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Urban domestic gardens (VIII) : environmental correlates of invertebrate abundance

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Abstract. Domestic gardens associated with residential zones form a major component of vegetated land in towns and cities. Such gardens may play a vital role in maintaining biodiversity in urban areas, but variation in the abundance of organisms in gardens has been little explored. We report the results from a case study of 61 domestic gardens in the city of Sheffield, UK. Across 22 invertebrate groups, the median number of individuals recorded per garden was 49, 178, and 1012 in litter collections, pitfall and Malaise trap samples, respectively. Abundance was analysed by stepwise multiple regression and hierarchical *tree* analysis in relation to garden and landscape variables. The amount of variation explained in regression models ranged from 4 to 56%, for data based on pitfall and litter samples, and from 16 to 92% for data from Malaise traps. In total, 31 out of 36 explanatory variables entered into stepwise regression models, and 29 of them did so more than once. Although there was strong evidence only for approximately half of such relationships, in these cases the two methods of analysis corroborated one another. General correlates of invertebrate abundance were lacking, and likely reasons for inconsistencies in the relationships are discussed in the context of sampling and species biology. Correlates of the greatest significance occurred at both landscape (e.g. altitude) and garden scales (e.g. area of canopy vegetation). These factors were associated with species richness as well as abundance.

Introduction

Urbanisation causes wholescale transformation of the local environment, through its impact upon natural vegetation, climate, hydrology, and primary production (Sukopp and Starfinger 1999; Kinzig and Grove 2001). The scale of urbanisation is great: urban areas cover about 4% of the Earth's land surface, more than 4.71 million km^2 (UNDP, UNEP, World Bank & WRI 2000) – roughly equivalent to 19 times the area of the UK, or half that of the USA. Urbanisation is also accelerating worldwide (particularly in global biodiversity hotspots, Liu et al. 2003), therefore comprehending its effects, and consequently reducing its impact, are important goals for ecologists and conservationists.

The consequences of urbanisation include changes in the richness, composition, and individual species' abundance of animal and plant assemblages.

Urbanisation generally reduces native species richness across taxa (e.g. Blair and Launer 1997; Denys and Schmidt 1998; Thompson and Jones 1999; Germaine and Wakeling 2001), although certain groups may be favoured by the creation of novel habitats (e.g. Gilbert 1990; Eversham et al. 1996). Urbanisation tends to increase the proportion of alien species in an assemblage (Roy et al. 1999) with the effect that overall biodiversity may even be enhanced (Pyšek 1993; Blair 1996).

Land in towns and cities that supports vegetation and has freely draining surfaces, generically termed ‘green space’, can reduce the impact of urbanisation. Green space has the potential to lessen detrimental effects on species assemblages by preserving or creating habitat, and by retaining corridors through the urban matrix. A major component of urban green space is formed by domestic gardens associated with residential zones. The few estimates available for UK cities indicate that domestic gardens comprise 19–27% of the entire urban area (Gaston et al. in press), therefore they may play a critical role in maintaining biodiversity in such regions.

Domestic gardens can contain rich plant and animal assemblages (e.g. Owen 1991; Miotk 1996; Saville 1997), but with the exception of birds (BTO Garden BirdWatch scheme, Cannon 2000), the factors related to variation in biodiversity remain poorly understood; studies have focussed on either single gardens (e.g. Allen 1964; Smith 1989; Owen 1991) or a small number of taxa (e.g. Davis 1978; Vickery 1995; Bailey et al. 1998). It is difficult to predict what the relative roles of ‘internal’ and ‘external’ factors may be for biodiversity, since gardens are managed at an individual level, and vary widely in land cover composition and management intensity (e.g. ‘cleanliness’). At the same time, gardens form interconnected tracts of green space, so that they are also influenced by the configuration of vegetated land at a wider scale. Thus gardens differ essentially from isolated patches of green space – the subject of many previous studies of urban biodiversity (e.g. McGeoch and Chown 1997; Miyashita 1998; Denys and Schmidt 1998) – because they constitute much of the urban matrix. Here we report results from a systematic assessment of patterns in invertebrate abundance across a substantial sample of domestic gardens in a major city in the UK, encompassing variation in urban location, density of the built environment and garden age, size and management.

This work is part of a larger study, the Biodiversity of Urban Gardens in Sheffield (BUGS) project, an investigation of the resource that domestic gardens provide for biodiversity and ecosystem functioning (Gaston et al. in press; Smith et al. in press a), the factors that influence the levels of plant biodiversity associated with different gardens (Thompson et al. 2003, 2004) and ways in which features of gardens can be manipulated to enhance biodiversity (Gaston et al. 2005). We have examined patterns in invertebrate biodiversity in terms of both richness, mainly at the species level (the subject of a companion paper: Smith et al. in press b) and abundance of major taxonomic groups, the subject of this report.

Knowledge of abundance is relevant to understanding biodiversity for several reasons. First, abundance and richness are rarely independent, and the persistence of species, or their extent of distribution is often related to their local abundance (Soulé et al. 1988; Denys and Schmidt 1998; Gaston et al. 2000). Second, variation in the total abundance of a taxonomic group is likely to partly reflect the suitability of a habitat, or the availability of resources, for the group's constituent species. Thus abundance may provide useful information about the role of gardens for particular taxa. Third, in terms of ecological function, it is likely that the abundance of groups (in addition to species richness) will significantly influence their contribution to particular 'ecological services' (e.g. pest control, pollination, litter breakdown), and hence the importance of those processes in gardens (Loreau et al. 2002). Fourth, one, possibly unique aspect of garden biodiversity is that most owners will come into their closest contact with wildlife via the garden; therefore what occurs in gardens has great potential to influence people's appreciation of their local environment (Cannon 1999). For many people their perception of garden wildlife will be strongly influenced by the occurrence of the most abundant (and obvious) groups (e.g. bumblebees), while the often subtle differences between species may go unnoticed. A final, pragmatic reason is that for many groups of invertebrates, the resolution of large quantities of sampled material to species level may involve a disproportionate effort, or even be impossible (for example with immature specimens). Therefore examination of abundance data provides a way of exploring the role of gardens as a habitat even for groups which lack full information on species richness.

Methods

Study site

The city of Sheffield, South Yorkshire, UK (53°23′ N, 1°28′ W; Ordnance Survey (O.S.) grid reference SK 38) lies in the centre of England; it is largely surrounded by agricultural land, except where the urban area merges with that of Rotherham to the north-east. The administrative boundaries of the city enclose an area of more than 360 km^2, including farmland and a portion of the Peak District National Park. The study was carried out in the rear gardens (hereafter called 'gardens') of private, owner-occupied houses in the predominantly urbanised region of the city (about 143 km^2, defined as those 1 km × 1 km cells having more than 25% coverage by residential or industrial zones, as judged from O.S. 1:25,000 scale maps, Figure 1). The study focussed on rear gardens because they formed the major garden component of most properties.

Sixty-one gardens were selected as a stratified sample from a convenience sample of 161 householders derived from contacts among ancillary, clerical and academic staff at the University of Sheffield, and from members of the public at lectures or displays (see Discussion about potential sources of bias). This

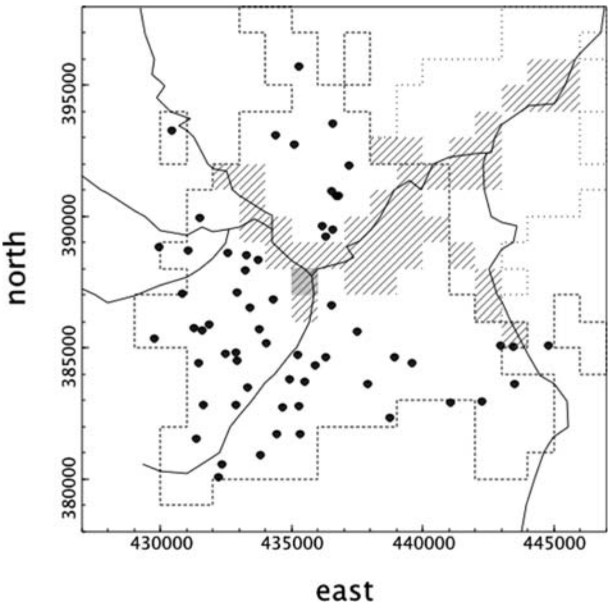

Figure 1. Map of the locations of the 61 study gardens in the predominantly urban area (heavy dashed line) of Sheffield, in relation to zones with > 50% industrial/commercial use (cross-hatching), principal rivers, and the adjoining town of Rotheram to the north-east (light dashed outline). The shaded square indicates 1 km^2 of the central business district, centred on the city hall. Map axes represent distances (m) on the Ordinance Survey national grid; the map covers 20 km by 20 km.

approach was chosen due to the great difficulty in the alternative of recruiting householders at random who were both sympathetic to research being conducted in their gardens, and able to offer daytime access. The sample size was the maximum permitted by the constraints of other aspects of the project (e.g. faunal sampling). By stratifying the sample along key axes of interest – house age and garden size – and selecting values along the entire length of each axis, our method enabled us to explore the influence on landcover composition of such axes, over their full ranges of variation. By this means the results from the study could be generalised to culturally similar areas in the UK even if the distribution of garden sizes differed. House age, approximate garden size, and location were the sole information used in generating the garden sample. Rear gardens ranged from 32 to 940 m^2 in area and their associated properties ranged from 5 to 165 years in age. Blocks of apartments were excluded from the study because they generally lacked private gardens.

Recording garden characteristics

Rear gardens were surveyed between July and September 2000. Principal dimensions were measured to the nearest 0.5 m, and a scale plan was drawn of each garden; this included the side portion on properties occupying corner plots. The plan incorporated boundaries (and their construction), buildings within the garden, and all forms of land use. The areas of each type of land use, and the lengths of linear features, were then estimated from the plan. Distance to the centre of the nearest 1 km×1 km cell having less than 25% coverage by residential or industrial zones was measured. Information on garden management and the intentional provision of resources for wildlife ('wildlife gardening') was gathered from garden owners using a questionnaire (see Appendix A for details). Altitude was recorded to the nearest 10 m, from O.S. 1:50,000 scale maps, and houses ranged between 40 and 250 m above sea level.

Recording vegetation

A complete list was made of all vascular plant taxa during the garden survey, and each taxon was allocated to alien or native categories (nomenclature and status followed Stace (1997) where possible, otherwise Wright 1984). Some plants were allocated to the native taxon (e.g. *Primula vulgaris*, *Aquilegia vulgaris*), even though many garden plants are of hybrid origin. Cultivars were not considered as separate taxa. Although the timing of the survey meant that some strict vernals (e.g. *Anemone blanda*) were missed, the remains of *Hyacinthoides*, *Narcissus* and *Tulipa* spp. were still visible. Measures of vegetation structure were produced by estimating the area covered by a canopy in the following height classes: <0.5, 0.5–1, 1–2, 2–3, and >3 m. The classes were mutually exclusive, and incorporated tree canopies (including those overhanging from outside the garden) but omitted mown lawn. The number of trees taller than 2 m was also recorded.

Garden measurements using digital data

The following variables were measured for each property using Ordnance Survey digital 'Land-line Plus' (1:1250) maps, imported to an ArcView GIS (Environmental Systems Research Institute, Inc.): total plot area, house area, and total garden area (calculated as the area of the plot excluding the house). A series of variables for land use surrounding each garden was also created. Measured for a circular area of 10,000 m^2 (1 ha) centred on each garden, the variables were: number of houses (where more than half of the area of the house was covered), area of roads, area of buildings, area of gardens (plots minus houses), and area of land not in the former categories. Within a 10,000 m^2 (1 ha) square plot centred on each garden, two other measures of local green space were taken from 1:1250 scale aerial photographs ('Cities Revealed', The GeoInformation Group, Cambridge, UK): the area of the contiguous block of green space in which the survey garden lay, and the total ground area of green space in the quadrat (non-built up, unmetalled ground, including gardens, parks, waste ground, woodland and landscaping).

Human population density was measured using POPSURF data at a 200 m grid cell resolution, based on 1991 UK population census data (Martin and Tate 1997). The value of the cell in which a garden lay was used as a measure of local population density. For three gardens where data were missing, a value was calculated from a bilinear interpolation of the four nearest cells.

Invertebrate sampling

Indices of the relative abundance of organisms in gardens (hereafter referred to as abundance) were measured by three methods, selected on the basis of their efficiency in gathering broadly comparable data for a wide range of taxa, across a large number of gardens simultaneously. These measures of abundance were valid for drawing comparisons between gardens, within taxa, where the sampled substrates were similar.

Pitfall trapping

White, disposable plastic coffee cups, 110 mm high and 70 mm wide at the rim, were used for pitfall traps. They were placed in triplicate in the cultivated borders of each of 60 out of the 61 gardens, as widely spaced as practicable. In one garden without borders, traps were placed along the boundary, which comprised fencing and a hedge. Each trap was half-filled with 50% alcohol, rather than ethylene glycol, due to the risk of being found by pets or children. When in use, each trap was covered with a ply-board rain shield, positioned 20 mm above the rim of the trap. Traps were run for 2 weeks at the beginning of each month, from June to October inclusive in 2000, resulting in a total of 15 samples for each garden.

Litter sampling

Samples of leaf litter and organic debris were collected in triplicate from each of the 61 gardens, on a single occasion between the end of July and mid-September 2000. Each sample was taken from a cultivated border, in a circular area of ca. 20 cm diameter, to a depth of ca. 5 cm, and samples within gardens were collected as far apart as possible. The surface substrate was collected if no litter was present. In one garden without borders, the samples were taken from the base of a boundary hedge. Organisms were extracted from the samples using Tullgren funnels, and collected into 70% ethyl alcohol. Organisms that remained in the dried litter samples, in particular snails, were recovered by hand searching.

Malaise trapping

Single Malaise traps (white roof, black walls) were erected in 16 out of the 61 gardens in order to sample flying insects (although samples also contained substantial numbers of arachnids); traps were placed in gardens that spanned the range of property sizes. Malaise traps were located in as standardised a manner as possible in each garden: at the edge of the lawn, with their long axis perpendicular to a border. The traps were operated for the first 2 weeks of June, July and September 2000 and invertebrates were collected in 70% ethyl alcohol.

The taxa sorted from samples were limited to those that could be easily allocated to a group without optical aids, or which would not have taken excessive time to extract; thus true fly (Diptera), springtail and mite families were largely excluded. Sorted specimens were generally grouped by family or order.

Analyses

As is often the case with analyses of this exploratory nature, there was a substantial number of independent variables of possible interest or importance. We examined our data for redundancy, and were able to remove a modest number of intercorrelated variables; in each case the retained variable had a clearer potential biological role, or had been measured with greater confidence. This enabled us to reduce the number of variables to 36, but further reductions would have become increasingly arbitrary as the pattern of intercorrelation was rather diffuse. This was reflected in the failure of a principal components analysis of the remaining independent variables to achieve useful reduction of the data.

In addition, the independent variables (excluding positional variables) were examined for evidence of spatial autocorrelation, but there was little evidence of anything other than weak, and idiosyncratic patterns. Essentially, there was no consistent pattern of gardens in close proximity being more similar in their characteristics than those which were far apart.

Whilst acknowledging that this left rather more variables than is ideal for model fitting, the approach to the analysis was exploratory: the primary aim was to identify what, if any, associations occurred between garden environments and relative abundance, and what evidence there was for general patterns across different groups of organisms. We chose not to try to control for the number of comparisons since, firstly, we were more interested in examining the full range of associations and their relative strengths; and secondly, the conceptual and methodological uncertainties with techniques for doing this would have resulted in arbitrary judgements as to how to apply such corrections (e.g. see Moran 2003). One consequence of this approach is that the weaker results must be viewed cautiously, and they are only presented in tables to give an overview. We used both multiple regression and tree modelling (binary recursive partitioning) to provide descriptive models of the relationships between the abundance of each group of organisms and the independent variables describing environmental characteristics. We are not suggesting that the models produced were either the only, or the best, for explaining the abundance of each group. However, for the first time they do provide a test of which types of garden features may be related to the abundance of various animal groups. The generality of these relationships and the existence of causal mechanisms remain to be explored.

Stepwise multiple regression was used to explore which environmental factors accounted for variation in abundance within each taxonomic group (see Appendix A for the list of factors). Data from triplicate samples (pitfall traps and litter samples) were pooled within each method, for each garden. Also, data were pooled across sampling times for pitfall and Malaise trap samples. Thus each taxon had one observation per sampling method in each garden, and each sampling method was analysed separately. For some sampling methods certain taxa were not analysed due to the small number of individuals. For example, although ants can form an important component of the invertebrate fauna in urban environments (Gibb and Hochuli 2002), they were omitted from the present study because they were absent from 65% of gardens, with only four gardens returning more than 20 individuals. Due to their numerical dominance in pitfall traps, and to their well-known ecology, ground beetles (Carabidae) were treated separately from other beetles.

Five of the independent variables had missing values for a few observations; if these factors failed to enter initial models they were removed in order to maximise degrees of freedom. The values of dependent variables were, when necessary, logarithmically transformed for analyses in order to homogenise variances and normalise residuals. Similarly, the areas of gardens and their internal land uses, of GIS-derived variables, lengths of internal walls and hedges, and proportions were logarithmically or arcsine square root transformed in order to linearise the relationship with the dependent variable.

Tree models (Crawley 2002; denoted *tree* for clarity) were used to check the robustness of our inferences from multiple regression. *Tree* models are well suited to situations where explanatory effects may be contingent, and effects are not simple linear responses. The process involved a sequential binary partitioning of the data with respect to the independent variables. The independent variable explaining the maximum deviance was selected first, and the data were split into two subgroups at a threshold value of this variable, such that the split gave the best reduction of total deviance in the group. This process was then repeated for each of the two subgroups, again selecting from all the independent variables, and continued with each successive subgroup until a group contained too few data to be further partitioned. Here we consider only the most important independent variables in each *tree* model, generally the results of the first two partitions (producing up to four groups, although partitioning sometimes stopped before). Fitting *tree* models was carried out using the *tree* package in R (Ihaka & Gentleman 1996).

Results

Twenty-two different invertebrate taxa were sorted across three sampling methods. The same nine taxa were identified from litter samples and pitfall traps, based on 5448 and 17,466 specimens respectively; 16 taxa were identified in Malaise traps, based on 15,570 individuals (Table 1). The median number of individuals recorded per garden (across taxa, for sorted groups) was 49, 178,

Table 1. Relative abundances of individuals from 22 different invertebrate taxa, and percentage occupancy of gardens, recorded in (panel a) litter samples – 61 gardens, (panel b) pitfall traps – 60 gardens, and (panel c) Malaise traps – 16 gardens.

	% gardens	Sum	Mean	Median	Minimum	Maximum
Panel a: litter samples						
Woodlice	100	3941	65.7	42.5	1	334
Snails	90.2	581	9.52	8	0	47
Millipedes	70.5	249	4.08	2	0	33
Beetles (others)	90.0	237	3.88	2	0	28
Spiders	90.2	224	3.67	3	0	20
Centipedes	60.6	89	1.46	1	0	9
Slugs	42.6	60	0.98	0	0	12
Harvestmen	36.0	50	0.82	0	0	6
Beetles (Carabidae)	16.6	17	0.28	0	0	4
Panel b: pitfall traps						
Woodlice	100	7903	132	70	4	1293
Slugs	100	3416	56.9	49	1	355
Beetles (Carabidae)	93.3	3144	52.4	27.5	0	272
Beetles (others)	100	1185	19.8	12.0	1	316
Spiders	100	842	14.0	10.0	1	67
Snails	83.3	436	7.27	4.5	0	59
Harvestmen	83.3	413	6.88	4	0	49
Millipedes	55.0	87	1.45	1	0	11
Centipedes	43.3	40	0.67	0	0	7
Panel c: Malaise traps						
Parasitoid wasps	100	3655	228.4	204.5	97	440
Hoverflies	100	2345	146.6	142.5	47	421
Moths	100	2080	130.0	101.5	45	317
True bugs	100	1223	76.4	62.0	25	288
Soldier-flies	93.8	1159	72.4	57.5	0	248
Bumble bees	100	1131	70.7	52.0	10	246
Social wasps	100	856	53.5	30.0	6	236
Beetles	100	672	42.0	36.5	14	100
Craneflies	100	645	40.3	32.5	5	82
Long-legged-flies	100	621	38.8	30.5	3	187
Sawflies	100	372	23.2	17.5	4	60
Spiders	100	338	21.1	17.5	6	47
Dance-flies	93.8	274	17.1	8.5	0	118
Solitary bees	75.0	80	5.00	2	0	27
Solitary wasps	81.2	61	3.81	2	0	21
Harvestmen	62.5	58	3.63	1.5	0	15

and 1012 in litter, pitfall and Malaise trap samples, respectively. Woodlice dominated the samples of ground-dwelling organisms. Comprising 72.3% of the total sorted litter samples, they were more than six times as abundant as the next taxon, snails; woodlice formed 45.2% of the total sorted pitfall samples, and were approximately four times more numerous than beetles or slugs. As might be expected from the mobility of organisms, pitfall traps recorded more individuals than litter samples in all sorted taxa except snails, centipedes, and millipedes. Flies were the dominant group in Malaise trap samples even before sorting (32.4% of the sorted catch, with hoverflies alone forming 15.1%), although parasitoid wasps were also strongly represented, accounting for 23.5% of the total sorted catch. In the following sections each invertebrate taxon is treated in turn, with results from regression analyses followed by those from the *tree* models.

Beetles (Arthropoda, Insecta: Coleoptera)

Ground beetles (Carabidae). Abundance of ground beetles in pitfall traps was positively related to the area of green space surrounding a garden, followed by the number of trees; habitat diversity was negatively related (Table 2, panel a). This result was partially reflected in the *tree* analysis (Table): the primary split was on the contiguous area of green space in which the garden lay, with secondary splits on garden ‘permeability’ (i.e. percentage of boundary not comprising walls) and number of alien plant taxa (panel a of Tables 3 and 4).

Beetles other than Carabidae. No variables entered the model for other beetles based solely on litter sampling. For pitfall traps, the only significant factor common to the regression on ground beetles was the area of green space, although the area of vegetation canopy above 2 m was also positively associated (and this variable is closely correlated to number of trees). The richness of native plant taxa, number of surrounding houses, and intensity of garden management were further positively associated with non-Carabidae abundance; distance on a northerly axis and area of hard surfaces in a garden were negatively related (Table 2, panel a). The area of canopy above 2 m high was also the primary split in the *tree* analysis, and the higher group only further subdivided on the area of hard surfaces (panel a of Tables 3 and 4). For beetles in Malaise traps, a negative relationship with altitude was the sole factor in the model, accounting for over half the variation in abundance (Table 2, panel b). This relationship was corroborated by the *tree* analysis, where altitude was also the only split (panel b of Tables 3 and 4).

Spiders (Arthropoda, Arachnida: Aranea)

Less than 10% of the variation in spider abundance was explained by the multiple regression, either for litter or pitfall data. Single factors entered each model: the proportion of vegetative material in litter samples for the former, and area of surrounding gardens for the latter (Table 2, panel a). For the *tree* analyses, the primary split for spiders in litter was the area of canopy above 2 m high; thereafter, the lower group divided on the size of the green space fragment. Concerning spiders in pitfall traps, data split on garden permeability, with the upper group further dividing on house age (panel a of Tables 3 and 4).

A strong, negative association with altitude, and a weaker positive relationship with length of garden walls, accounted for more than half the variation in spider abundance in Malaise trap samples (Table 2, panel b); altitude contributed 97% of that explained. The sole split in the *tree* analysis was on the garden perimeter–area ratio (panel b of Tables 3 and 4).

Harvestmen (Arthropoda, Arachnida: Opiliones)

The abundance of harvestmen in litter samples was related positively to garden size, proportion of permeable boundary and house age, but negatively to altitude. Only marginally significant factors entered the model based on pitfall samples (Table 2, panel a). In the *tree* analyses, harvestmen in litter were associated positively with area of vegetation above a level of 2 m; secondary splits were on the area of green space in the garden and the length of boundary abutting other gardens (panel a of Tables 3 and 4). For pitfall samples, harvestmen were more abundant in gardens with smaller proportions of boundary abutting green space. Native plant taxon richness and altitude formed the secondary splits (panel a of Tables 3 and 4). A greater proportion of the variation in abundance was explained for harvestmen in Malaise trap samples. Variation was positively related to the areas of lawn and vegetation canopy below 2 m and negatively to the area of surrounding gardens (Table 2, panel b). The latter result was corroborated by the *tree* analysis, with harvestmen being more abundant at sites with a smaller area of surrounding gardens (panel b of Tables 3 and 4).

Slugs (Mollusca: Gastropoda)

The abundance of slugs in pitfall traps was strongly positively related to the area of vegetation canopy above 2 m in height, and to the richness of alien plant taxa; the area of hard surfaces was strongly negatively related (Table 2, panel a). According to the *tree* analysis, slug abundance declined in gardens to the east, with data then splitting on the area of canopy above 2 m high and the structural diversity of the vegetation (panel a of Tables 3 and 4).

Snails (Mollusca: Gastropoda)

Models for snails in pitfall traps and litter explained very similar degrees of variation, and included relatively large numbers of factors (Table 2, panel a).

Table 2. Stepwise multiple regression: matrices showing the relationships between independent variables (environmental and housing characteristics; no. in italics refers to description of variable in Appendix A) and the relative abundance of individuals in invertebrate taxa (see Methods for details) for (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps.

Panel a: Pitfall trap and litter samples:		Ground beetles	Beetles (others)	Spiders	Spiders	Harvestmen	Harvestmen	Slugs	Snails	Snails	Centipedes	Centipedes	Millipedes	Woodlice	Woodlice
Source of data:		P	P	L	P	L	P	P	L	P	L	P	L	L	P
Model d.f.:		4, 54	6, 52	1, 59	1, 58	4, 54	3, 57	3, 56	7, 50	8, 46	2, 56	3, 54	1, 59	4, 56	2, 57
Model r^2_{adj}:		0.38	0.46	0.06	0.07	0.40	0.17	0.41	0.56	0.53	0.08	0.16	0.04	0.25	0.18
Alien taxon richness	*2*							**2**							
Native taxon richness	*3*		1												
Distance east	*5*								**−2**	**−2**					
Distance north	*6*		**−2**												**2**
House age	*7*					1									
Altitude	*8*					**−2**	(1)								
Habitat diversity	*10*	−1													
Structural diversity	*11*								1	1					
Garden area	*12*					**2**									
Perimeter–area ratio	*13*								**−2**						
Area of lawn	*14*									−1		1			
Area of hard surface	*16*		**−3**					**−3**				**−3**		1	
Presence of pond	*17*	(−1)					(1)			−1					
Presence of composting	*18*									1					1
Canopy < 2 m	*19*								−1						
Canopy > 2 m	*20*		**3**					**3**						**3**	
No. of trees	*21*	2													
Length of hedges	*23*								1	**3**					
Length of walls	*24*								1	**2**			(1)		
% permeable boundary	*26*					**2**									

% green on boundary	*27*						(−1)				(1)						
No. of houses	*29*		1														
Area of gardens	*30*				1						(−1)			−1			
Total green space	*31*	**3**	**2**											−1			
Green space fragment	*32*											(1)					
Management index	*33*		1						**−3**								
Use of slug pellets	*34*									**−3**							

Panel b: Malaise trap samples:		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Model d.f.:		1, 14	2, 12	3, 12	1, 14	3, 10	4, 9	4, 10	4, 11	3, 11	2, 13	3, 14	4, 11	3, 12	1, 14	2, 13	5, 10
Model r^2_{adj}:		0.54	0.63	0.56	0.16	0.86	0.81	0.91	0.64	0.86	0.48	0.60	0.90	0.52	0.41	0.58	0.92
Native taxon richness	*3*					**3**											**3**
Distance east	*5*										1	(1)					
Distance north	*6*								1	**3**							
House age	*7*												**−2**				
Altitude	*8*	**−3**	**−3**					**−3**					**3**				
Rural proximity	*9*											−1		**2**			
Habitat diversity	*10*										1					**3**	
Structural diversity	*11*															**−1**	
Garden area	*12*												**−3**				
Perimeter–area ratio	13							**2**									**−3**
Area of lawn	*14*			1			**2**										
Presence of pond	*17*				(1)												**2**
Presence of composting	*18*						**2**										
Canopy < 2 m	*19*			**2**													

Table 2. Continued.

Panel b: Malaise trap samples:		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Model d.f.:		1, 14	2, 12	3, 12	1, 14	3, 10	4, 9	4, 10	4, 11	3, 11	2, 13	3, 14	4, 11	3, 12	1, 14	2, 13	5, 10
Model r^2_{adj}:		0.54	0.63	0.56	0.16	0.86	0.81	0.91	0.64	0.86	0.48	0.60	0.90	0.52	0.41	0.58	0.92
Canopy > 2 m	*20*							**3**									
No. of trees	*21*								**2**	**3**			**3**		**2**		
Length of hedges	*23*								**−2**					(−1)			
Length of walls	*24*		(1)														
Local population density	*28*						**2**							1			**3**
No. of houses	*29*																**3**
Area of gardens	*30*			−1		**−2**	−1		−1								
Total green space	*31*							**3**									
Green space fragment	*32*									**−3**		1					
Wildlife index	*35*					**−2**											

In each cell, '+' or '–' indicate the direction of the relationship; for level of significance: **3** = $p < 0.001$, **2** = $p < 0.01$, 1 = $p < 0.05$, (1) = $0.10 > p > 0.05$.

Table 3. Tree analysis: matrices showing the relationships between independent variables (environmental and housing characteristics; no. in italics refers to Appendix A) and the relative abundance of individuals in invertebrate taxa (see Methods for details) for (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps.

Panel a: pitfall trap and litter samples

Source of data:		Ground beetles P	Beetles (others) P	Spiders L	Spiders P	Harvestmen L	Harvestmen P	Slugs P	Snails L	Snails P	Centipedes L	Centipedes P	Millipedes L	Woodlice L	Woodlice P
Alien taxon richness	*2*	B+													B–
Native taxon richness	*3*						B+								
Distance east	*5*							A–	B–	B–			B–		
Distance north	*6*														A+
House age	*7*				B+										
Altitude	*8*						B+								
Structural diversity	*11*							B–							
Area of lawn	*14*								B–						
Area vegetated	*15*					B–				A+					
Area of hard surface	*16*		B–												
Canopy > 2 m	*20*		A+	A+		A+		B+						B+	
No. of trees	*21*														
Boundary with gardens	*25*					B–									
% permeable boundary	*26*	B–			A+										
% green on boundary	*27*						A–								
Local population density	*28*											B–			
Area of gardens	*30*										A–				
Total green space	*31*												A– B+		
Green space fragment	*32*	A+		B–					A+					A+ B–	B+
Management index	*35*										B+	A–			

Table 3. Continued.

Panel b: Malaise trap samples		Beetles	Spiders	Harvestmen	Bumble bees	Solitary bees	Solitary wasps	Social wasps	Sawflies	Parasitoids	Moths	True bugs	Craneflies	Dance-flies	Long-legged flies	Soldier-flies	Hoverflies
Native taxon richness	*3*					A+	A+										
Distance east	*5*											A+					
Altitude	*8*	A−															
Perimeter–area ratio	*13*		A−		A−									A−			
Area vegetated	*15*															A−	
Presence of pond	*17*							A+							A+		A+
Canopy > 2 m	*20*												A+				
Length of walls	*24*									A+							
% boundary with gardens	*25*										A+						
No. of houses	*29*								A+								
Area of gardens	*30*			A−													

In each cell, ‘A’ and ‘B’ indicate the 1st and 2nd variables, respectively, on which the data split, and ‘+’ and ‘–’ show the direction of the relationship. Data for all groups from Malaise traps split only once.

Table 4. *Tree* analyses showing details for up to the first two partitions of data for the relative abundance of individuals in invertebrate taxa: (panel a) data from pitfall traps (P) and litter samples (L), and (panel b) data from Malaise traps (see Analyses for details).

Taxon		1st partition	Threshold		Above, below	2nd partition	Threshold		Above, below
Ground beetles	P	Green space fragment	936 m^2	+	28.4	% permeable boundary	90%	–	11.3
									46.7
					3.90	Alien taxon richness	49.3 species	+	8.34
									1.82
Beetles (others)	P	Canopy > 2 m	6.93 m^2	+	15.1	Area of hard surface	35.4 m^2	–	10.3
									23.8
					4.98	—			
Spiders	L	Canopy > 2 m	11.5 m^2	+	5.13	—			
					2.75	Green space fragment	2917 m^2	–	1.43
									3.96
Spiders	P	% permeable boundary	37%	+	19.1	House age	30 yrs	+	22.5
									11.8
					7.76	—			
Harvestmen	L	Canopy > 2 m	23.5 m^2	+	1.2	Area vegetated	18.4 m^2	–	0.0
									0.7
					0.2	Boundary with gardens	33.5 m	–	0.7
									2.7
Harvestmen	P	% green on boundary	0.89	–	4.3	Native taxon richness	50.0 species	+	7.2
									2.4
					12.0	Altitude	175 m	+	21.0
									7.2
Slugs	P	Distance east		–	37.3	Canopy > 2 m	8.9 m^2	+	42.8
									18.4
					82.4	Structural diversity	0.6	–	52.7
									129.1
Snails	L	Green space fragment	1441 m^2	+	9.7	Distance east		–	2.4
									12.0
					3.0	Area of lawn	38.0 m^2	–	1.52

Table 4. Continued.

Taxon		1st partition	Threshold		Above, below	2nd partition	Threshold		Above, below
									4.12
Snails	P	Area vegetated	172.4 m^2	+	17.9	—			
					4.2	Distance east		–	1.32
									4.84
Centipedes	L	Area of gardens	2854 m^2	–	1.2	Management index	9.5	+	1.7
									0.6
					3.6	—			
Centipedes	P	Management index	4.5	–	0.4	Local population density	2.35 ha^{-1}	–	0.4
									1.2
					2.2	—			
Millipedes	L	Total green space	4471 m^2	–	2.8	Total green space	7217 m^2	+	10.4
									1.8
					9.3	Distance east		–	4.3
									16.4
Woodlice	L	Green space fragment	1090 m^2	+	51.4	Canopy > 2 m	10.5 m^2	+	63.2
									21.2
					16.2	Green space fragment	374 m^2	–	9.0
									37.2
Woodlice	P	Distance north		+	160.7	Alien taxon richness	60.4 species	–	69.5
									313.3
					44.9	Green space fragment	936 m^2	+	58.2
									21.1

Columns show the independent variables at either the primary or secondary partitions, and their associated threshold values, directions of relationship ('+' and '-'), and values of sub-group means above and below the split.

Threshold values of the Distance east were relative and are not shown. Data for all groups from Malaise traps split only once. Pitfall trap and litter samples.

Table 5. Malaise trap samples.

Taxon	1st partition	Threshold		Above, below
Beetles	Altitude	140 m	–	23.6 46.6
Spiders	Perimeter–area ratio	0.295	–	13.0 28.1
Harvestmen	Area of gardens	5881 m^2	–	0.3 6.4
Bumble bees	Perimeter–area ratio	0.290	+	116.4 38.4
Solitary bees	Native taxon richness	50.4 species	+	6.3 1.9
Solitary wasps	Native taxon richness	43.9 species	+	3.4 1.4
Social wasps	Presence of pond		+	61.8 26.6
Sawflies	No. of houses	28.5 houses	+	31.1 14.9
Parasitoids	Length of walls	18.9 m	+	304.8 148.2
Moths	% boundary with gardens	91%	+	146.6 71.0
True bugs	Distance east		+	79.4 43.2
Craneflies	Canopy > 2 m	41.1 m^2	+	62.1 17.0
Dance-flies	Perimeter–area ratio	0.29	+	17.1 5.34
Long-legged-flies	Presence of pond		+	35.0 10.3
Soldier-flies	Area vegetated	105 m^2	–	13.8 93.5
Hoverflies	Presence of pond		+	182.4 88.7

Distance on an easterly axis, structural diversity of the vegetation, and lengths of hedges and walls in gardens were common to both models, though the latter two effects were greater for pitfall data. Respectively, the use of slug pellets (molluscicides) and the index of management intensity had strong negative relationships with snail abundance in pitfall traps and litter, accounting for 21 and 36% of explained variation in models.

The area of green space fragment was the primary split in the *tree* analysis for litter data, with the sub-groups splitting on distance east and area of lawn. For snails in pitfall traps, the data split on area of vegetated land uses in a garden. The lower group only then split on distance east, and as for litter data, snails were more abundant in the west (panel a of Tables 3 and 4).

Centipedes (Arthropoda: Chilopoda)

Centipede abundance in litter was not strongly related to any factors. The area of hard surfaces had the strongest, and negative, effect on centipede abundance in pitfall traps, while the area of lawn was weakly positively related (Table 2, panel a). The area of surrounding gardens was negatively related to abundance in litter in the *tree* analyses; only the data above the split bisected further, on index of garden management intensity. Abundance in pitfall traps was negatively associated with the index of garden management intensity; the data split further, for the upper group only, on local human population density (panel a of Tables 3 and 4).

Millipedes (Arthropoda: Diplopoda)

No variables were strongly related to millipede abundance in either litter or pitfall samples (Table 2, panel a). In the *tree* analysis, the primary split was on the surrounding area of green space, with secondary splits on area of green space and distance east (panel a of Tables 3 and 4).

Woodlice (Arthropoda: Crustacea, Isopoda)

The model for litter data for woodlice explained slightly more variation, with four factors, than that for pitfall traps, in which only two entered (Table 2, panel a). No factors were common to both models, the most important for litter was the positive relationship with extent of vegetation canopy above 2 m, while for pitfalls it was distance north. There was weak evidence for negative associations between abundance in litter and both the area of gardens and total green space. In the *tree* analyses (panel a of Tables 3 and 4), the litter data split first on green space fragment area, and secondarily on area of canopy above 2 m and, again, green space fragment area. The pitfall data split on distance north, and then on green space fragment area alien plant taxon richness.

Bumble bees (Arthropoda, Insecta, Hymenoptera: Apidae)

No significant relationships existed for bumble bee abundance (Table 2, panel b). The *tree* analysis indicated that abundance was greater in gardens with a large perimeter–area ratio (i.e. in smaller gardens, panel b of Tables 3 and 4).

Solitary bees (Arthropoda, Insecta, Hymenoptera: Apoidea)

Native plant richness was positively related to abundance of solitary bees, and explained 56% of variation in the regression model (Table 2, panel b); the area of gardens in the surroundings, and an index of wildlife gardening, were negatively related. Data divided also on native plant richness in the *tree* analysis (panel b of Tables 3 and 4).

Solitary wasps (Arthropoda, Insecta, Hymenoptera: Specoidea, Vespoidea)

The regression model also explained a large proportion of the variation in solitary wasp abundance. Positive relationships existed with area of lawn, the presence of composting, and local human population density. In common with solitary bees, abundance was negatively related to the area of surrounding gardens (Table 2, panel b). Similarly, the primary split in the *tree* analysis was native plant richness (panel b of Tables 3 and 4).

Social wasps (Arthropoda, Insecta, Hymenoptera: Vespidae)

Virtually all the variation in abundance of social wasps was explained by four factors (Table 2, panel b), of which two positively related ones, canopy vegetation above 2 m and area of surrounding green space, explained 34 and 26% respectively. Other variables strongly associated with social wasp abundance were altitude (negatively), and the garden perimeter–area ratio (positively). The sole split in the *tree* analysis was on the presence of ponds (panel b of Tables 3 and 4).

Sawflies (Arthropoda, Insecta, Hymenoptera: Symphyta)

Sawfly abundance was related positively to number of trees in a garden and distance north, and negatively to the length of hedges and area of surrounding gardens (Table 2, panel b); number of trees accounted for 32% of the variation in abundance. The number of houses in the surrounding 1 ha was the sole split in the *tree* analysis (panel b of Tables 3 and 4).

Parasitoid wasps (Arthropoda, Insecta, Hymenoptera: Ichneumonidae)

As for sawflies, number of trees and distance north were important effects in the regression model for parasitoid wasps, with trees explaining 61% of variation in abundance. Parasitoid abundance was negatively related to the area of green space in which the garden lay (Table 2, panel b). The *tree* analysis indicated that parasitoids were more abundant in gardens with a greater length of walls (panel b of Tables 3 and 4).

Moths (Arthropoda, Insecta: Lepidoptera, excluding butterflies, Papilionoidea)

There was some evidence for strong relationships for moths with the distance east and garden habitat diversity, which explained nearly half the variation in moth abundance (Table 2, panel b). The percentage of garden boundary abutting green space formed the primary split in the *tree* model (panel b of Tables 3 and 4).

True bugs (Arthropoda, Insecta: Hemiptera, excluding Sternorrhyncha)

True bug abundance was related positively to the area of green space in which a garden lay, and it increased towards the rural edge (Table 2, panel b). The *tree* analysis indicated a sole split on distance east (panel b of Tables 3 and 4).

Craneflies (Arthropoda, Insecta, Diptera: Tipulidae, Pediciidae, Limoniidae and Ptychopteridae)

The regression analysis for craneflies accounted for 90% of variation in abundance, and a positive association with the number of trees was twice as important as the next factor, altitude (also positive, unlike most cases with other taxa). Garden area and house age were strongly negatively related (Table 2, panel b). According to the *tree* analysis (panel b of Tables 3 and 4), craneflies were more abundant in gardens with more vegetation canopy above 2 m.

Dance-flies (Arthropoda, Insecta, Diptera: Empididae)

Distance from the rural edge and local human population density were positively associated with the abundance of dance-flies (Table 2, panel b). In the *tree* analysis perimeter–area ratio was the sole split (panel b of Tables 3 and 4).

Long-legged-flies (Arthropoda, Insecta, Diptera: Dolichopodidae)

The number of trees was the only factor related (positively) to abundance of long-legged-flies, accounting for 41% of variation (Table 2, panel b); in the *tree* model (panel b of Tables 3 and 4) long-legged-flies were more abundant in gardens with ponds compared to those without.

Soldier-flies (Arthropoda, Insecta, Diptera: Stratiomyidae)

Abundance was strongly positively related to habitat diversity in a garden, and weakly negatively related to structural diversity (Table 2, panel b). The *tree* model indicated that soldier-flies were more abundant in gardens with relatively less vegetated landcover (panel b of Tables 3 and 4).

Hoverflies (Arthropoda, Insecta, Diptera: Syrphidae)

Native plant richness, local human population density, number of houses and presence of ponds all had strong positive relations with hoverfly abundance, while the perimeter–area ratio of the garden was negatively associated (Table 2, panel b). In the *tree* model (panel b of Tables 3 and 4), hoverflies were very much more abundant in gardens containing ponds.

Discussion

Our need to work intensively in gardens for all the components of the BUGS project meant that survey gardens were drawn from owner-occupiers who were either relatively interested in their gardens or sympathetic to the presence of university researchers (but not necessarily motivated by their gardens). Our sample possessed relatively more large (detached) houses, and fewer small (terraced) ones: terraced, semi-detached and detached houses comprised 16, 56, and 28% of the sample respectively, compared to 50, 44, and 6% occurring in a random sample ($n = 218$) of Sheffield gardens (Gaston et al. in press). Thus the results of the study need to be interpreted in this context. Nevertheless, it is also clear that a substantial majority of UK residents invests time and interest in the garden: a random survey of Sheffield garden owners indicated that more than 75% enjoyed their garden environment, while less than 10% valued nothing about their garden (Dunnett and Qasim 2000). Our experience also revealed that owners' interest in the project or in wildlife issues did not necessarily match effort spent on the garden, due to constraints on time such as young children or a busy job. We therefore believe that our approach allowed us to survey the full range of variation in interest and creativity one might expect to encounter in a random sample (and possibly more): from gardens used daily to those largely untouched for 10 years; from gardens including wildlife meadows and ponds to those with nothing but a lawn. Further, our sample contained the full span of garden sizes as found in a random sample (Dunnett and Qasim 2000), which permitted us fully to investigate landcover in relation to garden area.

For the twenty-two invertebrate taxa examined, a broad range of factors were significantly related to their abundance in gardens. These factors operated across geographical scales, from characteristics of gardens and their management, to effects at the level of the landscape. Thirty-one out of 36 explanatory variables entered stepwise regression models at least once, and 29 did so more than once. As was found for similar analyses of species richness in the same study (Smith et al. in press b), the amount of variation explained by models varied, though in many cases it was reasonably large (Table 2). For data based on pitfall and litter samples, the total ranged from 4 to 56%, yet for Malaise traps it ranged from 16 to 92%, with the majority of models accounting for more than 50% of variation in abundance. Strong, consistent patterns did not emerge for the effects of factors across taxa. Results of the *tree* analyses partially supported the relationships identified in regression models (Table 3): in 16 out of 30 analyses (53%), the primary or secondary splits in the data occurred on variables, or closely correlated ones, that also featured in regressions.

Geographical scales of explanatory factors

The abundances of invertebrate taxa were related to variables external and internal to gardens. Of the former, the distances on easterly (snails and moths) and northerly (beetles other than Carabidae, sawflies and parasitoid wasps) axes represented the largest scales at which correlations occurred, over distances of more than 10 km. Altitude, varying by more than 200 m across the sample gardens, was strongly negatively related to the abundances in Malaise traps of beetles, spiders and social wasps, but positively to craneflies. Independent evidence for an effect of local climate on garden biodiversity is provided by the species composition of garden lawns in Sheffield. Most of the variation in the vascular plant composition of lawns was explained by Principal Components Analysis axes correlated with the west-east decline in altitude, such that plants of woodland or damp habitats were more common in the west, while weeds of waste ground were more common in the east (Thompson et al. 2004).

Measures of the extent of green space surrounding each study garden (within the 1 ha cell) featured strongly in models only occasionally: these were either the summed area of surrounding gardens (solitary bees), the summed area of all green space (beetles and social wasps), or the size of the contiguous green space fragment in which the garden lay (parasitoid wasps). Further, the directions of relationships were sometimes contrary to expectation if one predicted that green space area should have been positively correlated with the numbers of invertebrates in gardens. The general absence of strong effects for the suite of green space variables has two implications. Either the range of variation in green space extent was insufficient to detect effects, or other correlates of abundance were more important. As the total amount of green space ranged between 28 and 79% of the 1 ha cell centred on each garden, the second explanation seems more probable. Total green space was at least strongly related to the abundance of beetles in pitfall and litter samples, and to ground beetles in particular; but this finding is not supported by evidence for ground beetles in London gardens, where green space was measured at a larger scale (correlation of $\log_{10}$ abundance with % green space in a 20 ha cell, $r = -0.13$, $n = 15$, $p > 0.05$; from data in Davis 1978).

The majority of variables that correlated with abundance occurred at the scale of the garden itself (17 out of 23, 74%, for data from pitfall and litter samples, and 15 out of 24, 62%, for data from Malaise trap samples), and this pattern was reflected in the *tree* analyses too (11 out of 15 variables, 73%, on which data split for pitfall and litter data, and 8 out of 11, 73%, for Malaise trap data). The predominant factors were those associated with vegetation structure in gardens: canopy above 2 m was strongly positively related to beetles (other than Carabidae) and slugs in pitfall traps, while the area of hard surfaces was strongly negatively related to centipedes, beetles (other than Carabidae) and slugs in pitfall traps; woodlice in litter were also strongly positively related to canopy > 2 m. Sawflies, parasitoid wasps, craneflies and long-legged flies in Malaise trap samples were all strongly positively associated with the number of trees in gardens (itself closely correlated with canopy > 2 m, Smith et al. in press a). The significance of vegetation structure has been demonstrated previously for mammals: various height classes of vegetation were more important than measures of urbanisation in determining the abundances of small mammals in urban habitat patches (Dickman and Doncaster 1987). In contrast, the diversity of vegetation structures did not appear as important. Structural diversity probably is significant when considered across all taxa in a garden, whereas individual taxa are perhaps only associated with specific components of the vegetation.

On the basis of previous research in urban environments (e.g. McGeoch and Chown 1997; Miyashita et al. 1998), some garden variables that might have been expected to be important correlates of biodiversity in gardens played relatively minor roles. For example, measures of patch size and richness – garden area and land use diversity – entered models rarely. Garden area and house age were strongly negatively related to cranefly abundance alone, and habitat diversity was only strongly positively associated with soldier-flies. Such a result might have arisen because gardens comprise much of the surrounding habitat matrix; therefore the fauna recorded in a particular garden is not isolated from external populations, and thus less influenced by patch characteristics. It is possible that had we studied smaller organisms, such as the soil mesofauna, then effects due to the 'patch' sampled (e.g. a flower bed or area of uncut lawn) may have become apparent. Having said this, disturbance in gardens due to movements in soil and plant material, and during general redesign of gardens, are likely to homogenise invertebrate assemblages. The members of relatively sessile taxa, such as molluscs, centipedes and millipedes, were virtually ubiquitous in Sheffield gardens (Smith et al. in press b).

The species richness of plants in gardens also featured infrequently in models, although native plant richness formed strong positive relationships with the abundance of solitary bees and hoverflies, and these taxa are known to be closely associated with flora. This result was corroborated by the *tree* analysis, and by the strong relationship between the species richness of solitary bees and total plant richness (Smith et al. in press b; a further analysis, replacing native richness by % native taxa, to control for the positive correlation between the sizes of alien and native components, did not alter the result). Similarly, measures of garden management or disturbance – the use of slug pellets and the index of management intensity – were only strongly (negatively) related to snails in pitfall and litter traps respectively. The composition of litter was only weakly related to one out of the seven groups (spiders) in litter samples.

Although some plausible relationships are noted above, there were numerous cases where associations between an invertebrate group and an independent variable were obscure. For some of these cases the variables are probably correlated with other factors of real significance. Examples include slugs and woodlice related to canopy above 2 m, and snails related to the lengths of hedges and walls in gardens; all these instances could be linked to the provision of shelter or litter. Other explanatory variables, however, are less obvious, e.g. the association of garden perimeter–area ratio (greater in smaller gardens) with snails in litter, social wasps, and hoverflies. The presence of ponds and, again, perimeter–area ratio were the primary splits for 6 out of 16 groups in the *tree* analyses of Malaise trap data (Table 3, panel b), yet the reason for their inclusion is unclear.

Inconsistencies in explanatory factors

The correlates of invertebrate abundance were relatively inconsistent between taxa, and they mirror the results for species richness in the same study of Sheffield gardens (Smith et al. in press b). There are several possible reasons for this. First, as stressed previously, it is likely that some of the apparent associations were chance results: a large number of variables was examined, and evidence for many of the relationships was weak; respectively, only 44 and 66% of the significance values for factors in models of pitfall/litter and Malaise data had a probability <0.01. However, even for factors with strong evidence, the direction was often dependent on the taxon. Second, a wide range of taxa was studied: one would expect different factors to be associated with the abundance of taxa of dissimilar life histories and biology, e.g. predatory spiders compared to omnivorous molluscs. Third, the three sampling methods operated at different scales. Pitfall trapping and litter sampling were effective over relatively small areas, at the sampling point itself, or in the immediate vicinity. Therefore the taxa that such methods sampled, typically woodlice, millipedes, centipedes, and ground-dwelling beetles, arachnids and molluscs, should have better reflected local factors. In contrast, Malaise traps sampled a predominantly aerial, mobile fauna (likely to have originated from outside as well as within the garden), so that the recorded taxa should have reflected broader-scale factors. Although this latter prediction was confirmed for species richness (Smith et al. in press b), it was not borne out for abundance, where the number of factors related to the scale of the garden was similar between sampling methods.

Inferences from abundance and species richness

Urbanisation frequently leads to declines in species richness and in abundance within species. However, overall abundance of a taxon (as measured across species) may fall at a slower rate because certain species, often termed ‘urban exploiters', thrive in urban environments as other species disappear (Blair 1996; Denys and Schmidt 1998; Germaine and Wakeling 2001). Thus the abundance of organisms in a taxon may not necessarily be closely linked to the group's species richness. In the present study, some of the important explanatory factors related to abundance were also associated with species richness (Smith et al. in press b). The strongest cases were: canopy above 2 m and the number of trees for beetle abundance and species richness, respectively; distance east and altitude (which are negatively correlated) for beetle abundance and richness in Malaise traps; distance north for sawflies; altitude for spiders in Malaise traps; length of walls for snails; and plant richness for solitary bees. Such congruence suggests that where the abundance of particular invertebrate groups was high, numbers were enhanced due to a relatively large number of species, rather than to a small number of species that contributed a disproportionate number of individuals.

Indeed, when gardens were ranked according to abundance and species richness, 9 out of 16 invertebrate group-sampling method combinations (a subset of taxa, as species richness had not been evaluated for all) showed strong correlations between the two measures of biodiversity (Spearman Rank correlations on untransformed variables: beetles in pitfall traps: $r_s = 0.61$, $p < 0.001$; beetles in Malaise traps: $r_s = 0.78$, $p < 0.001$; spiders in litter: $r_s = 0.46$, $p < 0.001$; spiders in pitfall traps: $r_s = 0.63$, $p < 0.001$; spiders in Malaise traps: $r_s = 0.54$, $p < 0.05$; snails: $r_s = 0.69$, $p < 0.001$; millipedes: $r_s = 0.81$, $p < 0.001$; solitary bees: $r_s = 0.96$, $p < 0.001$; and solitary wasps: $r_s = 0.87$, $p < 0.001$). Correlations were not significant for slugs, centipedes, woodlice, bumble bees, sawflies, craneflies and true bugs; the first four of which were species-poor, but often very widespread and abundant groups. Thus for a range of relatively species-rich invertebrate groups, the significant correlations indicate that certain gardens are associated with both high species richness and abundance.

Conclusions

Many factors were related to invertebrate abundance in urban gardens, although very few assumed importance for more than a few taxa. This lack of evidence for general determinants of abundance is to be expected, as a consequence of the range of sampling methods used and the wide variety of invertebrate taxa examined, with their associated differences in mobility and resource requirements. The present study contrasts with work on habitat fragments, which has found strong effects related to patch characteristics; instead, urban gardens are interconnected over large areas and individual garden size is therefore less directly significant. In trying to extract those environmental correlates of greatest importance, the suite of variables associated with garden vegetation and its structure would be foremost. Providing mature vegetation and trees in urban gardens could be the best way of enhancing abundance in the widest possible range of taxa. Such action is largely under the control of garden owners, although the current trend in the UK for new houses to possess small gardens may discourage owners from planting trees. Further, as abundance was closely linked to species richness for a significant proportion of the taxa in this study, then appropriate garden management could have benefits for overall biodiversity.

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Appendix A. Independent variables used in analyses of relative abundance (see methods)

(1) Richness of higher plant taxa in garden; (2) richness of alien higher plant taxa in garden; (3) richness of native higher plant taxa in garden; (4) proportion of alien higher plant taxa; (5) easting, Ordnance Survey National Grid map coordinate; (6) northing, Ordnance Survey National Grid map coordinate; (7) age of house calculated in 2000; (8) altitude, m above sea level; (9) rural proximity: distance in km from centre of nearest 1 km cell with $<25\%$ urban land use; (10) habitat diversity: Simpson's diversity index for land uses in each garden; (11) structural diversity: Simpson's diversity index for vegetation canopy cover classes: <0.5, 0.5–1, 1–2, 2–3, and >3 m in each garden; (12) area of rear garden in m^2; (13) perimeter–area ratio: ratio of 'exposed' (i.e. excluding perimeter along rear of house) garden perimeter to garden area; (14) area of grass in rear garden (cut + uncut portions); (15) area of non-grass green space in rear garden (grass paths + cultivated border + vegetable patch + neglected/uncultivated); (16) area of non-green space in rear garden (hard paths + patios + green house + sheds + garage + decking); (17) presence of ponds in a rear garden (scored 1 or 0); (18) presence of compost bins or heaps in a rear garden (scored 1 or 0); (19) area of vegetation canopy 0–2 m (excluding mown grass); (20) area of vegetation canopy >2 m; (21) no. of trees >2 m tall in rear garden; (22) exposed perimeter length of rear garden (i.e. excluding perimeter along rear of house); (23) length of hedges in rear garden, m; (24) length of walls in rear garden, m; (25) length of garden boundary abutting other gardens, m; (26) proportion of garden boundary permeable to movement by animals (i.e. not composed of mortared walls); (27)

proportion of boundary abutting green space; (28) human population density (no. $40 \times 10^3 m^{-2}$, or 4 ha^{-1}), POPSURF 1991 census data; 26–29 recorded from GIS, for 1 ha circular plot centred on survey garden: (29) no. of houses (where > half of property is included), (30) area of domestic gardens, (31) area of all green space, (32) area of contiguous green space fragment; (33) management intensity index- summation of following values of management variables, data from questionnaire: (a) index of intensity of weeding (weak 1–5 strong), (b) index of intensity of pruning vegetation (weak 1–5 strong); (c) index of intensity of watering borders (weak 1–5 strong), (d) dead-heading flowers (scored 1 or 0), (e) collecting fallen leaves in autumn (scored 1 or 0), (f) use of fertiliser in garden (scored 1 or 0), (g) use of herbicides in garden (scored 1 or 0), (h) use of pesticides in garden (scored 1 or 0); (34) use of slug pellets (scored 1 or 0); (35) wildlife management index – summation of following wildlife gardening variables, data from questionnaire: (a) bird feeding (scored 1 or 0), (b) provision of nest box for birds (scored 1 or 0), (c) other management specifically to attract wildlife (scored 1 or 0); (36) estimate of proportion of vegetative matter in litter sample, averaged across replicates in a garden.

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