise the arrival, establishment and spread of IAS, and thereby of their ecological impacts (Cadotte et al., 2017; Padayachee et al., 2017). Still, well-designed studies are lacking, as well as studies investigating socio-economic spatial pattens, or considering the sub-urban environment as a separate and different class from the urban environment (Cadotte et al., 2017). Whilst IAS-habitat and IAS-native species interactions are well reported, biotic interactions between IAS are understudied (Simberloff and Holle, 1999). Another important knowledge gaps requiring research attention would be to understand how adaptive behaviours evolved from exposure to humans and urbanisation, such as boldness, may be translating into the natural environments surrounding invaded urban landscapes, and modify interspecific dynamics with native biota, potentially increasing invasive potential to previously resistant natural landscapes.

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