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Invertebrates in urban areas: A review

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Abstract. As urbanisation is set to continue, understanding the impact on wildlife becomes increasingly important if we are to be able to conserve biodiversity. As an excellent group of bioindicators, invertebrates can allow us to understand some of the forces in urban areas which impact upon biodiversity and wildlife populations. This paper discusses some of the trends in the abundance, diversity and richness of invertebrates related to urbanisation and the specific urban environmental and traffic factors which may be at play.

INTRODUCTION

In the UK, an urban area is defined as having a population of more than 10,000 (2009). Urban areas are made up of a high density of housing, commercial buildings, roads and other paved surfaces (Niemelä, 1999). In 2007, the UK population was greater than 60 million (National Statistics, 2007) compared with 49 million in 1996 (Department for Communities and Local Government, 2000). In 2000, 89.5% of the UK population lived in urban areas compared with 84.2% in 1950 with a predicted rise to 92.4% by 2030 (Population Division Department of Economic and Social Affairs, 2001). This rising UK, and in particular urban, population will lead to rising urbanisation, with a similar trend expected globally (Botkin & Beveridge, 1997). Urbanisation is defined as "the process by which urban ecosystems are created" (McIntyre et al., 2001). As urbanisation has occurred throughout history, habitat types within these areas have changed, meaning that wildlife is influenced. Some habitats have been lost altogether, while others have been reduced and new ones created. New habitats include urban green spaces. Urban areas are therefore a mosaic of land uses, including residential, commercial, industrial and infrastructural, interspersed with green spaces (Breuste et al., 2008). In 2001 it was estimated that UK urban parks alone covered between 127,000 and 147,000 ha (Department for Communities and Local Government, 2001). Urban domestic gardens may also be important urban green spaces and in Sheffield, UK, it is estimated that 33 km^2 or 23% of the area of the city is made up of gardens (Gaston et al., 2005). Other green spaces, such as roundabouts and roadside verges, are often not considered for their contribution to the green element of an urban area which could overlook a significant amount of more natural habitat. With increasing importance placed on the inclusion of urban parks and other urban green spaces in urban planning and increasing global biodiversity interest, studies into urban green spaces are highly relevant now and for the future.

As urbanisation increases, green spaces within urban areas will become increasingly important as wildlife habitats. Urban green spaces are important for biodiversity primarily as wildlife refugia and wildlife movement corridors (Zapparoli, 1997). Furthermore they are also genetic reservoirs which is important for conservation (Zapparoli, 1997). Wildlife can develop and flourish in urban areas so they should not be considered barren wastelands (Davis, 1976; Angold et al., 2006). Many wildlife species find urban areas offer favourable conditions for their survival while other species often adapt. Urbanisation can even increase biodiversity by increasing habitat diversity (Weller & Ganzhorn, 2004; Breuste et al., 2008). Artificial habitats, such as those found in urban areas, have been found to support 12–15% of Britain's scarce and rare species (Gibson, 1998). Urban green spaces are therefore extremely important in the urban environment and consequently it is reasonable that the ecological value of these areas should be included in urban planning and investments (Czechowski, 1982). Little is known, however, about the best methods to maximise these green spaces for use by wildlife which is an essential consideration for the future.

There is great invertebrate diversity within urban areas, including rare and important species (Owen & Owen, 1975; Davis, 1979; Chudzicka, 1986; Zapparoli, 1997; McIntyre, 2000; McIntyre & Hostetler, 2001; Jones, 2003; Helden & Leather, 2004). For example, a high number of insect species have been recorded in the historical literature (since the second half of the 19th century) in Rome, Italy, which may be due to the heterogeneity of the urban area or the suitable geographic (Fattorini, 2011). There are, however, some species which have not been recorded since the 1940s, possibly a result of loss of specialist habitats or diets or detrimental effects of urban conditions (Zapparoli, 1997). This highlights the importance of continued monitoring in urban areas. Davis (1978) noted the loss of invertebrates during the historic expansion of the area of London, UK, although the importance of parks, wasteland and gardens as refugia for invertebrates was highlighted. Brownfield sites, post industrial and urban, in England have been found to be important as refugia for invertebrates so the assumption that these areas are devoid of important and rare species is therefore false (Eyre et al., 2003b). This has been noted in other instances also (Owen & Owen, 1975; McGeoch & Chown, 1997; Hornung et al., 2007).

Most authors believe urbanisation has detrimental effects on invertebrate diversity and abundance (Davis, 1978; Pyle et al., 1981; McIntyre et al., 2001). Urban-rural gradients are often used to look for changes in diversity and abundance of invertebrate groups and provide a method of investigating effects of urbanisation (McDonnell & Pickett, 1990). Some studies have found no changes in the number of or the diversity of invertebrates with proximity to urban areas, however, and negative effects are not ubiquitous. Some examples of negative correlations of invertebrate measures in urban areas are displayed in Table 1. There are also effects on species composition in urban areas relative to non-urban, with increasing dominance of mainly generalist and opportunist species (Czechowski, 1982; Niemelä et al., 2002; Ishitami et al., 2003; Magura et al., 2004; Sadler et al., 2006; Elek & Lövei, 2007; Fujita et al., 2008; Magura et al., 2008a). Urban areas are also more likely to show variation in species composition whereas rural areas have a more stable diversity throughout the season (Klausnitzer & Richter, 1983). Negative correlations of invertebrate numbers in urban areas relative to non-urban, however, are not ubiquitous and some studies have shown little impact on populations or even positive correlations (Table 2).

INVERTEBRATES AS URBAN BIOINDICATORS

McIntyre (2000) summarises the importance of studying invertebrates in urban areas in five points: (1) As a diverse group they give a good indication of general biodiversity of an area. (2) Due to rapid generation times they can respond in a short time to anthropogenic changes to soil and vegetation. (3) They are easy to sample and sampling is not controversial in the public eye. (4) They are present at many trophic levels. (5) They are important in terms of sociology, agronomy and economy within habitats under anthropogenic change. In addition, McIntyre et al. (2001) also noted that invertebrates are important in cycling of organic matter, nutrient cycling, soil aeration and pollination. Thus, they influence the ecosystem function of urban areas. Furthermore, invertebrates act as a food source for higher trophic levels and changes in their numbers can influence both these organisms as well as plants (Jones & Paine, 2006). Invertebrates act as good bioindicators compared with many other animal groups (Zapparoli, 1997; Cameron & Leather, 2012). For insect herbivores they fulfil this role because they will respond directly to plant nutrients, defence chemicals, growth and communities (Jones & Paine, 2006).

As a focus group of terrestrial invertebrates, carabids (Coleoptera: Carabidae) make a particularly good bioindicator group. Carabids are sensitive and respond rapidly to disturbances and environmental change and therefore act as particularly good insect indicators of habitat quality (Lövei & Sunderland, 1996; Boscaini et al., 2000). They are present at different trophic levels (predators, herbivores, detritivores) (Lövei & Sunderland, 1996), are found in almost every habitat type and species can be either generalists or highly specialised (Lövei & Sunderland, 1996). This diversity allows detection of poor quality habitats. Carabids are further suited to be indicators because they are diverse and abundant, taxonomically well known and easily collected using pitfall traps (Rainio & Niemelä, 2003). Previous work has shown that their diversity indices are correlated with those of other Coleoptera (Oliver & Beattie, 1996) and other insect groups (Duelli & Obrist, 1998; Cameron & Leather, 2012). And birds (Gagne & Fahrig, 2011) Further to their use as bioindicators, they are economically important in their own right, being significant predators of agricultural pests and should be conserved (Lövei & Sunderland, 1996).

Much work has utilised them in this role previously and they have been used to measure effects of forest fragmentation (Desender & Bosmans, 1998; Fujita et al., 2008), forest management (Koivula, 2002; Fuller et al., 2008), climate change (Scott & Anderson, 2003), agricultural practices (Desender & Bosmans, 1998; Irmler, 2003), land cover variables (Eyre et al., 2003a, 2004; Eyre & Luff, 2004; Small et al., 2006), biodiversity (Pizzolotto, 1994; Duelli & Obrist, 1998), pollution (Heliövaara & Väisänen, 1993), insecticides (Frampton & Cilgi, 1994; Walsh, 1993), environmental classification (Casale, 1990; Dufrêne et al., 1990; Eyre & Luff, 1990; Mossakowski et al., 1990; Zulka, 1994), habitat quality (Heijerman & Turin, 1994), as well as many more. As noted above they have also been widely utilised as indicators of urbanisation.

As a frequently used bioindicator, carabid species richness would be expected to correlate with the diversity of other groups. Moreover, sites which are good for one group would be predicted to be good for other groups. Previous work has noted that plant diversity shows a positive correlation with carabids in urban woodlands (Croci et al., 2008), in Scottish road verges (Palmer et al., 2004), in arable field margins (Asteraki, 1994) and in small forest fragments in Finland (Halme & Niemelä, 1993). Invertebrate diversity and abundance as a whole and invertebrate predator and herbivore diversity and abundance have also been found to show this pattern (Siemann et al., 1998).

Flight is the primary mode of carabid dispersal for most species, especially into newly formed areas (den Boer, 1970; Lövei & Sunderland, 1996). Their flying ability is dimorphic between and within species: species can be macropterous (winged), brachypterous (short winged but essentially wingless) or dimorphic (containing both macropterous and brachypterous individuals). These differ-

TABLE 1. Examples of negative impacts of urbanisation/roadsides on invertebrate populations

Invertebrate	Pattern	Location	Urban areas	Reason	Reference
Arthropod species richness	Declined in urban	Private gardens	London, UK	Higher temperature, lower humidity, higher pollution, reduced winter sunshine, reduced precipitation in urban	Davis (1978, 1979)
Native bee species richness	Declined in urban	Urban gardens compared with reserves and non-urban	Bronx and East Harlem, USA, compared with New Jersey and New York state	Native bees are limited by urbanisation due to increased habitat loss and fragmentation, pollution, and prevalence of exotic species	Matteson et al. (2008)
The number of phytophagous insects	Declined in urban	On *Artemisia vulgaris* and *Tanacetum vulgare*	Bonn, Germany	Low site diversity and regular flooding in urban	Schmitz (1996)
Butterfly diversity, richness and number of specialists	Declined in urban	Secondary forests and cultivated lands compared with urban parks	Tsukuba City, Japan	High levels of human disturbance or "Intermediate disturbance hypothesis" (Connell, 1978), loss of specialist host plants	Kitahara & Fujii (1994)
Abundance of native specialist butterflies	Declined in urban between 1910 and 1973	Entire urban locality	Staten Island, USA	Loss of host plants and habitats, intrinsic cycling, mosquito insecticides, air pollution	Shapiro & Shapiro (1973)
Butterfly species and abundance	Declined in urban	Transects along the main avenues	Porto Alegre, Brazil	Pollution, urban climate and lower vegetation cover in urban localities	Ruszczyk (1986)
Gall occupation, larval density and species richness of gall-inhabiting Lepidoptera	Declined in urban	On *Acacia karroo*	Pretoria, South Africa	Anthropogenic disturbance	McGeoch & Chown (1997)
Elaterid species richness	Declined in urban	Urban green areas	Warsaw, Poland	Loss of forest habitat and clearance of wood in urban sites	Burakowski & Nowakowski (1981)
Lepidoptera species richness and abundance	Lower on reservations	Intersection reservations compared with grasslands, fields and field verges	Between Imatra and Lappeenranta, SE Finland	Surrounding environment and young age of intersections meaning less vegetation and low soil potassium	Valtonen et al. (2007)
Carabid diversity	Declined in urban	Grassland and graveyard sites	Alberta, Canada	Habitat alterations: loss of unmanaged grassland	Hartley et al. (2007)
Carabid species richness and abundance	Declined in urban	Mixed sites	Hiroshima City, Japan	Unfavourable conditions in urban areas for specialists	Ishitami et al. (2003)
Carabid species richness	Declined in urban	Forest and woodland patches	Helsinki, Finland; Sofia, Bulgaria; Edmonton, Canada	Urban sites are highly disturbed, homogenised, isolated, unfavourable to specialists	Niemelä et al. (2002)
Carabid species richness, abundance and diversity	Declined in urban		Helsinki, Finland	Increased fragmentation, pollution, temperature, recreational usage and exotic species and decreased moisture in urban areas plus many other factors	Venn et al. (2003)
Carabid abundance and diversity	Declined in urban	Woodland patches	Rennes, France	Increase in built surfaces and fragmentation in urban areas	Croci et al. (2008)
Carabid species richness and abundance	Declined in urban	Forest patches	Brussels, Belgium	Urban sites are fragmented and unfavourable to specialists	Gaublomme et al. (2008)
Carabid species richness	Declined in urban	Forest and woodland patches	Hamburg, Germany	Increased isolation of urban sites	Weller & Ganzhorn (2004)
Carabid species richness and diversity	Declined in urban	Oak-sycamore woodlands	Birmingham, UK	High fragmentation and disturbance in urban sites	Sadler et al. (2006)
Weevil diversity	Declined in urban	Willow species – rural to urban gradient	Beijing, China	High fragmentation	Su et al. (2011)

Table 2. Examples of neutral and positive impacts of urbanisation/roadsides on invertebrate populations.

Perceived change	Invertebrate	Pattern	Location	Urban areas	Reason	Reference
Neutral	Soil arthropod diversity and species richness	No pattern	Along the roadside of an expressway	Chicago, USA	Microhabitat differences and local disturbance are more important than urbanisation	Lussenhop (1973)
Neutral	Wasp species richness, abundance and community composition	No pattern	Remnant habitat in urban areas compared with continuous vegetation	Sydney, Australia	Wasps are resilient to urbanisation at this coarse scale	Christie & Hochuli (2009)
Neutral	Carabid abundance and species richness	No significant differences	Forest and woodland patches along an urbanisation gradient	Helsinki, Finland	None given	Alaruikka et al. (2002)
Neutral/community change	Woodlice species richness, abundance and diversity	No pattern, but increases in urban specialist abundance, with a corresponding decrease in forest specialists, was obscuring any pattern	Forested sites along an urbanisation gradient	Debrecen, Hungary	Changes in numbers can be complex relating to preference of disturbance level by individual species. Woodlice also will not follow the intermediate disturbance hypothesis (Connell, 1978) because they are decomposers	Hornung et al. (2007)
Highest at intermediate levels of urbanisation	Butterfly species richness	Highest at intermediate urbanisation level	Mixed sites along an urbanisation gradient	Palo Alto, USA	"Intermediate Disturbance Hypothesis" (Connell, 1978)	Blair & Launer (1997)
Positive	Species of carabid	Lower per trap in urban but total caught in the urban were higher	Urban park compared with suburban area and rural forest	Denmark	Colonisation and invasion of open habitat and generalist species	Elek & Lövei (2007)
Positive	Carabid species richness	Suburban had lowest, urban and rural were higher, although abundance decreased from rural to urban	Woodlands	Debrecen, Hungary	Due to the presence of open habitat species	Magura et al. (2004)
Positive	Spider species richness	Higher in urban sites compared with suburban or rural	Forest patches	Debrecen, Hungary	Due to the presence of open habitat species from the surrounding matric	Magura et al. (2010)
Positive	Butterfly species richness	Higher in tropical gardens	Tropical gardens compared with primary and secondary forest	Sierra Leone	Pruning maintains young leaves, presence of new food resources, gardens combine habitats not normally found together	Owen (1971)
Positive	Invertebrate species	Harbour many beneficial pollinators and predators of agricultural pests thus making them important sources of natural enemies	Roadside verges	Hertfordshire, UK	Contained suitable forage	Free et al. (1975)
Positive	Butterflies and Burnets	Breeding populations present	Roadside verges	Dorset and Hampshire, UK	Presence of suitable host plants and nectar sources	Munguira & Thomas (1992)
Positive	Carabids	Corridors between patches, rare species, some species preferred these sites over larger	Roadside heathlands	Netherlands	Presence of suitable habitat nearby	Vermeulen (1993)
Positive	Carabid early successional species	Highly disturbed roadside acts as refugia	Roadside verges	East Anglia, UK	Due to the bare ground and regular disturbance of the roadside environment	Eversham & Telfer (1994)
Positive	Beetle catches/ carabids	Beetles were mainly generalist carabids with a preference for open habitat but some rare and vulnerable species	Central reservations	Helsinki, Finland	None given	Koivula et al. (2005)

ences in flight ability can be utilised to investigate the effects of site factors related to mobility. As this is within a family it allows a more controlled comparison than comparing different groups. Carabids on newly emerged habitats in Dutch polders were skewed towards small and macropterous species suggesting that these are the best invading species (Ranta & Ås, 1982). Newly formed habitats made from sand mine spoil showed 74% of species were macropterous and 93% of individuals (Kielhorn et al., 1999). Carabid populations in unstable environments, therefore, appear to invest in flight (den Boer, 1970, 1987).

Previous work has indicated that there are fewer brachypterous species and/or individuals present within urban areas because they find it difficult to move between potentially isolated patches of habitat, and/or an increase in macropterous species and/or individuals. This has been noted in many different urban situations (Tischler, 1973; Kegel, 1990; Venn et al., 2003; Koivula et al., 2005; Sadler et al., 2006; Small et al., 2006; Fujita et al., 2008). Results for dimorphic species are more variable. In woodlands in Birmingham, UK there was no pattern in the numbers of wing dimorphic species numbers with increasing urbanisation (Sadler et al., 2006). Carabids in ruderal areas, street margins, parks and gardens in the centre of Berlin were found not to include any brachypterous species, although there were winged individuals of dimorphic species (Kegel, 1990). Carabids on central reservations of main roads in Helsinki, Finland were mainly macropterous or wing dimorphic species (Koivula et al., 2005). Dimorphic species have declined less over the last 50 to 100 years in Europe than macropterous or brachypterous species. This difference arises because the winged forms are able to disperse and colonise while the wingless forms have a high reproductive output (Kotze & O'Hara, 2003).

Flying individuals are less likely to return than walking individuals and this active selection against flying has been previously noted as a potential for isolated islands (den Boer, 1970). It has been suggested in road enclosed forest patches in Helsinki, Finland, that carabids from remnant populations may not be able or want to escape from patches (Koivula & Vermeulen, 2005). This may be the case for brachypterous species, especially as carabids do not like to cross tarmac and roads on foot (Mader, 1984; Mader et al., 1990; Koivula & Vermeulen, 2005). Increasing road density positively correlated with brachypterous species in unmanaged sites in Alberta, Canada (Hartley et al., 2007), indicating that isolation is less important in this case. This explanation relies on the fact that the brachypterous species are a remnant population (Kinnunen et al., 1996), however, and has survived since these urban green spaces were formed.

Carabids vary greatly in size [1.5 to 35 mm (Luff, 2007)], a characteristic which can be utilised to study the impact of site factors. Increasing disturbance is known to decrease body size by being detrimental to larger species (Gray, 1989; Blake et al., 1994; Lövei & Sunderland, 1996). Large species are more negatively affected by disturbance because of their low reproductive output, requirement for larger ranges, smaller populations and slow response to environmental change (Kotze & O'Hara, 2003). They also have a longer life cycle and therefore need stable resources (Blake et al., 1994). There is some overlap between investigations of carabid flight ability and size because smaller species are generally more likely to be flying species (Niemelä et al., 2002; Magura et al., 2004).

Because of the increasing disturbance, high fragmentation and decrease in habitat area of urban green spaces, examples of decline in size (both in terms of species size and mean size of individuals) measured along an urbanisation gradient into urban areas are common (Czechowski, 1982; Kegel, 1990; Alaruikka et al., 2002; Niemelä et al., 2002; Ishitami et al., 2003; Magura et al., 2004, 2006; Sadler et al., 2006; Elek & Lövei, 2007; Fujita et al., 2008).

URBAN EDGE EFFECTS

Although the majority of the edges of urban sites lie next to the road, little work has investigated edge effects on invertebrates as a whole group in urban areas. Green space at the road edge is likely to have very different abiotic and biotic conditions relative to away from the edge. There is increased temperature, decreased moisture, high emission levels, high turbulence, noise, dust, bright lights (especially from car headlights), high salinity (with associated changes in pH) and changes in the composition of plants and animals which increases resource competition, at the road edge (Braun & Flückiger, 1984; Mader, 1984; Mader et al., 1990). High road edge environmental stresses could lead to reduction in diversity according to Gray's (1989) disturbance hypothesis. There may be greater food at the site edge; specific host plants or prey items may exist there but not at the site interiors. Roadside plants can have elevated foliar nitrogen content following exposure to vehicle derived oxides of nitrogen due to direct uptake (Port & Thompson, 1980; Spencer et al., 1988) or stress (Bolsinger & Flückiger, 1989). Herbivores may do better on plants with a higher nitrogen content as this is frequently the limiting factor for their growth (Southwood, 1975; White, 1978; Mattson, 1980; Lightfoot & Whitford, 1990). Therefore, changes in abundance, richness and/or diversity of invertebrate populations at the immediate edge of green space is highly likely. Table 3 shows some examples of invertebrates measured at the edge of green space and away from roads.

FACTORS INFLUENCING URBAN INVEREBRATES

Site age

There is little indication how richness and abundance may be affected by site age, and results from studies investigating this are variable (Sattler et al., 2010). McIntyre (2000) hypothesises that invertebrate diversity should increase with the age of an urbanised site, at least in part because of the addition of exotic species. Also, as sites age, there is succession of the vegetation present (Val-

TABLE 3. Examples of the impact of the road edge on invertebrate populations.

Perceived impact	Invertebrate	Pattern	Location	Urban areas	Reason	Reference
Negative	Carabid abundance and relative biomass	Decreased	Next to motorways in agro-ecosystems	Moscow	Food deficiencies and accumulation of heavy metals at the road edge	Butovsky (1994)
Negative	Soil invertebrate abundance and richness	Increased away	Away from unpaved roads	Cherokee National Forest, Tennessee, USA	Reduced depth of leaf litter close to road	Haskell (2000)
Negative	Elaterid beetle species richness	Decreased in sites closer to the road	Park plots, housing estate plots, street-side plots	Warsaw, Poland	Increasing pollution	Nowakowski (1986)
Negative	Frequency of road crossings by carabids	Low levels of crossings	Undisturbed natural habitat next to roads	Odenwald and Westerwald, Germany	Changes in abiotic and biotic factors making roads less favourable	Mader (1984)
Negative	Road crossing by bumblebees	Avoid flying over roads	Conservation land in a metropolitan area	Boston, Massachusetts, US	Roads separate floral patches into separate populations and bees have high site fidelity	Bhattacharya et al. (2003)
Negative	Dead invertebrates	Many sightings	Roadsides	Athens in Athens County, Ohio, US	Killed by cars or dry out during crossing	Siebert & Conover (1991)
Negative	Dead invertebrates	Many sightings, especially dragonflies and butterflies	Roadsides	Highways in Bandipur National Park, Nagarahole National Park and Mysore, India	Killed by cars or dry out during crossing	Roa & Girish (2007)
Negative / Positive	Soil arthropods	Lower diversity but higher abundance	Roadside compared with a prairie and old field site away from the road.	Chicago, USA	Microhabitat differences such as soil bacteria and fungi and disturbance are more important than urbanisation gradients	Lussenhop (1973)
Neutral/ Negative	Collembola and Enchytraeid worms abundance, species and diversity	No patterns with distance from the road, although Acari increased in abundance further from the road	Roadside verges	Scotland, UK	Altered soil pH	Palmer et al. (2004)
Neutral	Number of arthropod orders	Did not change with increasing distance	Away from a gravel road	The Barrie Islands, Canada	Low resolution	Luce & Crowe (2001)
Neutral	Invertebrate abundance, number of orders	Unrelated to the distance from the edge	Green spaces	California, USA	Ability of invertebrates to disperse, resisting edge effects and some small sites are all "edge"	Bolger et al. (2000)
Neutral	Road crossings by butterflies	Frequent for many species although turbulence could influence them	Roadside verges	Dorset and Hampshire, UK	Mortalities are unlikely	Munguira & Thomas (1992)
Positive	Invertebrate abundance	Decreased with increasing distance	Away from a gravel road	The Barrie Islands, Canada	Represents a natural gap in the environment	Luce & Crowe (2001)
Positive	Invertebrate macrofauna diversity	Increase in invertebrate macrofauna diversity within the first 0.5 m from the road but no relationships beyond	Transects away from the A40	Southern England, UK	None givem	Muskett & Jones (1980)
Positive	Isopods, hemipterans, hymenopterans and collembolans	Greater numbers near the road, with the greatest differences found within the first 13 m	Transects away from the A40	Southern England, UK	May be escaping high density of natural enemies related to the inability of natural enemies to withstand pollution at the road edge	Muskett & Jones (1980)
Positive	Abundance of Coleoptera, non-ant Hymenoptera, spiders and Acari	Higher at edge	Green spaces	California, USA	Release from natural enemies	Bolger et al. (2000)

TABLE 3 continued.

Perceived impact	Invertebrate	Pattern	Location	Urban areas	Reason	Reference
Positive	Carabid species richness	Increased next to road	Mixed coniferous forests	Leksand, Sweden	Roadside verges are dispersal corridors and act as refugia for stenotopic species	Melis et al. (2010)
Positive	*Aphis pomi* density	Higher compared with away from reseravtion	On *Crataegus monogyna* on the central reservation of a motorway	Switzerland	Microclimate, especially increased temperature	Flückiger et al. (1978)
Positive	Ant diversity	Higher at the edge	Highway	South Africa	Decreased competition between ant species	Samways et al. (1997)
Positive	Aphids	Higher	Next to the road	Poland	Escaping predation	Przybylski (1979)
Positive	*Aphis pomi* abundance	Higher	Next to motorway	Switzerland	Decreased parasitism and predation by Coccinellidae, Syrphidae and Cecidomyidae	Braun & Flückiger (1984)
Positive	*Phalera bucephala* (the Buff Tip moth)	Higher	On *Fagus sylvatia* on central reservations and verges of motorways	UK	Enhanced plant nitrogen from vehicle emissions which is beneficial to this species	Port & Thompson (1980)
Positive	*Euproctis similis* (the Gold Tip moth)	Higher	On *Crataegus. monogyna* on central reservations and verges of motorways	UK	Enhanced plant nitrogen from vehicle emissions which is beneficial to this species	Port & Thompson (1980)
Positive	*Aphis fabae* abundance	Higher	On *Viburnum opulus* and *Phaseolus vulgaris* on motorway verges	Switzerland	Increased foliage organic nitrogen and phloem sap total amino acids which is beneficial to this species	Bolsinger & Flückiger (1987, 1989)
Positive	Numbers of invertebrate predators	Higher at the edge	Green spaces	California, USA	High numbers of the Argentine ant (*Lunepithema humile*) with young and brood ants which are a suitable prey, increased detritivores which are prey, which in turn related to greater numbers of non-native grass which provide detritus	Bolger et al. (2000)
Positive	Ant diversity	Higher at the edge	Highway verge	South Africa	High numbers of insect road-kill which provide a food resource	Samways et al. (1997)
Positive	Arboreal hemiptera	Rare species found	Roundabouts	Bracknell, UK	Provision of specific host plants	Helden & Leather (2004)

tonen et al., 2007) which may be related to increased habitat heterogeneity from stratification during vegetation succession (Odum, 1969; Synder & Hendrix, 2008) which in turn increases the niches available to invertebrates. Positive correlations between site age and invertebrates were found for Lepidoptera species richness on intersection reservations in south eastern Finland (Valtonen et al., 2007), leafhopper species diversity and evenness in parks in Warsaw, Poland (Chudzicka, 1986), and spider diversity on a university campus in Japan (Okuma & Kitazawa, 1982).

Negative correlations, however, were found for arthropod species richness in urban gardens in London (Davis, 1978) and invertebrate diversity and abundance in green spaces in California, USA (Bolger et al., 2000). This may be because invertebrates decline with time in urban fragments (Bolger et al., 2000). Species richness of carabids declined on older brownfield sites in the West Midlands, UK because of successional changes, including decreased habitat heterogeneity or vegetation succession (Small et al., 2006).

Woodlice have been previously found to be unaffected by urban site age (Bolger et al., 2000) although in general, woodlice diversity and abundance is expected to increase with site age (Synder & Hendrix, 2008). In California, the total number of orders was also unrelated to site age (Bolger et al., 2000)

Site age was also important in determining butterfly and moth communities on road intersection reservations in south east Finland (Valtonen et al., 2007) and grasshopper and leafhopper communities in urban brownfield sites in Bremen and Berlin in Germany (Strauss & Biedermann, 2006).

Site area

Site area is another important factor in determining invertebrate richness and abundance, particularly because it is informative to know how big green areas need to be to preserve natural levels of diversity (McIntyre, 2000).

The general rule applies that as area of a site increases, richness and abundance also increase according to the species-area relationship (Arrhenius, 1921; Gleason, 1922; Preston, 1962; McGuinness, 1984) and individual-area relationship (Connor et al., 2000). Positive correlations have been noted for invertebrate diversity and abundance in green spaces in California, USA (although number of orders showed no correlation) (Bolger et al., 2000), spider species richness in urban forest fragments in Yokohama and Tokyo, Japan (Miyashita et al., 1998), diversity of butterflies on roadside verges in south east Finland (Saarinen et al., 2005), Lepidoptera and Agromyzidae (Diptera) species richness on roundabouts in Bracknell, UK (Keep, 2006), species richness of Diptera and Coleoptera in city parks in Cincinnati, Ohio, USA (Faeth & Kane, 1978), number of social wasp colonies in urban gardens in Brazil (Alvarenga et al., 2010), carabid species richness in urban green spaces in Bracknell (Leather & Helden, 2005; Stamp, 2006) and carabid species richness in road enclosed forest patches in Helsinki, Finland (Koivula & Vermeulen, 2005).

Site area was also found to only be positively correlated with carabid species richness in rural forest sites and not urban sites along an urbanisation gradient in Brussels, Belgium (Gaublomme et al., 2008). This may be related to the presence of edge preferring carabid species was altering the expected species-area relationship (Lövei et al., 2006).

Butterfly communities on road verges in south east Finland were influenced by verge width which increased food sources and breeding habitat (Saarinen et al., 2005). Area of urban heathland patches in south-eastern Australia was important in determining the community composition of spiders and wasps and area of urban woodlands was important in determining spiders and ant communities (Gibb & Hochuli, 2002). Area affects carabid community composition: in forest fragments in Wog Wog, Australia (Davies & Margules, 1998), urban woodlands in Birmingham, UK (Sadler et al., 2006) and urban forests in Honshu, Japan (Fujita et al., 2008).

Fragmentation, isolation and surrounding land use

Fragmentation decreases the area of habitat available to invertebrates. Paths and other internal barriers could influence invertebrates within green space and this sort of internal fragmentation is less well studied than landscape wide fragmentation. Bumblebee movement investigated in Boston, Massachusetts, USA, found that individuals only cross roads and railways if they were displaced or forced to find new flower resources (Bhattacharya et al., 2003). Soil invertebrate abundance and richness increased away from unpaved roads in Cherokee National Forest, Tennessee, USA, probably as a result of thinning of the leaf litter (Haskell, 2000), and Luce & Crowe (2001) found increased invertebrate abundance closer to a gravel road in the Barrie Islands, Canada. Some species have a requirement for the interior of sites and invasion from outside (Niemelä, 2001). Thus, internal paths and concrete patches could alter invertebrate communities.

Isolation of green space and the surrounding land use has been shown to be important in determining invertebrate richness and abundance (Konvicka & Kadlec, 2011). McIntyre (2000) formed a number of hypotheses associated with isolation in urban areas: scarce or isolated habitat, especially host-plants, should have higher rates of occupation; green spaces which are near to natural habitat or on the edge of urban areas should be more easily colonised by invertebrates than sites in the city centre and therefore should show higher diversity (McIntyre, 2000). The best predictor of diversity in urban gardens in London, UK, was the proportion of land occupied by urban green spaces within 1 km of study sites. This was because where there was more urban green space, there was more likely to be enough suitable environment to sustain a population (Davis, 1979). Butterfly diversity in South West Manchester and Mersey Valley, Manchester, UK, decreased with increasing urban cover because of decreases in host plants and nectar sources (Hardy & Dennis, 1999). One key factor that influences carabids in urban areas is habitat fragmentation (Magura et al., 2004, 2008a, b; Weller & Ganzhorn, 2004; Sadler et al., 2006; Small et al., 2006; Croci et al., 2008; Fujita et al., 2008) with isolated sites with decreased species richness, abundance and/or diversity (Kinnunen et al., 1996; Weller & Ganzhorn, 2004). The matrix of built land is also inhospitable for invertebrates to cross and thus high levels of surrounding suitable habitat is beneficial (Sadler et al., 2006; Small et al., 2006; Croci et al., 2008).

Isolation was important for carabid community composition along an urbanisation gradient in Brussels, Belgium, with greater impact on this measure than in carabid species richness (Gaublomme et al., 2008). Isolation can alter the community because less isolated sites will receive more invasions (Spence et al., 1996; Magura & Tóthmérész, 1997; Magura et al., 2000, 2001; Niemelä, 2001; Magura, 2002; Ewers & Didham, 2006). By affecting colonisation and food resources, surrounding land use can also be important in determining invertebrate communities (Blair & Launer, 1997). Examples include: surrounding built environment for butterflies in Palo Alto, California, USA (Blair & Launer, 1997), distance to other green space for leafhoppers in Warsaw, Poland (Chudzicka, 1986), surrounding forest and agricultural cover for butterflies on road verges and road intersection reservations in south east Finland (Saarinen et al., 2005; Valtonen et al., 2007), and surrounding brownfield sites for grasshoppers and leafhoppers in Bremen and Berlin, Germany (Strauss & Biedermann, 2006).

Pollution / Traffic

Pollutants can influence invertebrates either directly or indirectly. Direct effects are rare (Ginevan et al., 1980; Feir & Hale, 1983). Indirect effects generally act via their food source. For example, indirect effects on herbivores could include changes in the number of the preferred host plant, and/or changes to plant quality and surface texture but also they may be influenced by changes at higher trophic levels. In turn, changes in herbivores influence the higher trophic levels and the rest of the community

(Flückiger et al., 2002). The exact mechanisms of how these plant-herbivore interactions work and how higher trophic interactions act are highly complex and poorly understood (Flückiger et al., 2002). According to McIntyre (2000) invertebrate diversity should decrease with increasing level of pollution.

Numerous studies have shown that roadside plants have elevated foliar nitrogen content following exposure to vehicle derived oxides of nitrogen due to direct uptake (Port & Thompson, 1980; Spencer et al., 1988) or stress related changes in biochemistry caused by the roadside conditions (Bolsinger & Flückiger, 1989). This in turn leads to high herbivore abundance because most groups are nitrogen limited (Southwood, 1975; White, 1978; Mattson, 1980; Lightfoot & Whitford, 1990). Examples include, the Buff Tip moth [*Phalera bucephala* (Noctuidae)) and the Gold Tip moth (*Euproctis similis* (Lymantriidae)] on roadside *Fagus sylvatica* and *Crataegus monogyna*, respectively (Port & Thompson, 1980), aphid numbers on potted *Lolium perenne* (Spencer et al., 1988) and *Aphis pomi* on *Crataegus* spp. on motorway central reservations (Flückiger et al., 1978; Braun & Flückiger, 1984). Studies which fumigated plants with pollutants such as exhaust fumes, O_3, SO_2, CO_2 and NO_x found that herbivores did better and/or showed a preference for them (Dohmen et al., 1984; Trumble et al., 1987; Warrington, 1987; Warrington et al., 1987; Chappelka et al., 1988; Houlden et al., 1990; McNeill & Whittaker, 1990; Warrington & Whittaker, 1990; Holopainen et al., 1991; Flückiger et al., 2002), although this was not universal (Braun & Flückiger, 1989; Brown et al., 1993; Heliövaara & Väisänen, 1993; Holopainen et al., 1994; Salt & Whittaker, 1995; Masters & McNeill, 1996; Bezemer & Jones, 1998; Whittaker, 1999; Viskari et al., 2000; Flückiger et al., 2002).

Vehicle derived heavy metals are an important roadside pollutant. Heavy metal contamination can often result in a loss of invertebrates (Culliney et al., 1986; Tyler et al., 1989; Heliövaara & Väisänen, 1993) and micro-invertebrates in forests in New York, USA, decreased in total abundance with increasing heavy metal concentrations (Pouyat et al., 1994). Total abundance, however, is often unchanged following compensation by tolerant species. Roadsides soil with elevated heavy metal concentrations from vehicles do not always show decreased soil and litter fauna (Williamson & Evans, 1973) but heavy metals from other sources have been correlated with declines in arthropod diversity (Tyler et al., 1989; Pouyat et al., 1994). Some arthropods, such as oribatid mites, earthworms, nematodes and Collembola, seem to be more susceptible to heavy metals (Bengtsson et al., 1985, 1986; Tyler et al., 1989) and heavy metals have been found to decrease woodlice abundance, diversity and biomass (Paoletti & Hassall, 1999). There may also be changes in preferences: terrestrial algae near the M40 contained high concentrations of metals but grazing insect larvae preferred control algae (Sims & Reynolds, 1999).

Surprisingly little work has been carried out on the effect of traffic on invertebrates although it can be expected that turbulence from traffic might affect flight (Braun & Flückiger, 1984) and traffic itself could lead to insect deaths (Seibert & Conover, 1991; Rao & Girish, 2007). Species richness of epigenic beetles along an A type road was higher than along a highway (Bohac et al., 2004). Some examples in the literature note no influence of traffic flow on invertebrates, however: road verge populations of butterflies and burnets in Dorset and Hampshire, UK (Munguira & Thomas, 1992; Thomas et al., 2002), richness, abundance and diversity of butterflies and diurnal moths in south east Finland (Saarinen et al., 2005) and foraging insects on verges of the M1 in Hertfordshire, UK (Free et al., 1975). Acari on roadsides in Scotland, however, had higher species richness with lower traffic although Collembola and Enchytraeid worms had higher species richness and abundance on the low traffic sites (Palmer et al., 2004). One study found that carabid species richness was higher beside a dual carriageway rather than single carriage way or non-trunk road, although this was attributed to habitat heterogeneity (Palmer et al., 2004) and another found high traffic sites had higher abundance relative to low traffic areas (Melis et al., 2010). Furthermore, traffic affected carabid community composition in road enclosed forest patches (Koivula & Vermeulen, 2005). Traffic may also influence the microclimate of the roadside environment (previously discussed).

Grass mowing

Mowing of lawns is usually the primary management of urban green spaces. Some studies have found that certain invertebrate species prefer disturbances such as mowing (Tischler, 1973; Czechowski, 1982) although others concluded that this favoured exotic ruderal species such as the pavement ant (*Tetramorium caespitum*) (King & Green, 1995). Another study actually notes that there was greatest species diversity at intermediate levels of disturbance (Connell, 1978; Blair & Launer, 1997).

In general, however, it is considered a harmful factor because it is an intense disturbance event and would thus negatively impact on invertebrate diversity (Gray, 1989). Mowing influences both the structure and composition of vegetation (Chudzicka, 1986). Furthermore, tall grass has more invertebrate species, individuals and greater diversity and cutting is a non-selective, catastrophic event resulting in a uniform sward (Morris, 2000).

The literature is replete with examples where decreased mowing and/or longer vegetation has benefited communities. For example, butterflies and burnets on roadside verges in Dorset and Hampshire, UK, were found to decline sharply after mowing (Munguira & Thomas, 1992) and on road verges in south east Finland, increased meadow diurnal moths were seen along road verges with taller vegetation for shelter and meadow butterflies were more common when there were more nectar sources (Saarinen et al., 2005). Other studies have compared cut and uncut plots: Acari and Enchytraeid worms had higher abundance on uncut roadsides compared with cut in Scotland, UK (Palmer et al., 2004). More detailed studies show a continuum of management intensity: snail species richness and abundance in urban gardens in Sheffield, UK, was negatively related to increased intensity of management (Smith et al., 2006a, b); lawns in green spaces in Warsaw, Poland, which were less intensely managed (both in terms of mowing and other management) had increased species diversity of leafhoppers (Chudzicka, 1986); higher species richness and abundance of Hemiptera in green spaces in Bracknell, UK, were found in sites with less frequent mowing (Helden & Leather, 2004); less frequently mown sites in Bracknell had higher carabid abundance (Stamp, 2006); carabid species diversity increased with decreasing mowing in urban parks in Helsinki, Finland (Venn & Rokala, 2005); urban areas in Warsaw, Poland where greenery was less managed, a higher diversity of carabids was found and the structure of the community resembled that of unmanaged rural sites (Czechowski, 1982); and in Berlin, Germany carabid species numbers were higher in unmanaged and weed covered urban sites (Kegel, 1990).

These increases may be due to a number of reasons: increased shelter from predators and parasitoids, increased habitat layers and therefore niches, increased food for herbivores, increased prey for predators or parasites, changes in microclimate and more sites for oviposition (Czechowski, 1982; Chudzicka, 1986; Epstein & Kulman, 1990; Lövei & Sunderland, 1996; Morris, 2000; Brose, 2003; Haysom et al., 2004; Helden & Leather, 2004; Magura et al., 2004, 2008a). Further to this, mowing itself may kill off invertebrates (Czechowski, 1982), some species are sensitive to disturbance (Luff, 2007) and some species choose to migrate out of sites with frequent mowing (Hartley et al., 2007)

Gray (1989) noted that opportunistic species can become dominant with increasing disturbance. Leafhopper communities in green spaces in Warsaw, Poland, were determined by intensity of grass management, with more intense management leading to dominance by a few species (Chudzicka, 1986). Diurnal moth communities on road verges in south east Finland were affected by intensity of mowing (Saarinen et al., 2005). Much work has indicated the increases in winged and small carabid species with increasing disturbance such as mowing (den Boer, 1970; Gray, 1989; Blake et al., 1994; Venn & Rokala, 2005; Hartley et al., 2007), for example the size of carabids in uncut areas of urban parks in Helsinki, Finland were found to increase relative to cut areas (Venn & Rokala, 2005). Venn & Rokala (2005) found carabids formed two different communities types in mown lawns (dominated by thermophilic grassland species) and in uncut meadows (dominated by deciduous woodlands species).

Mowing also affects the structure and resources of grassland which has been found to be important for butterflies in Singapore (Koh & Sodhi, 2004), invertebrates in green space in Melbourne, Australia (Kazemi et al., 2009), for grasshoppers and leafhoppers in urban brownfields in Bremen and Berlin, Germany (Strauss & Biedermann, 2006), for nectar resources for butterflies on road verges in south east Finland (Saarinen et al., 2005), and for vegetation height and nectar resources for butterflies and moths on intersection reservations in south east Finland (Valtonen et al., 2007).

Cultivated plants, other exotics and green roofs

Urban landscapes are characterised by a large proportion of non-native plant species (Owen, 1983; Smith et al, 2006; Shrewsbury & Leather, 2012), and this can have profound effects on habitat diversity and insect occurrence (Gaston et al., 2005; Raupp et al., 2010). This can operate in two ways, native insects utilising non-native plants, e.g. the butterfly *Poanes melane* is largely dependent on the Australian grass, *Rytidosperma racemosum* in urban and suburban California (Shapiro, 2006), and it has been estimated that over 40% of butterflies in these settings utilise non-native plants as hosts (Shapiro, 2002; Graves & Shapiro, 2003). Conversely invasive insect pests can be introduced via nursery plants as evidenced by the establishment of the African Lycaenid, *Cacyreus marshalli* in Majorca (Monteys, 1992).

The increasing use of green roofs in towns and cities (Hunter & Hunter, 2008) has also led to an increase in insect diversity in what would otherwise be unsuitable habitats (Kadas, 2011). Green roofs support a wide variety of invertebrates and although probably no more diverse than other brown-field sites can act as additional *refugia* for arthropod biodiversity in cities (McIvor & Lundholm, 2011).

CONCLUSIONS

This paper aims to highlight just some of the factors which may influence the ability of green space to be wildlife reserves and how invertebrate bioindicators could be used in studies such as this. It is obvious that there is potential for increasing the effectiveness of these sites to act as reserves and this will become increasingly important with rising urbanisation. Appropriate management can not only retain biodiversity at current levels, but can increase the numbers of rare and uncommon species and increase the abundance of many species.

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