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Review

Amphibian ecology and conservation in the urbanising world: A review

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ABSTRACT

Urbanisation currently threatens over one-third of the world's known amphibian species. The main threats of urbanisation to amphibian populations are habitat loss, habitat fragmentation and isolation, and degradation of habitat quality. A complex array of interacting biotic and abiotic factors impact amphibians in urban and urbanising landscapes. These can lead to a decrease in species richness and the abundance of individual species towards the centre of cities and towns. The ability of amphibians to disperse can be significantly reduced in urban and suburban landscapes. However, different species exhibit markedly different responses to urbanisation. Amphibian species that are habitat generalists or have relatively low dispersal requirements appear to be better able to survive in urban and suburban landscapes. There is insufficient information on the ecology of amphibians in urban and suburban areas, particularly in the tropics and sub-tropics, despite worldwide declines reported over past decades. Future research of amphibians in urban and suburban landscapes would greatly benefit by using long-term studies at sites along urban–rural gradients, conducted at both local and landscape scales. Research needs to be directed to the developing world in the tropics and sub-tropics, which has the highest rates of urbanisation. Research into amphibian ecology and conservation in the urbanising world would be improved through experimental approaches to determine the proximate causes of species' responses to human modification of the landscape. Maintaining viable populations of amphibians in urban and suburban landscapes will require conservation strategies that consider key urbanisation processes (i.e. habitat availability and habitat quality) and the key responses and adaptations to urbanisation (i.e. species availability and species response). Conservation strategies for amphibians in urban and suburban landscapes need to include actions to prevent further loss and degradation of both terrestrial and aquatic habitat, and to reconnect the landscape to facilitate dispersal and long-term regional persistence of amphibian populations and communities.

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1. Introduction

Urbanisation is currently affecting many of the earth's ecosystems and is expected to continue to increase rapidly well into the future (United Nations Human Settlements Programme, 2004). It is estimated that the world's urban population will reach almost 5 billion by 2030 with the bulk of the increases occurring in undeveloped countries and in cities with less than half a million inhabitants (UNFPA, 2007). Urbanisation is a complex process driven by an increase in human density that generates significant changes in the chemical, physical, and ecological conditions in areas of human development, and specifically results in the creation of new land cover and new biotic assemblages of plants and animals, and it can alter the types and frequency of disturbance regimes (McDonnell and Pickett, 1993; Kinzig and Grove, 2001). The process of urbanisation occurs as large cities grow, but also occurs in city-rural fringes and small towns and villages. Census surveys of countries around the world commonly use a density of 400 human individuals/km^2 to define an urban area (Demographia, 2008), but there are many other factors such as density of buildings, roads and other types of infrastructure that contribute to creating urban environments (McDonnell and Pickett, 1993). McIntyre et al. (2000) and Hahs and McDonnell (2006) have contributed toward developing a standard set of measures to characterise urbanisation, but as of yet there is no one universal definition.

Urbanisation can cause habitat loss and fragmentation (McKinney, 2002, 2006), change hydrology via the construction of impervious surfaces, thus increasing runoff, increase sedimentation and pollution of streams and wetlands (Paul and Meyer, 2001; Miltner et al., 2004), and modify soils (Effland and Pouyat, 1997). Urbanisation may also result in an increase in the establishment of exotic and domesticated plants and animals (Pickett et al., 2001; McKinney, 2006), and in climatic differentials between urban and less-populated surrounding rural areas (McDonnell et al., 1993; Grimm et al., 2008). Urbanisation is therefore currently one of the most pervasive causes of natural ecosystem disturbance and change worldwide, and thus presents a major threat to biota (Czech et al., 2000; Miller and Hobbs, 2002).

Amphibians have the highest proportion of species on the verge of extinction among the world's vertebrates (Stuart et al., 2004), currently estimated as one in three species under the 2004 IUCN Red List (Baillie et al., 2004). Globally, amphibians have suffered massive, widespread, often unexplained, and probably irreversible, declines over the last several decades (see Collins and Storfer, 2003; Beebee and Griffiths, 2005 for recent reviews on amphibian declines). In total, 21% of amphibian species are critically endangered or endangered, whereas the proportions for mammals and birds are only 10% and 5%, respectively, and this high level of threat might be an underestimate, as 23% of amphibians could not be assessed because of insufficient data (Baillie et al., 2004). Habitat loss, fragmentation and degradation, which often result from urbanisation, currently impact 88% of threatened amphibians (Baillie et al., 2004), and are therefore among the greatest threats to amphibian populations (Stuart et al., 2004; Beebee and Griffiths, 2005; Cushman, 2006). For example, the global amphibian assessment (GAA) lists 2197 amphibians of a total 5918 as being threatened by urbanisation through infrastructure development (IUCN, Conservation International, and NatureServe, 2006). It is clear that urbanisation will remain a dominant threat to amphibians worldwide, as human transformation of the landscape continues to expand and intensify.

Amphibians often comprise a significant proportion of the vertebrate biomass in forest and wetland ecosystems, as well as being important carnivores and prey species (Burton and Likens, 1975; Gibbons et al., 2006). Despite their importance to ecosystem function and the widespread declines observed for many species, however, amphibians are among the least studied taxonomic groups in urban and suburban areas (Pickett et al., 2001; McDonnell and Hahs, in press).

While many of the direct and indirect impacts of human development on amphibians have been addressed within recent reviews (e.g. Cushman, 2006), there have been no explicit reviews to date of the impact of urbanisation on amphibians or on the ecology and conservation of amphibians in urban and suburban areas (but see Windmiller and Calhoun, 2007, for a discussion on conserving amphibians in urban landscapes of the northeastern USA). The aim of this paper is to review the current literature on the ecology and conservation of amphibians in urban and suburban landscapes. Due to the complexity of potential impacts on amphibians in human settlements and the variety of potential responses to these impacts by different taxa, we have presented the results of our review in the context of a hierarchical framework that recognises four critical components that affect the persistence of amphibian populations in urban and suburban landscapes: (a) habitat availability; (b) habitat quality; (c) species availability; and (d) species response (Fig. 1). This framework provides a tool to assess the current knowledge base on the ecology of amphibians and their response to urbanisation. In addition, this framework assists in identifying gaps in our knowledge and future research opportunities, and it serves to inform the development of conservation strategies for amphibians in urban and suburban areas. This framework is a tool to identify broad generalisations regarding the response of amphibians to urbanisation. There will of course be species with unique or specific life-history traits and behaviour that are exceptional, and therefore, difficult to include in any generalisations. This paper has been separated into two sections. The first half of the paper presents the results of our literature review on the ecology and conservation of amphibians in urban and suburban landscapes, while the second half

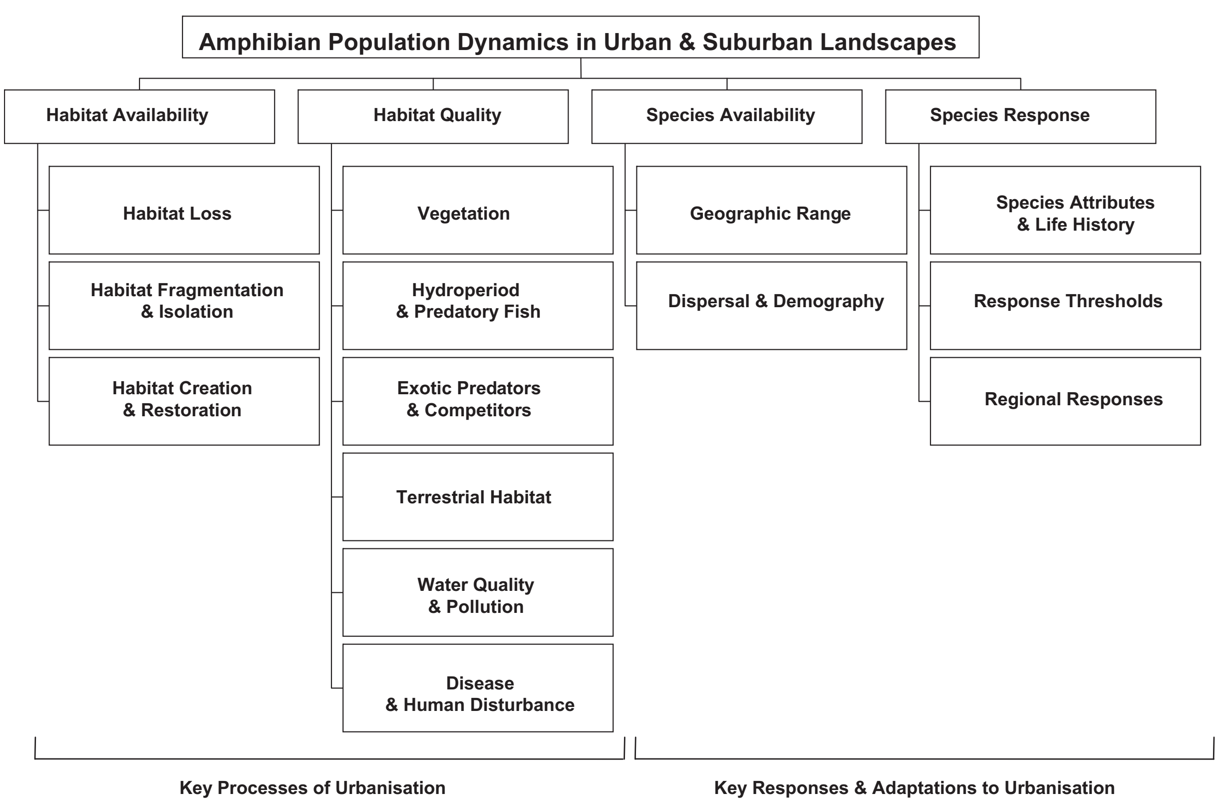

Fig. 1 – Conceptual framework for assessing existing knowledge of amphibian ecology and conservation in urban and suburban landscapes. This framework identifies key knowledge gaps and future research opportunities to develop conservation strategies for amphibians in urban and suburban areas.

discusses future opportunities and challenges regarding the study of amphibians in these areas.

2. Ecology and conservation of amphibians in urban and suburban landscapes

2.1. Habitat availability

The maintenance and survival of amphibian populations in urban and suburban landscapes requires the availability of suitable aquatic habitats, such as a waterbody (pond, dam or lake), wetland (swamp, marsh) or stream, and terrestrial habitats (Wells, 2007). The amount and type of amphibian habitat available in a landscape is affected by several processes that occur in urban and suburban environments including: (1) habitat loss; (2) habitat fragmentation and isolation; and (3) habitat creation and restoration.

2.1.1. Habitat loss, fragmentation and isolation

Urbanisation eliminates large portions of habitat from the landscape; the remaining patches are often fragmented and isolated, and remaining animal populations are smaller (Radeloff, 2005). The importance of habitat loss and fragmentation in the decline of local populations of amphibians has been outlined in recent reviews (Cushman, 2006; Gardner et al., 2007). Gardner et al. (2007) identified a gradient of increasing severity of impact on amphibian species richness with decreasing structural and habitat complexity arising from habitat loss. Many amphibian populations are naturally patchy across the landscape at local scales, which may comprise larger networks of metapopulations towards regional scales (Marsh and Trenham, 2001; Smith and Green, 2005). Moreover, many amphibian species depend on the linking of complementary habitats at multiple spatial scales to successfully fulfil their complex life cycle requirements, and their populations are thus structured as patchy networks or metapopulations (Pope et al., 2000; Marsh and Trenham, 2001). Urbanisation reduces the ability of these networks of populations to function due to the construction of roads and urban infrastructure such as buildings, fences and open areas that inhibit or discourage amphibian dispersal (Vos and Chardon, 1998).

Nearly all studies we reviewed reported a negative relationship between urbanisation and amphibian species richness, presence/absence, abundance or community structure (see Table 1). Overall amphibian decline in an area is directly associated with changes in landscape structure due to urbanisation that results in decreased wetland area and density, and increased wetland isolation, decreased wetland vegetation, forest cover and other upland terrestrial habitat (Lehtinen et al., 1999; Rubbo and Kiesecker, 2005; Parris, 2006; Gagné and Fahrig, 2007).

Studies into changes in amphibian habitat over time have reported an inverse relationship between urbanisation and extant habitat. Gibbs (2000) conducted an analysis of wetland mosaics along an urban–rural gradient in the New York city region, USA, and reported reductions in wetland density and an increase in nearest-neighbour habitat distances associated with the shift in human settlement patterns from rural to urban. Wood et al. (2003) attributed the decline of the great crested newt (*Triturus cristatus*) in the UK to the loss of pond habitat caused by urban development. They proposed that these critical temporary pond habitats are at greater threat in the UK than any other small waterbody because they are typically shallow, vulnerable to soil drainage, and are highly susceptible to pollution. Similarly, vernal pools, which constitute habitat for many amphibian species across the northeastern USA, are also at risk of destruction from urbanisation due in part to their diminutive size and short hydroperiods (Grant, 2005), and because they are rarely afforded protection (Dodd and Smith, 2003; Semlitsch, 2003; Windmiller and Calhoun, 2007). Small temporary wetlands (<4.0 ha) are critically important for amphibian breeding success and may function as stepping-stones to reduce interwetland distances (Gibbs, 1993, 2000; Semlitsch and Bodie, 1998), and thus every effort should be made to preserve and even enhance these habitats in urban and suburban landscapes in order to maintain local, regional and global amphibian biodiversity.

Habitat loss, fragmentation and isolation may also affect population genetic structure. For example, the landscape genetics of *Physalaemus cuvieri* in the Brazilian Cerrado show a signature of effects of human occupation and habitat loss on genetic differentiation at the regional scale, with discontinuities to gene flow in two particular regions with more intense habitat loss and older human settlement (Telles et al., 2007).

2.1.2. Habitat creation and restoration

Amphibians with broad habitat requirements may be able to persist within urban landscapes because they are able to use artificial habitats such as garden ponds, ornamental lakes and dams, retention ponds and drains. Indeed, there is evidence that some species have benefited from the construction of ponds and wetlands, particularly during the early phase of urbanisation when colonisation by amphibians is less impeded, because they may replace the function of rural or natural ponds destroyed during the process. For example, the common frog (*Rana temporaria*) in Britain persists in urban and suburban areas more so than in rural areas, which is most likely due to the abundance of garden ponds (Carrier and Beebee, 2003).

However, waterbodies, wetlands and streams in urban and suburban areas are often limited in their suitability for amphibian species with more specific habitat requirements because many are artificially stocked with exotic fish, have inappropriate hydrological regimes, receive contaminated runoff (fertilisers, sediment, pesticides, road surface grease and oil, heavy metals), and have high human visitation rates and artificial lighting, which disrupts breeding activity (Knutson, 1999; Rodríguez-Prieto and Fernández-Juricic, 2005; Rubbo and Kiesecker, 2005; Baker and Richardson, 2006). Moreover, the physical structure of urban ponds may exclude some species. For example, a vertical pond wall may mean that a pond is suitable only for tree frogs because they are able to climb out when emigrating (Parris, 2006). Urban wetlands are also often surrounded by roads and urban-related infrastructure that can form barriers to amphibian dispersal, potentially rendering them inaccessible to species with moderate to high dispersal requirements (Rubbo and

Table 1 – Response of amphibian species richness, presence/absence, abundance and community structure to explanatory variables recorded in 40 empirical studies

Explanatory variable	Dependent variables	Response	Number of studies	Source
Urbanisation	Species richness, presence/absence, abundance, community structure	Decrease	24	Atauri and de Lucio (2001), Bowles et al. (2006), Bunnell and Zampella (1999), Delis et al. (1996), Gagné and Fahrig (2007), Hodgkison et al. (2007a,b), Houlahan and Findlay (2003), Knutson et al. (1999), Lehtinen et al. (1999), Mensing et al. (1998), Miller et al. (2007), Parris (2006), Pearl et al. (2005), Pellet et al. (2004a,b), Price et al. (2004), Reinelt et al. (1998), Richter and Azous (1995), Riley et al. (2005), Rubbo and Kiesecker (2005), Skidds et al. (2007), Willson and Dorcas (2003), Woodford and Meyer (2003)
	Presence/absence	Increase/decrease	1	Van Buskirk (2005)
Forest cover	Species richness, presence/absence, abundance, community structure	Increase	14	Baldwin et al. (2006b), Drinnan (2005), Gibbs (1998), Herrmann et al. (2005), Hodgkison et al. (2007a,b), Homan et al. (2004), Houlahan and Findlay (2003), Knutson et al. (1999), Lehtinen et al. (1999), Otto et al. (2007), Rubbo and Kiesecker (2005), Skidds et al. (2007), Van Buskirk (2005)
	Presence/absence	Increase/decrease	3	Guerry and Hunter (2002), Pearl et al. (2005), Price et al. (2004)
Canopy cover/shading	Species richness, presence/absence	Decrease	7	Bradford et al. (2003), Burne and Griffin (2005), Ficetola and De Bernardi (2004), Pearl et al. (2005), Pellet et al. (2004b), Skidds et al. (2007), Van Buskirk (2005)
Wetland vegetation	Presence/absence, abundance	Increase	8	Bradford et al. (2003), Burne and Griffin (2005), Healey et al. (1997), Houlahan and Findlay (2003), Parris (2006), Pearl et al. (2005), Price et al. (2004), Skidds et al. (2007)
	Presence/absence	Decrease	1	Galatowitsch et al. (1999)
	Abundance	Decrease	1	Mensing et al. (1998)
Area	Species richness, presence/absence, abundance	Increase	11	Bradford et al. (2003), Burne and Griffin (2005), Drinnan (2005), Gagné and Fahrig (2007), Herrmann et al. (2005), Houlahan and Findlay (2003), Knutson et al. (1999), Nyström et al. (2002), Parris (2006), Price et al. (2004), Skidds et al. (2007)
	Species richness	Decrease	1	Babbit (2005)
Isolation	Species richness, presence/absence	Decrease	4	Burne and Griffin (2005), Ficetola and De Bernardi (2004), Houlahan and Findlay (2003), Lehtinen et al. (1999)
	Abundance	Increase	1	Baldwin et al. (2006b), Homan et al. (2004)

Hydroperiod (permanence)	Species richness, presence/absence	Increase	7	Babbit (2005), Burne and Griffin (2005), Herrmann et al. (2005), Nyström et al. (2002), Reinelt et al. (1998), Skidds et al. (2007), Van Buskirk (2005)
	Presence/absence	Increase/decrease	2	Pearl et al. (2005), Rubbo and Kiesecker (2005)
	Species richness, presence/absence	Decrease	2	Ficetola and De Bernardi (2004), Richter and Azous (1995)
	Presence/absence	Intermediate	2	Otto et al. (2007), Van Buskirk (2005)
	Abundance	Increase	1	Baldwin et al. (2006b)
Fish presence	Species richness, presence/absence	Decrease	6	Ensabella et al. (2003), Ficetola and De Bernardi (2004), Lehtinen et al. (1999), Nyström et al. (2002), Pearl et al. (2005), Van Buskirk (2005)
Conductivity	Presence/absence	Decrease	4	Bradford et al. (2003), Ensabella et al. (2003), Pearl et al. (2005), Pellet et al. (2004b)
pH	Presence/absence	Increase	2	Bradford et al. (2003), Otto et al. (2007)
Nutrients	Species richness	Decrease	2	Ensabella et al. (2003), Houlahan and Findlay (2003)
Total phosphorus	Presence/absence	Increase	1	Nyström et al. (2002)

Only studies that produced explanatory variables included in the best or statistically significant amphibian–habitat models are shown.

Kiesecker, 2005). Therefore, species with specific habitat or life-history requirements may be attracted to constructed habitat of inferior habitat quality, and thus created ponds may function as habitat traps or sinks (Battin, 2004).

Restoration activities may improve the ecological function of urban ponds and wetlands, despite their limitations. For example, wetlands in an urban area of Minnesota, USA, were successfully restored by destroying portions of drainage tile or filling ditch systems and allowing water to re-flood the basins, and were subsequently colonised by amphibians conditional on distance to source ponds (Lehtinen and Galatowitsch, 2001). Restoration of wetlands on the Danube Island, Austria, was successful in attracting a suite of amphibian species where fish were absent (Chovanec et al., 2000). The ability of restored wetlands in urban landscapes to provide suitable habitat for amphibians requires the creation and maintenance of appropriate levels of habitat succession, suitable fluctuations in hydroperiod, availability of upland terrestrial habitat, good water quality, connectivity to surrounding populations, and the absence of native and exotic predatory fish (Beebee, 1996; Porej and Hetherington, 2005; Vasconcelos and Calhoun, 2006; Petranka et al., 2007). The restoration of metapopulations of amphibians at the landscape scale is critical for larger-scale and long-term recovery of amphibians (Semlitsch, 2002), although this poses a serious challenge in highly modified urban landscapes. There is also the possibility of re-introducing amphibians into restored waterbodies, wetlands and streams in urban and suburban areas via translocated stock, although this action raises ethical issues and concerns with transport of diseases, in addition to whether restoration fully satisfies the ecological requirements of the target species and provided adequate connectivity in the landscape (Marsh and Trenham, 2001; Seigel and Dodd, 2002; Calhoun and Hunter, 2003).

2.2. *Habitat quality*

The quality of amphibian habitat is influenced by the amount and type of vegetation in the waterbody, wetland or stream and surrounding terrestrial habitat, the hydroperiod, water quality, the presence of predators and competitors, the prevalence of diseases and the nature and frequency of human disturbances. Amphibian habitat provides resources for breeding and non-breeding activities, such as foraging and dispersal, and shelter and overwintering sites (Wells, 2007). Species with complex life cycles, such as pond-breeding amphibians, may depend on landscape complementation, where different breeding and non-breeding habitats are linked through movement, to complete their life cycles (Pope et al., 2000). Amphibians with simple life cycles, such as terrestrial salamanders with direct development, may require specialised habitat types (Wyman, 2003). Poor quality habitats may not support viable populations and these marginal habitats could potentially become species sinks depleting the larger-scale metapopulation (McKinney, 2002).

2.2.1. *Vegetation*

Urbanisation may result in the loss of aquatic vegetation within ponds, wetlands and streams, or the loss of forest and other upland terrestrial plant communities from the landscape. Aquatic vegetation provides shelter for larval and adult amphibians, and oviposition sites (Egan and Paton, 2004; Skidds et al., 2007), whereas terrestrial vegetation fringing ponds and wetlands, and upland plant communities, provide opportunities for dispersal, food, shelter and overwintering sites once individuals have metamorphosed (deMaynadier and Hunter, 1999). Forested wetlands also provide habitat for wetland-dependent amphibians in urbanising areas (Baldwin et al., 2006a). Along streams, changes in bed sediments, nutrient enrichment, and turbidity contribute to a reduction in the diversity of stream macrophytes (Suren, 2000), and large woody debris is also reduced in urban streams (Paul and Meyer, 2001).

In addition to vegetation removal, modifications to the structure and composition of vegetation in and around urban waterbodies, wetlands and streams have implications for the ability of amphibian populations to persist. For example, overstorey vegetation composed of exotic species of planted trees may encroach on urban ponds and result in increased pond shading, whereas weeds may smother the surface area of ponds, outcompete native aquatic species and reduce foraging success (Maerz et al., 2005). Pond shading can lower water temperatures, reduce the concentration of dissolved oxygen, and decrease the abundance of periphyton, a common food source for larval amphibians, thereby depressing larval growth rates and activity levels (Skelly et al., 2002; Thurgate and Pechmann, 2007). Many amphibian species in North America that favour open, early successional habitats are usually absent from ponds where forest canopies have closed over the pond basin (Skelly et al., 1999; Halverson et al., 2003; Werner et al., 2007), and there is also a negative relationship between canopy cover and similar species in urban and suburban areas (see Table 1). In urban areas, waterbodies, wetlands and streams may also be shaded by buildings, bridges and other urban-related infrastructure. Conversely, some forest-dependent amphibians (e.g. plethodontid salamanders) require mature forests with a closed canopy that provide cool, moist terrestrial microhabitats to complete their life cycle, and so are impacted by the removal of shady forest (see Table 1). Moreover, there are species that can inhabit ponds along the entire gradient of vegetation succession, such as the wood frog (*Rana sylvatica*), which is a canopy generalist (Skelly et al., 2002).

2.2.2. *Hydroperiod*

Hydroperiod, the length of time a waterbody, wetland or stream continuously holds water, is known to strongly influence the structure and composition of amphibian communities (Wellborn et al., 1996; Werner et al., 2007). Hydroperiod is likely to invoke the strongest and most contrasting responses across amphibian communities in urban and suburban areas. For example, some species require ephemeral ponds for breeding that hold water briefly (e.g. one or two months), whereas others require permanent aquatic habitats that never dry out. Rubbo and Kiesecker (2005) suggested that hydroperiod may play a significant role in determining amphibian distributions across urbanisation gradients owing to the complex life-histories of individual species and the relationship between predatory fish and wetland permanency. Altered waterbody and stream hydrology is a common outcome of urbanisation, involving changes in the extent, duration, frequency and timing of inundation, and quantity and flow of water, respectively. For example, urban development in the Portland area of Oregon, USA, has resulted in the conversion of large, shallow, well-vegetated ephemeral wetlands to smaller, deeper, less-vegetated and more stable permanent wetlands which are commonly inhabited by fish (Kentula et al., 2004). The loss of temporary natural wetlands in this region has reduced habitat quality for several amphibians that have rapid larval development (e.g. long-toed salamander, *Ambystoma macrodactylum*), but increased pond permanence has enabled species with longer larval periods to persist (e.g. bullfrogs, *Rana catesbeiana*; Pearl et al., 2005). Urbanisation has been reported to result in similar modifications to wetlands in other regions (e.g. central Pennsylvania, USA); typically, converted or created waterbodies and wetlands have increased hydroperiod (i.e. permanency; Rubbo and Kiesecker, 2005). Conversely, there may be reduced flow of streams in urbanising watersheds, which may have contributed to decreased larval abundance of southern two-lined salamanders (*Eurycea cirrigera*) in Wake County, North Carolina, USA (Miller et al., 2007).

Stormwater management in urban watersheds can alter the hydroperiod of urban wetlands by increasing the likelihood of wetlands drying out, particularly during dry seasons, by redirecting water that previously entered wetlands to stormwater management retention or detention facilities, or directly into streams (Hogan and Walbridge, 2007). Direct hydrological changes to urban and suburban waterbodies and wetlands may also occur by filling, ditching, diking and draining (Ehrenfeld, 2000). These practices may lower the reproductive success of amphibians in urban and suburban areas if larvae are unable to metamorphose prior to the wetland drying, or spawning may not occur at all if the wetlands are dry. Metamorphosed amphibians may desiccate under these conditions if they are unable to move to other wetlands or to moist microhabitats in the surrounding upland.

Stream hydrology can be greatly modified in urban and suburban catchments; increased surface runoff often results in rapid flood peaks, thereby increasing flood magnitude and frequency (Paul and Meyer, 2001; Allan, 2004). Miller et al. (2007) posit that a combination of increased peak flows and sedimentation, reduced base flow and chemical changes likely reduce the abundance of salamanders in urban and suburban streams. Increased flood frequency and magnitude can result in scour of the stream banks, which removes coarse woody debris and disturbs instream vegetation (Ehrenfeld, 2000). Impacts of altered stream flow regimes on stream-dwelling amphibians may include loss of shelter and breeding sites, reduced prey abundance, and adults and larvae may be flushed downstream by high flow rates following heavy rains (Willson and Dorcas, 2003). The encroachment of urbanisation into riparian zones has the potential to reduce the quality of habitat for amphibians and lead to population declines. For example, Price et al. (2006) suggested that the increased rate of urbanisation from 1972 to 2000 near Davidson, North Carolina, USA, may be responsible for the significant and rapid decline in stream salamander populations reported from this region.

2.2.3. Predators and competitors

The presence of predatory fish, particularly non-native species, in waterbodies, wetlands and streams often results in a decrease in the presence and diversity of amphibians (see Table 1). The aquatic larvae of many amphibians are vulnerable to predation by exotic species of fish (Knapp and Matthews, 2000; Gillespie, 2001; Kats and Ferrer, 2003). Predatory fish are often absent from waterbodies and wetlands with short hydroperiods because they are frequently dry, whereas predatory fish tend to persist in more permanent waterbodies, which is often the dominant type of waterbody in urban and suburban areas (Kentula et al., 2004). For example, Rubbo and Kiesecker (2005) reported that fish were more common in permanent wetlands in urban and suburban areas than in less permanent rural wetlands in central Pennsylvania, USA. Accordingly, they found that urban wetlands had lower larval amphibian species richness than rural wetlands. Many urban and suburban waterbodies, wetlands and streams are also actively and accidentally stocked with exotic fish (Paul and Meyer, 2001; Ficetola and De Bernardi, 2004; Rubbo and Kiesecker, 2005) which reduces their suitability as habitat for amphibians that cannot co-exist with fish (Kiesecker, 2003). For example, the construction of permanent ponds and the introduction of non-native fish into wetlands in the Willamette Valley, Oregon, USA, which has promoted the spread of non-native bullfrogs, have been implicated in the decline of the Oregon spotted frog (*Rana pretiosa*; Adams, 1999; Pearl et al., 2005).

Introduced invertebrates may also impact amphibian populations in urban and suburban areas through predation. For example, Riley et al. (2005) found that the presence of exotic crayfish (*Procambarus clarkia*) was shown to reduce the abundance of California tree frogs (*Hyla cadaverina*) in urban streams in southern California, USA. They also suggested that urbanisation had increased water depth and flow, resulting in more permanent streams, which allowed crayfish to persist, even in dry years.

In addition to the negative impacts of exotic fish and invertebrates on amphibian habitat quality, domestic pets, especially those that have become feral, may invoke high mortality on local amphibian populations. For example, Woods et al. (2003) estimated that a British population of approximately 9 million domestic cats killed 4–6 million reptiles and amphibians during a five-month survey period.

Introduced amphibians may also compete with native amphibian species for limited resources in urban areas, and ultimately displace local populations (Kiesecker, 2003). For example, modification of wetlands in western North America frequently benefits introduced bullfrogs because large, shallow, ephemeral wetlands are commonly converted to smaller permanent ponds (e.g. retention ponds), which provides the conditions required for successful bullfrog breeding (Adams, 1999; Kiesecker et al., 2001). Reduced vegetation and the spatial clumping of edge vegetation in the permanent ponds appear to intensify competition between larvae of the introduced bullfrog and the native red-legged frogs (*Rana aurora*). This more open habitat may also intensify predation by adult bullfrogs on larval and juvenile red-legged frogs (Kiesecker et al., 2001).

2.2.4. Terrestrial habitat

Many amphibians require terrestrial non-breeding habitat to access essential resources such as shelter and food as well as overwintering sites, and upland habitat may be a critical element of the habitat mosaic of pond-breeding amphibians (Semlitsch, 2000). These non-aquatic habitats (e.g. forests, grasslands) can be located adjacent to waterbodies, wetlands and streams, or they can occur over hundreds of metres to kilometres from aquatic-breeding sites depending upon the species (Semlitsch, 1998; Trenham and Shaffer, 2005; Rittenhouse and Semlitsch, 2007). For example, Baldwin et al. (2006a) reported that the wood frog selected forested wetlands as summer refugia following use of breeding pools in spring; postbreeding movements ranged from 102 to 340 m and included stopovers in upland forest floors. Terrestrial habitats also provide the necessary resources (rocks, woody debris and rotten logs) for amphibians with direct development that does not involve an aquatic larval stage (e.g. plethodontid salamanders; Wyman, 2003). Thus, maintaining amphibian populations in urban and suburban landscapes requires the conservation of not only aquatic habitats but these terrestrial habitats as well.

The quality of terrestrial habitat also determines whether amphibians can successfully disperse from breeding sites to upland forests and other wetlands in the surrounding landscape. The movement and survival of amphibians in the terrestrial environment is the critical component that ensures successful dispersal and recolonisation within regional metapopulations (Semlitsch, 2003), however, maintaining connectivity over terrestrial habitats is extremely challenging in urban and suburban landscapes (Gibbs, 2000). Urban and suburban areas contain a suite of formidable barriers to amphibian movement. Dense networks of roads, buildings, fences and other physical barriers prevent many amphibians from successfully dispersing among the multiple habitat patches they need to access in order to fulfil critical life cycle processes (Knutson et al., 1999; Dodd and Smith, 2003). Juvenile amphibians are often the most highly dispersive life stage of many species and are therefore at greatest risk of mortality in the upland habitat matrix, and many species avoid crossing open areas while emigrating (Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005). Amphibians are susceptible to being killed while crossing roads, and road mortality may have significant impacts on amphibian populations in urban and suburban areas, especially close to breeding sites (Carr and Fahrig, 2001; Hels and Buchwald, 2001; Eigenbrod et al., 2008). For example, using population projections based on spotted salamander (*Ambystoma maculatum*) life tables, Gibbs and Shriver (2005) showed that an annual risk of road mortality for adults of >10% can lead to local population extirpation, and estimated that 22–73% of populations in central and western Massachusetts, USA, would be exposed to at least this threshold level of risk.

2.2.5. Water quality and pollution

Amphibians are generally regarded as being highly sensitive to environmental pollutants due to their biphasic life cycle and physiological requirements (Phillips, 1990; Blaustein et al., 1994). Many waterbodies, wetlands and streams in urban and suburban areas receive stormwater runoff from large areas of impervious surfaces such as roads, parking lots, buildings and open space composed of asphalt and concrete, which may contain a wide range of pollutants including heavy metals, phosphorus, fertilisers, pesticides, suspended solids, hydrocarbons and salts (Paul and Meyer, 2001). Aside from direct application, pesticides may be deposited in urban and suburban areas due to atmospheric transport from surrounding agricultural land (Boone and Bridges, 2003). Larvae of aquatic-breeding amphibians and aquatic amphibians are most at risk of potential contamination because they are confined to the aquatic environment (Semlitsch, 2000). However, it has been suggested that terrestrial salamanders with direct development may also be sensitive to environmental contaminants, such as soil acidification arising from the deposition of airborne pollutants (Wyman, 2003).

Previous studies have documented the effect of sediments, nitrogen pollution and heavy metals on amphibians in urban areas, which have been shown to lower survivorship, growth and development rates (Boone and Bridges, 2003; Casey et al., 2005; Massal et al., 2007). For example, Snodgrass et al. (2008) exposed embryonic and larval amphibians to sediments collected from stormwater retention ponds, which had elevated levels of metals (e.g. zinc, lead and copper). They recorded 100% mortality in a species that is sensitive to urbanisation (*Rana sylvatica*), whereas *Bufo americanus*, which is relatively insensitive to urbanisation, suffered relatively minor lethal effects and metamorphosed at a smaller size. However, a smaller size at metamorphosis can reduce survival to maturity and reproductive fitness, and therefore, impact on population dynamics (Smith, 1987; Berven, 1990). Snodgrass et al. (2008) suggested that stormwater retention ponds could act as ecological traps for pond-breeding amphibians such as *R. sylvatica* because stormwater ponds present cues that might be attractive (i.e. they contain vegetation and surface waters) and accumulate pollutants that may prove toxic. Differential sensitivity to water quality and pollutants may therefore occur within amphibian communities where some species are more sensitive than others (Marco et al., 1999; Hamer et al., 2004; Griffis-Kyle and Ritchie, 2007). The presence of dissolved metals and salts in water (i.e. high conductivity) and high nutrient loads negatively affect amphibian populations in urban and suburban areas (see Table 1). Finally, the increasing proportion of urban land use in a catchment generally decreases algal species diversity due to a reduction in water quality (Paul and Meyer, 2001), which would potentially decrease the amount of food for larval amphibians.

2.2.6. *Disease*

The most enigmatic pathogen to emerge as a potential agent in global amphibian declines since the 1970s is the chytrid fungus *Batrachochytrium dendrobatidis* (Bd), which causes the infectious disease chytridiomycosis in amphibians. This pathogen has been implicated in the mass mortalities in several amphibian species around the world (Daszak et al., 2003; Muths et al., 2003). In urban and suburban landscapes, Bd may be transported by humans to areas supporting naive amphibian populations through inadvertent or deliberate introduction of amphibians to new regions via releases of pet species (Carey et al., 2003). For example, Daszak et al. (2004) demonstrated that bullfrogs can be infected by Bd, but are relatively resistant to chytridiomycosis, which is lethal to many other amphibian species. By demonstrating that bullfrogs are likely to be efficient carriers of this pathogen, their results showed that this host species is important in the spread of chytridiomycosis, particularly by commercial activities.

The virulence and density of pathogens such as Ranaviruses and trematode parasites in amphibian populations has been shown to become intensified in urban and suburban areas supporting disturbed or degraded habitats (Johnson et al., 1999; Carey et al., 2003). Many of these pathogens are distributed among amphibian populations via the introduction of invasive species such as fish (e.g. trout and aquarium fish) and infected amphibians (e.g. exotic bullfrogs; Kiesecker, 2003). King et al. (2007), however, reported that urbanisation may hinder parasite transmission to frogs by limiting access of other vertebrate hosts of their parasites to wetlands.

2.2.7. *Human disturbance*

Amphibians are known to respond to physical disturbance by humans (Rodríguez-Prieto and Fernández-Juricic, 2005), artificial light (Baker and Richardson, 2006) and noise pollution (Sun and Narins, 2005; Bee and Swanson, 2007), all of which may disrupt breeding behaviour, thereby potentially reducing recruitment rates and thus affecting population dynamics. For example, Baker and Richardson (2006) demonstrated that male green frogs (*Rana clamitans melanota*) produced fewer advertisement calls and moved more frequently when exposed to artificial light compared to ambient light conditions. In a study of a mixed-species anuran calling assemblage in central Thailand, Sun and Narins (2005) showed that man-made acoustic interference (e.g. road traffic, airplanes) may directly affect anuran chorus behaviour. Urban streams and wetlands can experience high human visitation rates, either because of active recreational viewing or incidental visits. For example, Rodríguez-Prieto and Fernández-Juricic (2005) assessed the effects of recreational activities on Iberian frogs (*Rana iberica*) in the Guadarrama Mountains of central Spain. By simulating different levels of human visitation to stream banks, they found an 80% and 100% decrease in stream bank use with a fivefold and a 12-fold increase in direct disturbance rate, respectively. Amphibians may also be collected by humans for food, fishing bait or as pets in urban and suburban areas, which may reduce population size or introduce species into previously uninhabited regions (Jensen and Camp, 2003).

2.3. **Species availability**

If amphibians are to inhabit urban and suburban areas they need to currently exist within these environments or there needs to be nearby populations that can colonise suitable habitats. The presence of amphibians in cities and towns is thus directly affected by the geographic range of each species and their ability to disperse and survive in fragmented urban and suburban landscapes.

2.3.1. Geographic range

In considering the effects of urbanisation on amphibians and the ecology of amphibians in urban areas, it is imperative to understand whether the natural range of a species actually included sites now covered by cities and towns. For example, populations may occupy less favourable habitat on the periphery of their natural range, where they tend to be more fragmented (Channell and Lomolino, 2000). It therefore seems unlikely that local populations of species in urban and suburban areas that are on the edge of their natural distribution will persist. However, given the "heat island" effect of cities and the wider implications of global warming (Grimm et al., 2008), amphibian species whose natural range did not include areas now occupied by urban and suburban land, due to unsuitable low temperature, for example, may be able to establish new populations. These species may be introduced accidentally or intentionally into urban and suburban areas from outside their natural range via human-facilitated dispersal resulting from commercial or recreational activities. For example, pet amphibians may escape or be intentionally released into novel habitats, whereas amphibians may be accidentally transported long distances in goods such as fruit and vegetables (Kiesecker, 2003).

2.3.2. Amphibian dispersal and demography in fragmented urban landscapes

Amphibian dispersal in urban and suburban areas is likely to be severely impeded, which has the potential to negatively impact the demography of extant populations. The inability of species to disperse across urban and suburban landscapes is also of particular concern in light of the predicted impacts of global climate change on the current geographic ranges of many animal species (Parmesan, 2006). Of critical importance to successful dispersal among habitat patches in urban and suburban landscapes is the degree and nature of connectivity. Compton et al. (2007) developed a model of connectivity among vernal pools for four salamanders in Massachusetts, USA, taking landscape resistance into account, and reported relatively high resistance values for dispersing juveniles and migrating adults across urban land cover. Joly et al. (2003) also modelled high coefficients of resistance for movement of common toads (*Bufo bufo*) in urban areas of the Rhône floodplain, France. Pyke (2005) developed a decision support system to assess movement of the California tiger salamander (*Ambystoma californiense*) along potential linkages relative to land cover threats and found the best linkages provided lots of natural land cover and few roads.

Smith and Green (2005) reported that amphibian migrants may occasionally disperse >10 km and therefore connect populations. However, given the constraints imposed on amphibian dispersal in urban and suburban landscapes, long-distance dispersal (>10 km) may not be possible for extant populations in these areas. Therefore, the ability of populations to function as metapopulations may be impeded, and dispersal may be limited to between habitat patches <10 km in urban and suburban landscapes. Although movement >1 km frequently occurs in amphibian populations, Smith and Green (2005) also reported 44% of amphibian species they reviewed moved <400 m. The implications of site fidelity in amphibians in urban and suburban areas are wide ranging. For example, many individuals may remain faithful to breeding sites, or may emigrate short distances to natal ponds from upland habitat (Smith and Green, 2006; Gamble et al., 2007). The loss of these sites due to urbanisation may affect local populations situated kilometres away. Ultimately, recruitment may not occur at remnant or artificial sites, and these populations may become extinct because of impairments to the rescue effect and source-sink dynamics (Brown and Kodric-Brown, 1977; Pulliam, 1988).

Amphibian species regarded to have the best dispersal ability may be the ones most sensitive to habitat fragmentation. For example, Gibbs (1998), in a study of the distribution of woodland amphibians along a forest fragmentation gradient in southern Connecticut, USA, found that the most sedentary species, the terrestrial-breeding redback salamander (*Plethodon cinereus*), was among the two species most resistant to habitat fragmentation, whereas the most dispersive species, the pond-breeding red-spotted newt (*Notophthalmus v. viridescens*) was least resistant and did not persist below a forest cover threshold of about 50%. High dispersal requirements in amphibians may increase the probability of a species colonising a newly-created habitat of sub-optimal quality in urban and suburban areas (e.g. ecological traps: fish-infested or polluted ponds; Battin, 2004; Snodgrass et al., 2008), or may reduce survivorship from the increased chance of individuals encountering roads (Hels and Buchwald, 2001). Finally, amphibian populations in urban and suburban areas have been shown to have lower genetic diversity than populations in natural areas as a result of inbreeding depression caused by human-induced fragmentation and decreased population size (Hitchings and Beebee, 1997; Arens et al., 2007; Noël et al., 2007).

2.4. Species response

Most empirical studies on the effects of urbanisation on amphibians reported a decrease in species richness, and individual species presence and abundance, with increases in the degree of urbanisation (see Table 1). Community structure is altered, often simplified, and genetic variability is eroded with an increase in urbanisation. The persistence of species in urban and suburban landscapes depends on species attributes and life histories, as well as their ability to respond to the changing environmental conditions resulting from the creation of human settlements.

2.4.1. Species attributes and life-history

There are often vastly different responses to urbanisation and other related variables across the amphibian community. Rubbo and Kiesecker (2005) hypothesised that specific attributes of some species render them more susceptible to urbanisation-induced habitat changes. For example, in their study of amphibian breeding distribution along an urban–rural gradient, they reported that species frequently found in urban or suburban wetlands may be more resilient to urban development as they are habitat generalists (e.g. bullfrogs). These "urban-adapted" species likely dominate the amphibian communities of cities and towns, whereas "urban-avoiders" are more sensitive to human disturbance and may be unable to persist (McKinney, 2002). Species associated with forested habitat (e.g. ambystomatid salamanders and wood frogs) appeared to be more sensitive to urbanisation because these amphibians have life-history stages that require forested habitat adjacent to breeding sites (Rubbo and Kiesecker, 2005). These species also have relatively high dispersal requirements due to their complex life-history (Gibbs, 1998). Ultimately, the magnitude and direction of impacts of urbanisation on individual species will depend on that species' life-history attributes, sensitivities to environmental disturbances, interspecies interactions and dispersal requirements (Garden et al., 2006).

The modification of waterbody, wetland and stream hydroperiod is a frequent outcome of urbanisation (Paul and Meyer, 2001; Kentula et al., 2004). The ability of individual amphibian species to cope with modifications to hydroperiod will be strongly dependent on their adaptive traits and behaviour, or if adult reproduction is timed to avoid periods when waterbodies are occupied by fish predators (Semlitsch, 2002). Survival to metamorphosis will increase for tadpoles of species that can accelerate time to metamorphosis in a drying pond, or have appropriate defence (chemical or morphological) or behavioural mechanisms to avoid fish predators in more permanent ponds (Relyea, 2001; Werner et al., 2007). For example, bullfrogs are able to persist in permanent wetlands in urbanised landscapes of the eastern USA because their larvae are unpalatable to fish predators and they have behavioural mechanisms to avoid fish, whereas eastern newts (*Notophthalmus viridescens*) breed in short-hydroperiod ponds where fish are usually absent, because their larvae have no defence mechanisms to avoid predation by fish (Rubbo and Kiesecker, 2005). Pearl et al. (2005) found that species with rapid larval development, such as the Pacific tree frog (*Pseudacris regilla*) and long-toed salamander, were associated with wetlands lacking non-native fish in the urban landscape of the Willamette Valley, Oregon, because they have no predator-avoidance traits. Many amphibian species that have evolved in the absence of predatory fish are unlikely to possess traits to cope with novel fish predators, such as exotic species, and the use of sub-optimal habitat (e.g. fish-infested ponds) may lead to local declines (Hamer et al., 2002).

2.4.2. *Response thresholds*

Amphibians may exhibit responses to urbanisation at specific thresholds of disturbance. For example, Willson and Dorcas (2003) found a threshold effect on the abundance of one species of salamander (southern two-lined salamander) when the amount of watershed composed of disturbed habitat reached about 20%, and suggested that plethodontid salamanders may be appropriate indicators of the level of disturbance within a watershed. Riley et al. (2005) found that the effects of urbanisation on stream amphibians appeared to be related to a threshold level of development within the watershed. They found that California newts (*Taricha torosa*) and California tree frogs were conspicuously absent from streams where the watershed was covered with >8% urban land uses. In a study of a fragmented urban landscape in southeastern Australia, Drinnan (2005) observed thresholds in the size of remnant bushland at approximately 4 ha for frog species richness, below which it rapidly decreased, although thresholds of 50 ha were observed for urban-sensitive species. There was also an inverse linear relationship between distance to other large reserves and species richness. Thresholds for connectivity among remnant patches in an urban landscape are likely to be largely dictated by a species' ability to disperse through an often inhospitable matrix of urban infrastructure (e.g. roads, buildings and car parks), or its ability to use habitat features that may provide some degree of connectivity (e.g. drains, parks and gardens).

2.4.3. *Regional responses to urbanisation*

The different abilities of amphibians to cope with the effects of urbanisation are likely to generate regionally contrasting long-term trends in their community dynamics. Urban-adapted species may persist whereas urban-sensitive species may not or may have high turnover. In an assessment of changes in frog and toad populations over 30 years in New York State, USA, Gibbs et al. (2005) reported that the disappearance of populations of two species was associated with elevated levels of urban development. Yet, despite the substantial loss of wetlands at the regional level, there was an overall increasing trend in wetland occupancy by many species. White and Burgin (2004) reported that the number of frog species has declined in urban reserves in Sydney, Australia, since urbanisation, and that tree frogs were more negatively impacted than terrestrial species, largely in response to infilling and water pollution. However, in another account of the changes in amphibian species assemblages in southeastern Australia, Tait et al. (2005) found no evidence of extinction, even after 166 years of significant habitat alteration and waterway pollution. Differences in species responses to urbanisation are also shown in the ability of the common frog to persist in urban habitats in Britain (e.g. garden ponds), whereas populations of the common toad have been substantially reduced in number and genetic diversity in the latter decades of the 20th century (Hitchings and Beebee, 1998; Carrier et al., 2003). Moreover, there may be a time lag of several decades between changes to amphibian habitat on urban and suburban land and a species-specific response (Löfvenhaft et al., 2004).

3. The study of amphibians in urban and suburban landscapes: future opportunities and challenges

Several critical issues need to be addressed to advance the study of amphibians in urban and suburban landscapes, including: (1) the limited scope of our knowledge base because most amphibian studies are conducted in temperate environments, with relatively few in tropical and sub-tropical environments; (2) a lack of standardisation regarding how researchers define "urban"; and (3) the need to define and standardise an appropriate landscape scale for the study of amphibians. Appreciation of these issues will help identify future directions for amphibian research in urban and suburban landscapes.

3.1. *Geographic bias*

The current literature on urbanisation and amphibians has a strong geographic bias, and the overwhelming majority of studies originate in temperate areas, generally North America, Europe and Australia, which is not surprising due to the concentration of researchers in these relatively affluent regions. The high level of research effort in these areas is largely disproportional to the number of amphibian species assessed as being threatened by urbanisation worldwide. Approximately 85% of amphibian species threatened by urbanisation occur in the tropics, compared to around 15% in temperate areas (IUCN, Conservation International, and NatureServe, 2006). Many regions of the earth supporting the richest assemblages of amphibians (e.g. tropics) are currently undergoing the highest rates of landscape modification by humans (Gallant et al., 2007). However, studies into the impact of urbanisation on amphibians in tropical and sub-tropical regions are rare. We found only one empirical study on amphibians and urbanisation in a tropical region (Ruiz-Jaén and Aide, 2006). There are currently no studies in English that report urbanisation and amphibians in Africa, Asia or South America, despite the acceleration of urbanisation and the high number of endangered species in these regions (Young et al., 2001, 2004; UNFPA, 2007). Urbanisation is currently responsible for widespread habitat loss in Brazil and is probably the main threat to amphibians in South America (Silvano and Segalla, 2005). Urban areas in China are currently expanding at a rapid rate (Shen et al., 2005), but the impact of the recent massive levels of urbanisation of Chinese cities on amphibians is unknown outside of China.

3.2. *Defining urbanisation in amphibian studies*

Few empirical studies that examined the impact of urbanisation on amphibians explicitly defined "urbanisation" or "urban land". In most cases, the definition of "urban land" is either not stated and only assumed, or is ambiguous, and therefore there is little consistency among studies. Ambiguities in definition and using general and indefinite terms present difficulties in documenting the effects of urbanisation across studies and in meta-analyses. The urbanisation metric most widely used was the proportion of the surrounding landscape covered by urban land. For example, Pearl et al. (2005) quantified the percentage of residential and commercial land, whereas Houlahan and Findlay (2003) quantified building density adjacent to wetlands as indicators of urbanisation. Gagné and Fahrig (2007) defined urban landscapes as having >50% urban land cover, which included residential, commercial and industrial land uses. In assessing the effects of urbanisation on the distribution and abundance of amphibians in streams, Riley et al. (2005) measured the degree of urbanisation within a catchment watershed by calculating the percentage of area upstream that consisted of urban land uses (industrial, commercial, residential, transportation and floodway areas). Streams in watersheds with >8% cover of urban land uses were classified as urban. These problems in defining what constitutes "urban" appear to be inherent in many ecological studies (McIntyre et al., 2000; Theobald, 2004).

Previous studies on urbanisation in ecology have defined urban and suburban areas using human population densities (e.g. McDonnell et al., 1997). Only two papers we reviewed included a measure of human demography; Rubbo and Kiesecker (2005) defined urbanisation using population densities of $\geqslant$450 people per km^2, and Gibbs (2000) used human population densities to assess the relationship between human density and wetland density, proximity and aggregate area along an urban–rural gradient. These two examples therefore highlight the need for progress into considering the social aspect of human-dominated landscapes when assessing amphibian distribution.

Seven studies used road density or cover surrounding ponds as a surrogate of urbanisation, as it is often correlated with the density of urban infrastructure. However, difficulties may arise when using this metric as it may not be possible to determine whether roads or roads in combination with associated human-made structures are affecting amphibian dispersal patterns (Parris, 2006).

Few empirical studies explicitly assessed amphibian–habitat relationships or assessed historical changes to amphibian habitat using urban–rural gradients (but see Gibbs, 2000; Rubbo and Kiesecker, 2005), despite the concept being commonly used to investigate the effects of urbanisation on ecological patterns and processes (McDonnell and Pickett, 1990). Most studies reported the consequences of urbanisation by comparing an urban area to relatively undisturbed or "natural" land use classes (e.g. forest). These studies, however, may not detect the full suite of potential impacts on amphibians from urbanisation, because often there are no clear boundaries between "urban" and "natural" areas (McIntyre et al., 2000).

3.3. *Defining and standardising appropriate landscape scales for the study of amphibians*

The spatial scale over which metrics of urbanisation were measured generally reflected the mean dispersal distances of species included in the studies, and that previous amphibian–habitat studies had shown effects on species richness, presence/absence or abundance at similar scales. In some cases, scales were also chosen to maximise sample size (e.g. Gagné and Fahrig, 2007), or were selected due to the resolution and availability of pre-existing data (e.g. Mensing et al., 1998). Knutson et al. (1999) recorded urban land within a 1000 m buffer radius around each pond as this was the smallest resolution that the scale limitations of the spatial data would allow. The area they measured was much larger than the home range for most anurans but smaller than the maximum dispersal distance recorded and therefore represented a reasonable area of landscape influence from a metapopulation perspective.

The mean maximum scale used in 19 studies that measured urbanisation as a landscape variable within a defined radius around each site was 1432 ± 1249 m (±SD, range: 300–5000 m). This may be insufficient to capture the landscape-level effects on amphibian populations in urban areas, as a recent review on amphibian dispersal highlighted that many species are capable of movements >2 km and some up to 10 km (Smith and Green, 2005). Because the effects of urbanisation on amphibian populations may extend far beyond the scales currently applied in most studies, they may be failing to capture the full response of individual species and communities to urbanisation. For example, Pellet et al. (2004a) found that urban areas, road surfaces and traffic loads had a strong adverse effect on presence of the threatened European tree frog (*Hyla arborea*), even at relatively far distances from ponds (up to 1 km).

3.4. *Future research directions*

The results of our review indicate that the continued urbanisation of landscapes around the world currently threatens many amphibian species. Despite habitat change being among the primary causes of amphibian decline, and that the persistence of many species depends upon conserving populations in human-dominated landscapes, there has been a recent shift in the focus of research on amphibian decline away from the consequences of habitat loss, because of the popularity in researching the causes of "enigmatic" population declines (Gardner et al., 2007). Not only are there few studies on the effects of habitat change on amphibians, there are even fewer on the effects of urbanisation, which is currently the main driver of habitat loss in many parts of the world. We propose the following six recommendations for future studies on amphibians in urban and suburban areas:

1. Greater application of long-term studies on population dynamics in urban and suburban areas may redress the clear bias towards short-term (1–3 years) studies on amphibian–habitat relationships that currently dominate the literature.
2. Greater use of the urban–rural gradient approach would help identify important factors in amphibian–urbanisation relationships and thresholds at various spatial scales (McDonnell and Pickett, 1990; McDonnell and Hahs, in press). Explicit and quantitative definitions of "urbanisation" and "urban" within these studies would remove ambiguity and promote comparative studies of amphibians in urban landscapes.
3. There is a tremendous opportunity and need for future research efforts in urban and suburban areas in tropical environments. Clearly, empirical research on amphibian–habitat relationships in urban and suburban areas of the tropics is required. However, little information exists on the distribution, natural history, life-history or ecology of many amphibians in the tropics, and many tropical areas have yet to be inventoried (Crump, 2003; Silvano and Segalla, 2005).
4. Because most empirical studies reviewed were correlative, the mechanisms of causality between predictor (e.g. urbanisation metrics) and response variables were unknown and can only be hypothesised. Gardner et al. (2007) contend that our ability to mitigate the negative impacts of human activities and develop much needed strategies for the conservation of amphibians depends critically on our understanding of the proximate ecological mechanisms that are responsible for the loss of species, such as the loss of breeding sites and the inability to disperse across hostile landscapes. For example, the use of proximal predictors more closely related to the physiology of the species may provide stronger insight (Pellet et al., 2004a). Manipulative studies that incorporate experimental designs may narrow the current gap in knowledge of proximate causes and responses of amphibian distribution in urban landscapes. Determining the genetic status of extant populations in urban and suburban areas may also offer a means of assessing their long-term viability.
5. Studies need to sample at both the local (<1 km) and landscape (⩾1–10 km) scales in order to capture variability in patterns and abundance that may result from urbanisation, and these studies should consider the scale of movement of the species in the community assemblage. These local and landscape scales have been recommended, respectively, for population-level and metapopulation or landscape-level management of pond-breeding amphibians (Semlitsch, 2008).
6. We advocate caution when assessing impacts of urbanisation using composite measures of diversity alone (e.g. species richness and biodiversity indices), especially when these are derived using ecologically-contrasting taxa that share no functional similarities. Species richness has been a popular metric of assessing the importance of habitat change for amphibians (see Gardner et al., 2007), whereas Cushman (2006) highlighted the importance of assessing species-specific responses to habitat loss and fragmentation. We see greater utility in using complementary response variables such as individual species presence/absence or abundance, together with an overall measure of community diversity. This may enable a better interpretation of the impacts of urbanisation on amphibians.

4. Conclusion

In order to maintain amphibian diversity in urban and suburban landscapes we need to: (1) prevent further habitat loss and degradation of habitat quality, including aquatic and terrestrial habitat; (2) ensure the availability of targeted species of amphibians to maintain viable metapopulations and regional communities, and/or individuals for reintroduction into restored or newly-created habitats; and (3) develop strategies to reconnect the landscape and allow amphibians to disperse between suitable habitats.

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