Biodiversity and Conservation (2006) 15:2415–2438
DOI 10.1007/s10531-004-5014-0

Urban domestic gardens (VI): environmental correlates of invertebrate species richness

RICHARD M. SMITH*, PHILIP H. WARREN, KEN THOMPSON and KEVIN J. GASTON

*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK; *Author for correspondence (e-mail: r.m.smith@sheffield.ac.uk; phone: + 44-1904-793679)*

Received 5 December 2003; accepted in revised form 10 October 2004

Key words: Backyard, Biodiversity, Green space, Home garden, Scale, *tree* analysis, Urbanisation

Abstract. Domestic gardens associated with residential zones form a major component of undeveloped land in towns and cities. Such gardens may play a vital role in maintaining biodiversity in urban areas, but explanations for the variation in the richness of species assemblages in gardens are lacking. We report the results from a case study of 12 invertebrate groups in 61 domestic gardens in the city of Sheffield, UK. The mean number of species within a taxon, recorded per garden, was no greater than 3, 10, and 20 species in litter, pitfall trap and Malaise trap samples, respectively. Relatively speciose groups exhibited high turnover between gardens, with typically 50% of the group occurring only once. In contrast, several species-poor taxa were virtually ubiquitous. Species richness was analysed by multiple regression and hierarchical *tree* analysis in relation to garden and landscape variables. In general, the two methods of analysis corroborated one another. In total, 22 explanatory variables entered into regression models, although 12 of them only did so once. The amount of variation in species richness explained in models was generally quite high, with the factors involved operating over a range of scales. However, the patterns that emerged were not consistent across taxa. The most important predictors of species richness, of relevance to land use planners, were components of garden vegetation, especially the abundance of trees. Likely reasons for inconsistencies in the relationships are discussed in the context of sampling and species biology.

Introduction

Urbanisation causes wholesale transformation of the local environment, affecting it at a fundamental level by altering habitat, climate, hydrology, and primary production (Sukopp and Starfinger 1999; Kinzig and Grove 2001). An important consequence is change in the composition of species assemblages. Urbanisation generally reduces native species richness across plant and animal taxa (Blair 1996; Denys and Schmidt 1998; Roy et al. 1999; Germaine and Wakeling 2001), although certain groups may be favoured by the creation of novel habitats (e.g. lichens, Gilbert 1990; ground beetles, Eversham et al. 1996) and overall biodiversity may be enhanced by the presence of alien species (Pyšek 1993).

Undeveloped land in towns and cities, generically termed ‘green space’, supports vegetation and ‘unsealed’ surfaces, and it can ameliorate the detrimental effects of urbanisation on species assemblages by preserving or creating habitat, and by maintaining corridors for movement through the urban matrix. Domestic gardens associated with residential zones form a major component of urban green space. The few estimates available for UK cities indicate that domestic gardens comprise 19–27% of the entire urban area (Gaston et al. in press b), therefore they may play a critical role in maintaining biodiversity in such regions (e.g. Owen 1991; Miotk 1996; Saville 1997; Owen 2002). With the exception of birds (BTO Garden BirdWatch scheme, Cannon 2000) evidence is limited when trying to explain variation in the richness of garden assemblages. It is either based on long-term data from single gardens (e.g. Allen 1964; Smith 1989; Owen 1991) or on short term data from multiple gardens for a very restricted range of taxa (e.g. Davis 1978; Vickery 1995; Bailey et al. 1998). In order to understand the contributions of different factors related to species richness in urban gardens it is necessary to sample a suite of gardens and taxa simultaneously.

Previous studies in urban environments have demonstrated that the features of habitat patches, such as their size (McGeoch and Chown 1997; Miyashita et al. 1998) and degree of isolation (Soulé et al. 1988; Denys and Schmidt 1998; Fernández-Juricic 2000) are significant factors in determining species richness. Conditions surrounding patches, such as building density, are also influential factors (Jokimäki 1999; Germaine and Wakeling 2001). In the case of urban domestic gardens, it is difficult to predict what the relative roles of 'internal' and 'external' factors may be, since gardens are managed at an individual level, yet they form interconnected tracts of green space. Therefore gardens differ essentially from other components of green space because they constitute much of the urban matrix, rather than existing as isolated patches of habitat.

In this paper we investigate the factors associated with variation in invertebrate species richness in urban domestic gardens, using the city of Sheffield as a case study. This study constitutes part of the Biodiversity of Urban Gardens in Sheffield (BUGS) project, a wider investigation of the resource that domestic gardens provide for biodiversity and ecosystem functioning (Gaston et al. in press b; Smith et al. in press), the factors that influence the levels of 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. in press a).

Methods

Study site

The city of Sheffield, South Yorkshire, UK (53° 23′ N, 1° 28′ W; OS 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 61 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 by eye from Ordnance Survey 1:25000 scale maps) (Figure 1). The study focussed on rear gardens, which form the major garden component of most properties.

Sixty-one gardens were selected from a pool 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. This 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. Our method also

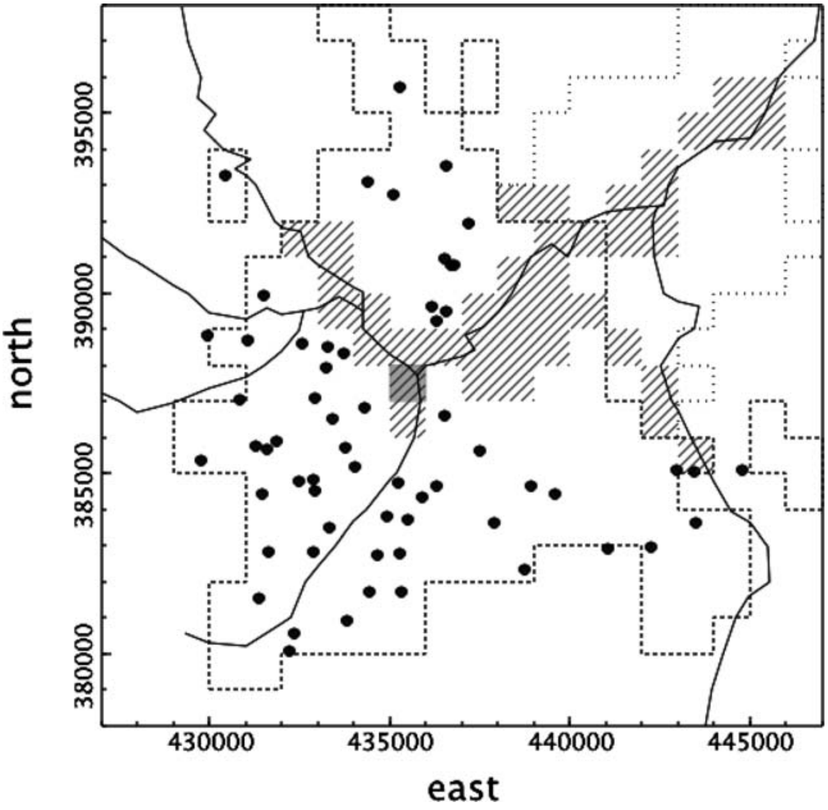

Figure 1. Map of the locations of the 61 study gardens in the predominantly urban area (heavy dashed line) of Sheffield, in relation to zones with > 50% industrial/commercial use (cross-hatching), principal rivers, and the adjoining town of Rotheram to the north-east (light dashed outline). The shaded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

enabled us to maximise variation in the environmental axes of interest, e.g. house age, garden size, and location across the urban area. Housing was characterised as terraced (two or more adjoining dwellings), semi-detached (one adjoining dwelling), and detached (no adjoining dwellings); they comprised 16, 56, and 28% of the sample, respectively (compared to a random sample of 50, 44, and 6% ($n = 218$) taken from all Sheffield gardens, Gaston et al. in press b). Rear gardens ranged from 32–940 m^2 in area and their associated properties ranged from 5–165 years in age. Altitude was recorded to the nearest 10 m, from Ordnance Survey 1:50,000 scale maps, and gardens ranged between 40 and 250 m above sea level.

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, of which 22 were recognised (Smith et al. ms.). The areas of each type of land use, and the lengths of linear features, were 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 1 for details).

Recording the garden flora and 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 m, 0.5–1 m, 1–2 m, 2–3 m, 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 a Geographic Information System (GIS)

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. A circular area of 10,000 m^2 (1 ha, radius c. 56 m), centred on each garden, was believed sufficient to sample the local land uses that might exert an effect on the invertebrates recorded in a garden; this scale of sampling was also adequate in detecting changes in housing density. The variables were: number of houses (where more than half of the area of the house was covered), area of road and pavement, 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.

Species sampling

The taxa studied in gardens were limited to those that could be identified by the appropriate specialists, or for which reference specimens could be checked.

Leaf-mining insects

This guild of insects was recorded during the inventory of garden plants, in 56 out of the 61 gardens; species were identified from characteristics of the mine, and by rearing adults. Tree species were included by searching foliage up to c. 2 m from the ground.

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 opened for the first 2 weeks of each month, June to October inclusive in 2000, resulting in a total of 15 samples (3 locations × 5 months) for each garden.

Litter sampling

Samples of leaf litter and organic debris were collected in triplicate from each of the 61 gardens between the end of July and mid-September 2000. Each sample was taken from a cultivated border, in a circular area of c. 20 cm diameter, to a depth of c. 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 60 gardens in order to sample flying insects (although samples also contained substantial numbers of arachnids); traps were placed in gardens where householders were willing to accommodate them, and those gardens 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 two weeks of June, July and September 2000 and invertebrates were collected in 70% ethyl alcohol.

Litter, pitfall and Malaise sampling were all selected for their efficiency in gathering standardised data for a wide range of taxa, across a large number of gardens simultaneously. They sampled species richness per unit area (species density; for Malaise traps, based on the area of netting obstructing insect flight paths), although in the cases of pitfall and Malaise traps the area would have varied according to the differential mobilities of the sampled faunas. Nevertheless, the methods remained comparable between gardens because the sampling locations and habitat were similar. With certain exceptions (such as leaf-miners – see above) sampling total garden richness requires considerable resources, can be hard to standardise, and would have been difficult to achieve for the large number of gardens in the survey. However, the scales at which species richness was measured for each group need to be borne in mind when considering the results.

Analyses

We attempted to control the number of independent variables of possible importance by removing closely correlated, and hence redundant, variables.

In each case we retained the variable with the clearer potential biological role, or for which we were most confident of the measurement process. We reduced the number of variables to 32, but a principal components analysis on these failed to reduce the data usefully; nine principal components were required to account for 75% of the variance, and the influences of the original variables on components were typically small (correlation of < 0.3). Although this number of variables was not ideal for model fitting, the aim of the analysis was to identify what, if any, associations occurred between garden environments and species richness, and whether general patterns appeared across different groups of organisms. In addition, the independent variables (excluding positional variables) were checked for evidence of spatial autocorrelation, but there was no consistent pattern for gardens close to each other being more similar than those which were far apart.

The rigour of the analysis was increased by using two modelling approaches and observing how closely the results compared. We used multiple regression and binary recursive partitioning (tree modelling – see below) to provide descriptive models of the relationships between the richness of each group of organisms and the independent variables describing environmental characteristics. The generality of these relationships and the existence of causal mechanisms remain to be explored.

Stepwise multiple regression was used to examine which environmental factors accounted for variation in species richness within each taxonomic group (see Appendix 1 for the list of factors). 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. Data from triplicate samples (pitfall traps and litter samples) were pooled for each garden, and data for all methods were pooled across months. The data for centipedes, millipedes and woodlice, and for spiders, harvestmen and pseudoscorpions were combined, because the number of species per garden was too low to analyse when the taxa were treated individually (Table 1). Similarly, data from litter samples and pitfall traps were amalgamated within a taxon where the number of species was low. The two methods both sampled the ground-dwelling assemblage, and sampling effort within methods was identical across gardens. Whilst none of these data pooling steps was ideal, it was preferable to analyse the data at the most practicable level possible rather than discard significant parts of the sampled taxa.

The values of dependent variables were, when necessary, logarithmically transformed for analyses in order to homogenise variances and normalise residuals. 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 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

Table 1. Invertebrate taxa recorded from (a) litter samples (61 gardens), (b) pitfall traps (60 gardens), and (c) Malaise traps (16 gardens).

Taxon	No. of individuals	No. of species	Mean no. of species garden^{-1}	Minimum no. of species garden^{-1}	Maximum no. of species garden^{-1}
(a) *Litter samples*					
Beetles	254	62	2.4	0	8
Slugs	60	4	0.7	0	3
Snails	581	17	2.8	0	8
Spiders	224	20	0.77	0	3
Harvestmen	50	7	0.44	0	2
Pseudoscorpions	16	3	0.23	0	2
Centipedes	89	6	0.80	0	3
Millipedes	249	10	1.3	0	4
Woodlice	3941	8	2.6	0	5
(b) *Pitfall traps*					
Beetles	4329	139	9.4	2	20
Slugs	3416	13	4.9	1	7
Snails	436	13	4.2	0	10
Spiders	842	57	5.1	1	15
Harvestmen	413	14	1.6	0	4
Pseudoscorpions	1	1	0.02	0	1
Centipedes	40	5	1.2	0	3
Millipedes	87	9	1.9	0	6
Woodlice	7903	8	3.4	1	6
(c) *Malaise traps*					
Beetles	672	147	19.9	11	45
Spiders	338	39	6.1	2	11
Harvestmen	56	4	1.0	0	3
Bumblebees	1131	9	6.0	4	8
Sawflies	372	37	7.8	3	17
Craneflies	645	47	10.3	4	17
True bugs	1223	81	13.9	9	20
Solitary bees	80	21	2.8	0	11
Solitary wasps	61	20	2.4	0	10

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).

Results

The same nine principal higher taxa were identified from litter samples and pitfall traps, based on 5464 and 17467 specimens, respectively; nine main taxa were identified in Malaise traps, based on 4578 individuals (Table 1). Species richness was generally low, compared to what might have been expected from garden faunal lists (e.g. Owen 1991): the mean number of species, within a taxon, recorded per garden was no greater than 3, 10, and 20 species in litter, pitfall and Malaise samples, respectively. Indeed, the maximum number of species per taxon in a garden never exceeded 8, 20, and 45 in litter, pitfall and Malaise samples, respectively.

The number of species recorded per garden was generally low compared to the species list summed over all gardens (e.g. spiders and beetles in pitfall traps and litter samples, Table 1), indicating high turnover in species composition between gardens. In taxa where more than 19 species were recorded, around a half of those species occurred in just a single garden – for pitfall plus litter (Figure 2): beetles 48%; spiders 42%; and in malaise traps (Figure 3): spiders 62%, craneflies 46%, sawflies 53%, true bugs 43%, solitary bees 57%, and solitary wasps 45%. In contrast, many members of relatively species-poor taxa were widely distributed across gardens, e.g. isopods and molluscs in pitfall and litter samples (Figure 2), and bumblebees in Malaise traps (Figure 3).

Leaf-mining insects (Arthropoda, Insecta: Diptera, Lepidoptera, Coleoptera, Hymenoptera)

Fifty-four leaf-mining species were recorded across 56 gardens, occurring on 104 plant taxa. The leaf-miner species were represented by flies (Diptera, 55.5%), moths (Lepidoptera, 33.3%), sawflies (Hymenoptera, Symphyta: 9.26%), and beetles (Coleoptera, 1.85%).

The number of trees > 2 m high in a garden explained 73% of the total variation in leaf-miner species richness; this was more than 10 times the variation as for other factors (Figure 4, Table 2). The *tree* analysis corroborated the above result: the primary split occurred for canopy vegetation above 2 m high, a measure which reflects well the canopy contributed by trees. The data were separated into groups above and below 47.5 m^2 of canopy > 2 m, with means of 12.1 and 4.2 leaf-mining species, respectively. The latter group was further split along the variable for vegetation > 2 m (means of 5.3 and 2.9 species above and below 10.5 m^2), whilst the former split on the proportion of boundary that abutted green space (means of 13.6 and 7.6 species above and below a threshold of 78%).

Beetles (Arthropoda, Insecta: Coleoptera)

The model for combined pitfall trap and litter sample data (Table 2) indicated that positive relationships with beetle species richness were, most importantly,

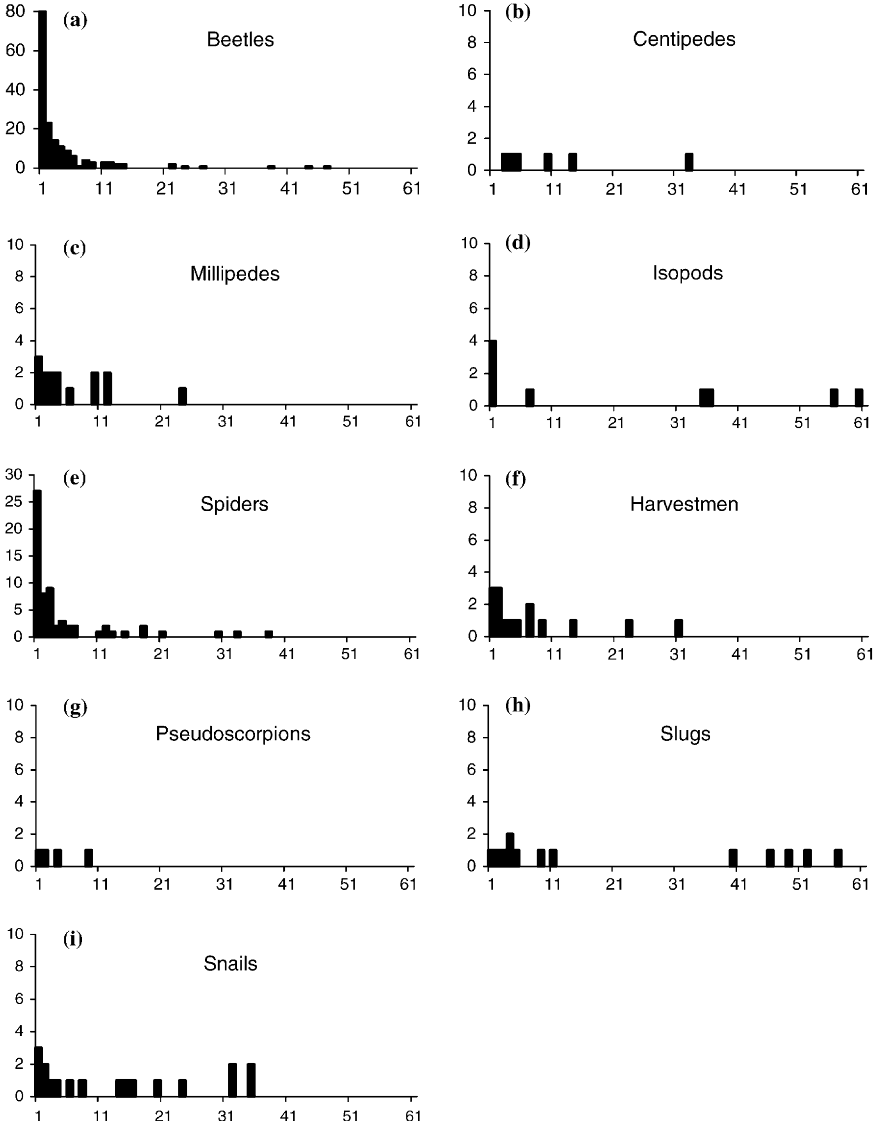

Figure 2. Species occupancy across gardens for taxa sampled by pitfall traps and in litter (combined data), for (a) beetles, (b) centipedes, (c) millipedes, (d) isopods, (e) spiders, (f) harvestmen, (g) pseudoscorpions, (h) slugs, (i) snails. The *x*-axis shows number of gardens, and the *y*-axis shows the number of species. Note that the *y*-axis scale is not constant.

the number of trees, then the presence of composting; house age and garden area were both negatively related to species richness. The significance of trees was supported by the *tree* analysis. This separated observations unevenly along the axis of canopy vegetation >2 m high (closely correlated to the number of

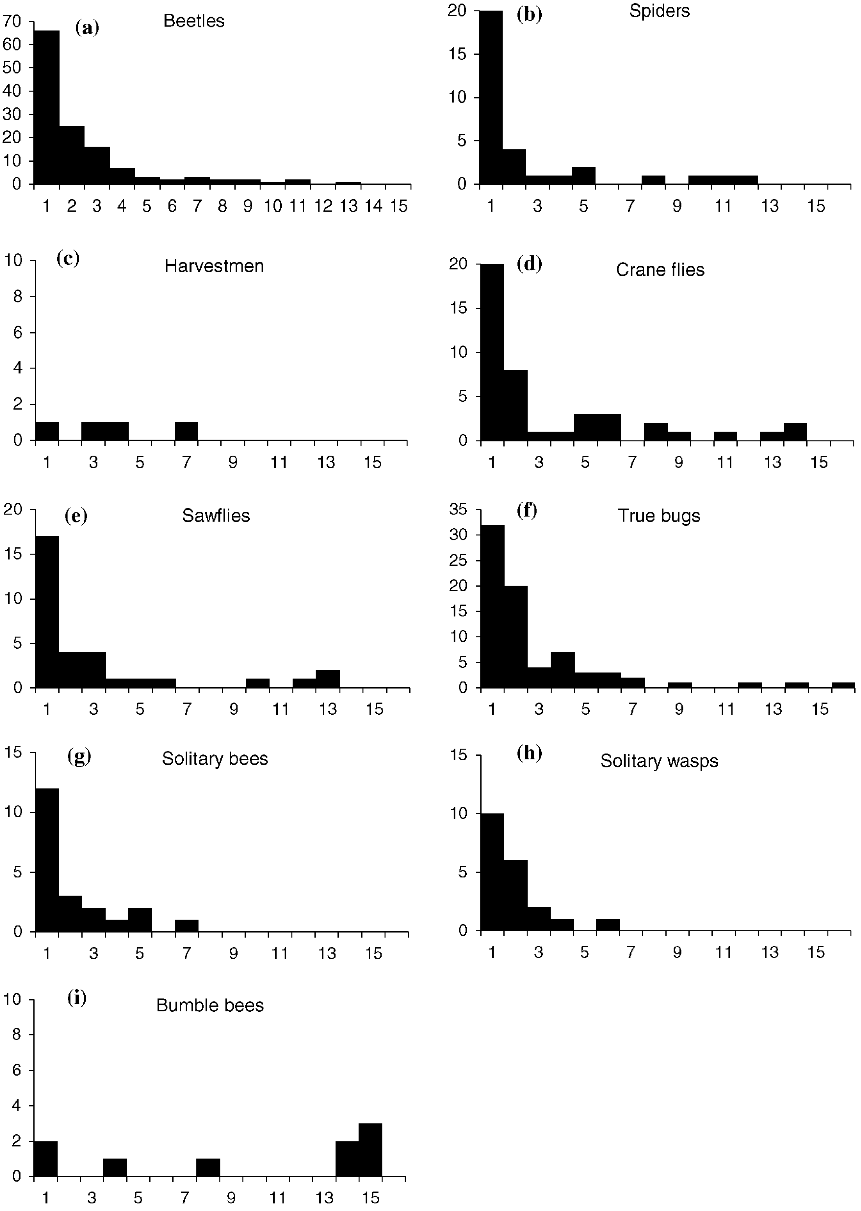

Figure 3. Species occupancy across gardens for taxa sampled by Malaise traps, for (a) beetles, (b) spiders, (c) harvestmen, (d) crane flies, (e) sawflies (f) true bugs, (g) solitary bees, (h) solitary wasps, (i) bumble bees. The x-axis shows number of gardens, and the y-axis shows the number of species. Note that the y-axis scale is not constant.

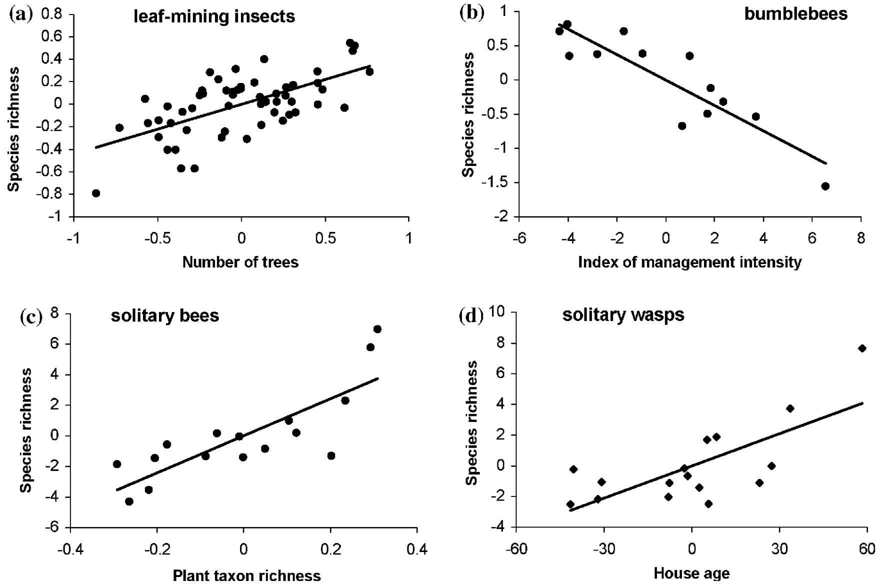

Figure 4. Partial leverage plots (SAS 8.1, SAS Institute Inc., Cary, NC, USA) showing examples of relationships between species richness and internal garden characteristics: (a) leaf-mining insects and number of trees > 2 m high, (b) bumblebees and an index of management intensity, (c) solitary bees and floral taxon richness, and (d) solitary wasps and house age. Plots are derived from stepwise multiple regression models (Table 2) where the *x*-axis represents the residuals of the explanatory variable from a model that regresses that explanatory variable on the remaining explanatory variables. The *y*-axis represents the residuals of the dependent variable calculated from a model with the explanatory variable (of the *x*-axis) omitted.

trees), into a small group below 6.9 m^2 in extent (a terminal node, mean 6.3 beetle species) and a larger one, above (mean 12.3 species). The latter further subdivided into groups with, respectively, means of 20.0 and 11.4 species within and beyond a threshold of 0.86 km to the urban edge.

Considering the data from pitfall traps alone, greater variation in beetle species richness was explained (36%, Table 2). The number of trees > 2 m high in a garden was also the dominant factor, but stronger than in the previous model. Further, the remaining factors of importance were different: negative influence due to the area of hard surfaces within the garden, and a positive effect of the extent of surrounding green space.

A substantial proportion of variation in beetle species richness in Malaise traps (84%) was explained by position on an easterly axis, the presence of composting, and to a lesser extent, the length of a garden's boundary shared by neighbouring gardens (Figure 5, Table 2). The primary, and only, split in the *tree* analysis occurred for local human population density above and below 14.8 people ha^{-1}, for which respective group means were 14.6 and 25 beetle species (i.e. higher richness was associated with gardens in less densely populated locations).

Table 2. A matrix showing the strengths of the effects of independent variables (environmental and housing characteristics) on the species richness' of invertebrate taxa, analysed by stepwise multiple regression (see Methods for details).

Taxon	Leaf-miners	Beetles	Beetles	Beetles	Arachnids	Arachnids	Arachnids	Slugs	Snails	Centipedes millipedes and isopods	Bumblebees	Sawflies	Craneflies	True bugs	Solitary bees	Solitary wasps
Source of data		P, L	P	M	P, L	P	M	P, L	P, L	P, L	M	M	M	M	M	M
Model d.f.	5, 50	4, 55	6, 48	3, 12	1, 58	1, 58	2, 13	6, 47	5, 52	2, 57	3, 9	3, 12	2, 13	1, 14	3, 12	2, 13
Model r^2_{adj}	0.61	0.28	0.36	0.84	0.10	0.09	0.62	0.47	0.42	0.19	0.88	0.70	0.44	0.22	0.63	0.45
Plant taxon richness															3	
Distance east				3												1
Distance north			(−1)									3				
House age		−1						−1								2
Altitude	−1						−3		1	1				−1		
Rural proximity												−1				
Garden area		−1														
Habitat diversity											3					
Structural diversity							2									
Perimeter-area ratio								2								
No. of houses			(1)												2	
Area of gardens									(−1)							
Area of lawn												2				
Area of hard surface			−2		2	2										
Presence of pond													2			
Presence of composting	−1	1		2				1								
Canopy < 2 m															(1)	
Canopy > 2 m										2						

Table 2. Continued.

Taxon	Leaf-miners	Beetles	Beetles	Beetles	Arachnids	Arachnids	Arachnids	Slugs	Snails	Centipedes millipedes and isopods	Bumblebees	Sawflies	Craneflies	True bugs	Solitary bees	Solitary wasps
Source of data		P, L	P	M	P, L	P	M	P, L	P, L	P, L	M	M	M	M	M	M
Model d.f.	5, 50	4, 55	6, 48	3, 12	1, 58	1, 58	2, 13	6, 47	5, 52	2, 57	3, 9	3, 12	2, 13	1, 14	3, 12	2, 13
Model r^2_{adj}	0.61	0.28	0.36	0.84	0.10	0.09	0.62	0.47	0.42	0.19	0.88	0.70	0.44	0.22	0.63	0.45
No. of trees	3	2	3						3							
Length of walls	1							1	2							
Length of gardens on boundary	(1)			1												
Local population density								1					−1			
Area of green space			2								2					
Management index			1						−1		−3					
Wildlife index								2								

Sources of data are: Pitfall traps (P), Malaise traps (M) and Litter samples (L). Negative relationships are indicated by –; for level of significance: 3 = $p < 0.001$, 2 = $p < 0.01$, 1 = $p < 0.05$, (1) = $0.10 > p > 0.05$.

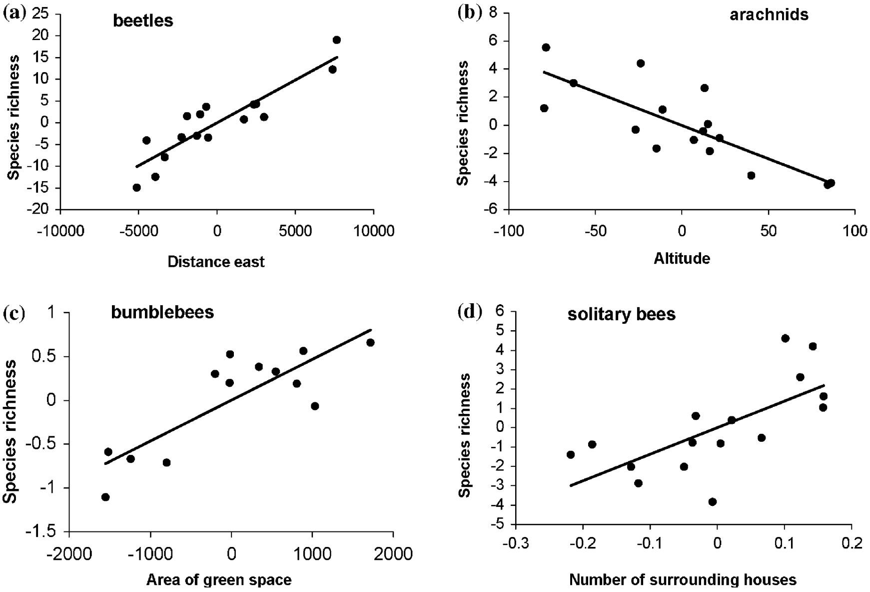

Figure 5. Partial leverage plots (SAS 8.1, SAS Institute Inc., Cary, NC, USA) showing examples of relationships between species richness and features of the environment external to gardens: (a) beetles in Malaise traps and the distance east, (b) arachnids in Malaise traps and altitude, (c) bumblebees and the area of green space in the surrounding 1 ha, and (d) solitary bees and the number of houses in the surrounding 1 ha. Plot axes derived as for Figure 4.

Arachnids (Arthropoda, Arachnida: Aranea, Opiliones, and Pseudoscorpiones)

Little of the variation in arachnid species richness was explained – either for pitfall trap data alone (9%), or for combined pitfall and litter data (10%) – being positively related only to the area of hard surfaces in a garden (Table 2). This was confirmed by the primary split of the *tree* analysis on the same variable, above and below 38.5 m^2 of hard surface, with respective group means of 9.4 and 6.2 arachnid species. The former group split further into subsets with means of 13.2 and 8.3 species below and above 48 m^2 of vegetation under 2 m high. The group associated with relatively less hard surface subdivided into sets with means of 4.9 and 8.0 species below and above 5333 m^2 of gardens in the surrounding 1 ha.

Arachnid species richness in Malaise traps was related positively to the structural diversity of the vegetation and strongly, negatively to altitude (Figure 5, table 2). The *tree* analysis revealed a single, primary split for extent of canopy vegetation more than 2 m high, at 54.0 m^2 . However, the means for the two groups were contrary to what might be expected if arachnid species richness was related to the extent of available canopy habitat: with means of 7.8 species below the split, and only 4.2 above.

Slugs and snails (Mollusca: Gastropoda)

Combined data from pitfall traps and litter samples for slugs showed that species richness was related to factors internal and external to gardens (Table 2). Positive relationships with the perimeter–area ratio of the garden (which is greater in small gardens) and local human population density suggest a general effect of the housing environment. Further, species richness was higher in younger housing. Within gardens, slug species richness was positively related to the presence of composting, the length of walls, and an index of wildlife gardening. Local human population density also featured as the primary split in the *tree* analysis, at virtually the same place as for beetles in Malaise traps (14.5 people ha^{-1}). Species richness was marginally greater at higher population densities: a group mean of 5.4 species compared to 4.4 below the split. Both of these groups then split unevenly on the variable east, and in each case the smaller, more westerly set had slightly higher species richness (lower population group: 5.5 compared to 4.1 species; higher population group: 6.2 compared to 5.0 species).

The length of walls was the only explanatory factor common to slug and snail species richness. However, length of walls accounted for less than half the snail species richness variation as explained by the number of trees. Small positive and negative effects were exerted, respectively, by altitude and the intensity of garden management (Table 2). The *tree* analysis reiterated the significance of number of trees: the relatively small number of gardens which contained more than 17.5 trees possessed nearly double the number of species – 6.2 vs. 3.6. The latter group split further on an easterly axis, with gardens to the west and east having means of 6.2 and 3.3 species, respectively.

Centipedes, millipedes and woodlice (Arthropoda: Chilopoda, Diplopoda and Crustacea (Isopoda))

Little variation was explained in the combined data for centipedes, millipedes and woodlice, the only relationships being positive ones for altitude, and more importantly, the extent of canopy above 2 m (Table 2). The *tree* analysis indicated that species richness was greater in gardens to the west (mean 7.6 species) than to the east (mean 5.6 species); this corroborates the regression analysis, since altitude and distance west are positively correlated ($r = 0.64$, $n = 59$, $p < 0.001$). The westerly gardens then subdivided along a northerly axis, with group means of 6.9 species to the south and 9.1 to the north. The easterly gardens split into sets with means of 6.8 and 5.0 species above and below a threshold garden management index of 11.5, i.e. relatively intensively managed gardens in the east of Sheffield supported marginally more species.

Bumblebees (Arthropoda, Insecta, Hymenoptera: Apidae)

Bumblebee species richness from Malaise traps was strongly positively related to habitat diversity in gardens, and strongly negatively related to the intensity of garden management; the area of surrounding green space was an additional positive correlate (Figures 4 and 5, Table 2). The sole split in the *tree* analysis was for habitat diversity too, with a mean species richness of 7.0 in relatively diverse gardens compared to 5.6 in relatively homogeneous ones.

Sawflies (Arthropoda, Insecta, Hymenoptera: Symphyta)

The distance north was the most important (positive) predictor of sawfly species richness, accounting for 52% of the variation explained by the model. Species richness was also positively related to the area of lawn in a garden, and there was weak evidence for a negative effect the further a garden occurred from the edge of the urban area (Table 2). The *tree* analysis indicated a split above and below an alien floral richness of 50.4 taxa, with means of 11.0 and 5.86 sawfly species for respective groups.

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

Cranefly species richness was related positively to the presence of ponds, and to a lesser extent, negatively to human population density (Table 2). As for the *tree* analysis for sawflies, cranefly species richness was greater in gardens with more alien plant taxa (14.3 cranefly species above a split of 43.9 plant taxa, and 6.8 species below).

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

A negative effect of altitude was the only factor associated with species richness in true bugs (Table 2), although the sole split in the *tree* analysis was for the number of trees. Below 14.9 trees the group mean was 15.1 species, whereas above the split the mean number of species was only 11.8.

Solitary bees (Arthropoda, Insecta, Hymenoptera: Apoidea)

The species richness of solitary bees was positively related, in order of strength, to the taxon richness of garden plants (Figure 4), the number of surrounding houses (Figure 5), and (marginally) to the extent of canopy vegetation below 2 m high (Table 2). The importance of the garden flora was supported by a single primary split in the *tree* analysis, where above and below a threshold of 50.4 native taxa, gardens had means of 3.8 and 1.0 species, respectively.

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

Solitary wasp species richness was positively related to house age and the distance east (Figure 4, Table 2). However, the tree analysis gave the same result as for solitary bees: a single primary split for native plant richness, with means of 2.3 and 0.4 wasp species above and below 43.9 plant taxa.

Discussion

The results from 16 analyses of 12 invertebrate groups showed that both factors within, and external to, gardens were significantly related to species richness within gardens. In total, 22 explanatory variables entered into stepwise regression models, although 12 of them only did so once. The amount of variation in species richness explained in models was generally reasonably high (Table 2), especially for data based on Malaise traps, where it ranged from 22–88%. However, consistent patterns did not emerge for the effects of factors across taxa, and in some cases relationships existed in opposite directions for different taxa (e.g. the length of walls, and altitude).

The factors external to gardens operated across a range of scales. Beetle and sawfly species richness in Malaise traps were associated with garden position on east-west and north-south axes, respectively, representing spatial correlations occurring over more than 10 km. Such broad influence has been shown for bird assemblages on an urban gradient, independently of the effect of habitat (Cooper 2002). There was evidence for a very general environmental effect of altitude in 5 out of the 16 analyses, although it only possessed a strong (negative) relationship with the species richness of arachnids caught in Malaise traps. Decreasing altitude was given as the cause for butterfly species richness to increase with urbanisation, across the Greater Manchester conurbation, since species-poor uplands bounded the urban area (Hardy and Dennis 1999).

At a more local scale, the quantity of green space in the surrounding 1 ha (including garden habitats) was related to the species richness of beetles in pitfall traps and bumble bees, whilst no variation was explained by the area of gardens alone. The extent of urban cover (i.e. built or sealed surfaces) has been widely cited as having a negative effect upon native species richness: at local scales in butterflies (Blair and Launer 1997; Hardy and Dennis 1999), birds in urban parks (Jokimäki 1999), lizards in residential areas (Germaine and Wakeling 2001), and ground beetles in urban London (Davis 1978). In the present study, effects of other measures of urban cover were also apparent. Local human population density correlated with slug species richness positively and craneflies negatively, although number of houses (in the surrounding 1 ha) was positively associated with solitary bee richness.

It is striking that several important aspects of the garden environment did not appear prominently in the analyses. Overall plant taxon richness, habitat diversity and structural diversity of the vegetation did so only once, and the number of alien or native plant species only in *tree* analyses. Even so, other features of garden vegetation were significant, particularly the number of trees >2 m high. Tree species supported 35% of the leaf-miners recorded, therefore gardens containing more tree specimens were more likely to harbour suitable hosts. As the number of trees and total garden plant richness are positively correlated, via their relationships with garden size (unpublished data), then trees probably also captured variation in the number of other plant hosts. In this respect, garden area indirectly influences the resources available to certain invertebrate guilds. While the richness of solitary bees was strongly related to plant taxon richness (most likely due to the wider range of floral resources available), this feature of gardens need not necessarily be restricted by size, as planting is under the control of garden owners.

Of the internal garden features related to invertebrate species richness, not all have obvious associations with particular taxa. It is likely that some factors are correlated with other features of real significance. For example, the influence of canopy >2 m high on centipedes, millipedes and woodlice could be construed as a variety of effects, such as provision of shade and litter. The presence of composting as a factor is readily explicable for beetle richness in Malaise traps, since compost heaps provide specialised microhabitats and resources in gardens (Ødegaard and Tømmerås 2000); but explanations for the relationship between compost heaps and the richness of leaf-mining insects; the richness of arachnids and the area of hard surfaces; between the richness of sawflies and the area of lawn, and between cranefly richness and the presence of ponds, are not at all obvious. The occurrence of such associations, for which mechanisms are difficult to suggest, reinforces the caution necessary in speculating about the causality of both these relationships and also those for which plausible causal links can be postulated. As emphasised initially this is, necessarily, an exploratory analysis documenting the patterns among richness and features of the garden environment, and there remains much work to be done to test the generality and causality in these patterns.

Perhaps the most striking feature of the results is the variation among taxa in the variables with which species richness is associated. There are a number of reasons why this might be the case. It is of course possible that a few of the apparent associations are chance results; many variables are examined, and some of the relationships are weak. 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 us making arbitrary judgements about how to apply such corrections (e.g. see Moran 2003). One consequence of this approach is that the weaker results must be viewed with some caution.

However, even among the stronger relationships, there is considerable variation in the factors involved and the direction of the association. The most obvious reason for this is that different factors are important for different groups of organisms. This could be as a result of the spatial scale at which the environment is likely to affect them (and at which we sampled), and of course the biological characteristics of the different taxa.

The autecology of most invertebrates is so poorly resolved that it is rarely known what resources species are using in gardens, and whether they occur as permanent residents, are using gardens for important stages of their life histories, or if they are simply casual or accidental visitors. For example, the high occupancy of gardens by most of the bumblebees recorded suggested that, even if they rarely nest in such habitats (Owen 1991), they are very mobile and readily exploit gardens. The availability of nectar resources and potential nest sites would explain the observed association of bumblebees to the amount of green space surrounding the garden. However, it is not clear why they were related negatively to the index of management intensity within gardens (being mobile, temporary visitors), or positively to land use diversity, which was largely unrelated to their resource requirements. Ironically, ground-active arachnids, centipedes, millipedes and woodlice are easily recognised as garden residents, yet their species richness' were poorly explained by variables describing the environments within the gardens where they were found.

In addition, the scale at which each sampling method operated will interact with the spatial scale at which species are using gardens, potentially contributing further to the variation in explanatory factors. Pitfall trapping and litter sampling were effective at relatively small scales, at the sampling point itself, or in its immediate vicinity. Thus the taxa that such methods sampled – typically woodlice, millipedes, centipedes, and ground-dwelling beetles, arachnids and molluscs – would have been expected to reflect local factors. In contrast, Malaise traps sampled a predominantly aerial fauna (presumably derived from a wider area than the garden itself), so that the recorded taxa should have reflected broader-scale factors. Indeed, for explanatory models of taxa sampled by Malaise traps, the most important relationships were with external garden factors in half of such models; in contrast, for taxa sampled by other methods, the more significant relationships all existed with factors internal to the garden (Table 2).

We believe that this potential combination of factors differing in importance to different taxa, and the differing scales at which they utilise garden environments, probably underpins much of the variation in the variables that feature in the results. However, we would also stress that this applies whether or not the taxon is responding to the variable we measured, or to one or more other factors with which that variable is associated.

A final observation is that this study differed in two important ways from those that have explicitly addressed the effect of urbanisation on species richness: first, it was based largely in residential zones and thus probably captured a smaller range of landscape variation than do studies of urban gradients (e.g. Blair 1996; McGeoch and Chown 1997; Germaine and Wakeling 2001). The latter seek to maximise the range of degree of urbanisation, from truly rural sites or nature reserves to the central business district, so that effects relating to urban cover should be more pronounced. Second, the analysis of habitat or resource fragments, be they host plants (Denys and Schmidt 1998), encapsulated semi-natural vegetation (Soulé et al. 1988; Miyashita et al. 1998; Honnay et al. 1999) or other green space (Jokimäki 1999), has emphasised the roles of isolation and fragment area on species assemblages. These assemblages are considered scarce in the surrounding urban matrix, and therefore governed by extinction and colonisation processes at the scale of the patch. In contrast, urban gardens characteristically form much of the matrix of residential zones, and are connected over large areas. Therefore invertebrates in a particular garden should reflect the species pool outside the boundaries of that garden better than if it was an isolated habitat fragment. For example, in Davis' (1978) study of ground beetles in gardens in London, the effect of distance to the urban edge was lost when the amount of open space in the surrounding 1 km radius was considered. In the present study, there was only evidence for a weak relationship with garden area in one of the five ground-active taxa studied (beetles in pitfall and litter samples, for which the sampling was spatially related to a garden's area); yet this actually showed a negative correlation with garden area. Similarly, proximity to the urban edge was weakly associated with only one taxon – sawflies, in which species richness declined away from the countryside.

In conclusion, the lack of evidence for general correlates of invertebrate species richness in urban gardens reinforces the view that different invertebrate taxa respond to specific resource requirements, both within and around gardens. Urban domestic gardens differ from other types of urban green space because they constitute the urban matrix, rather than being fragments within it. Therefore recommendations to enhance the quality of garden habitats for urban biodiversity may best be focussed upon their configuration in the urban area, to ensure that green space is distributed throughout the urban zone. If specific garden features are to be encouraged for invertebrates, then vegetation – especially tree cover – is likely to provide benefits for the widest range of taxa. Since tree cover is positively associated with garden size (Smith et al. in press), then attention should be given to providing sufficient garden space in new residential developments.

Acknowledgements

This work was supported by funding from the URGENT programme of the Natural Environment Research Council (grant GST/02/2592). We are extremely grateful to the householders who made their gardens available and to the following experts for their immense assistance in identifying specimens: M. Archer, K. Bland, D. Budworth, R. Cameron, J. Coldwell, J. Flanagan, J. Hodgson, I. Kenny, A. Lazenby, S. Price, P. Richards, E. Smith, P. Smithers, E. Thorpe and A. Willis. A. Jones kindly provided measurements of human population density. We also thank L. Bates, L. Bega, J. Carpenter, S. Colsell, R. Elliot, L. Jowett, J. Shutt, L. Worthington, T. Yardley and two anonymous referees for their help with this research, comments and discussion.

Appendix 1. Independent variables used in analyses of species richness (see Methods)

One 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 distance east, Ordnance Survey National Grid map coordinate; 5 distance north, Ordnance Survey National Grid map coordinate; 6 age of house calculated in 2000; 7 altitude, m above sea level; 8 rural proximity: distance in km from centre of nearest 1 km cell with $<25\%$ urban land use; 9 habitat diversity: Simpson's diversity index for land uses in each garden; 10 structural diversity: Simpson's diversity index for vegetation canopy cover classes: <0.5 m, 0.5–1 m, 1–2 m, 2–3 m, and >3 m in each garden; 11 area of rear garden in m^2; 12 perimeter–area ratio: ratio of 'exposed' (i.e. excluding perimeter along rear of house) garden perimeter to garden area; 13 area of grass in rear garden (cut + uncut portions); 14 area of non-grass green space in rear garden (grass paths + cultivated border + vegetable patch + neglected/uncultivated); 15 area of hard surfaces in rear garden (hard paths + patios + green house + sheds + garage + decking); 16 presence of ponds in a rear garden (scored 1 or 0); 17 presence of compost bins or heaps in a rear garden (scored 1 or 0); 18 area of vegetation canopy 0–2 m (excluding mown grass); 19 area of vegetation canopy >2 m; 20 no. of trees >2 m tall in rear garden; 21 exposed perimeter length of rear garden (i.e. excluding perimeter along rear of house); 22 length of hedges in rear garden, m; 23 length of walls in rear garden, m; 24 length of garden boundary abutting other gardens, m; 25 human population density (no. 40×10^3 m^{-2}, or 4 ha^{-1}), POPSURF 1991 census data. *Recorded from GIS, for 1 ha circular plot centred on survey garden:* 26 no. of houses (where $>$half of property is included), 27 area of domestic gardens, 28 area of all green space, 29 area of contiguous green space fragment; 30 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) removing dead flower heads (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); 31 use of slug pellets (scored 1 or 0, used in analyses of molluscs only); 32 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).

References

Allen A.A. 1964. The Coleoptera of a suburban garden. Entomol. Rec. J. Variation 76: 261–4.

Bailey S.E.R., North M.C. and Cook L.M. 1998. Slugs and snails and thrushes' anvils: children's surveys of slugs and snails. J. Conchol. Special Publication 2: 171–178.

Blair R.B. 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6: 506–519.

Blair R.B. and Launer A.E. 1997. Butterfly assemblages and human land use: species assemblages along an urban gradient. Biol. Conserv. 80: 113–125.

Cannon A. 2000. Garden BirdWatch Handbook, 2nd ed. British Trust for Ornithology, Thetford.

Cooper D.S. 2002. Geographic associations of breeding bird distribution in an urban open space. Biol. Conserv. 104: 205–210.

Crawley M.J. 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. John Wiley and sons, Chichester, UK.

Davis B.N.K. 1978. Urbanisation and the diversity of insects. In: Mound L.A. and Waloff N. (eds), Diversity of Insect Faunas. Blackwell Scientific, Oxford, pp. 126–138.

Denys C. and Schmidt H. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113: 269–277.

Eversham B.C., Roy D.B. and Telfer M.G. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Ann. Zool. Fenn. 33: 149–156.

Fernández-Juricic E. 2000. Avifaunal use of wooded streets in an urban landscape. Conserv. Biol. 14: 513–521.

Gaston K.J., Smith R.M., Thompson K. and Warren P.H. in press a. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodivers. Conserv. in press.

Gaston K.J., Warren P.H., Thompson K. and Smith R.M. in press b. Urban domestic gardens (IV): the extent of the resource and its associated features. Biodivers. Conserv. in press.

Germaine S.S. and Wakeling B.F. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol. Conserv. 97: 229–237.

Gilbert O.L. 1990. The lichen flora of urban wasteland. Lichenologist 22: 87–101.

Hardy P.B. and Dennis R.L.H. 1999. The impact of urban development on butterflies within a city region. Biodivers. Conserv. 8: 1261–1279.

Honnay O., Endels P., Vereecken H. and Hermy M. 1999. The role of patch area and habitat diversity in explaining native plant species richness in disturbed forest patches in northern Belgium. Divers. Distrib. 5: 129–141.

Jokimäki J. 1999. Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosyst. 3: 21–34.

Kinzig A.P. and Grove J.M. 2001. Urban–suburban ecology. In: Levin S.A. (ed.), Encyclopaedia of Biodiversity, Vol. 5. Academic Press, San Diego, pp. 733–745.

Martin D. and Tate N. 1997. Surpop V2.0: Introduction. http://census.ac.uk/cdu/surpop.htm.

McGeoch M.A. and Chown S.L. 1997. Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: the importance of reserves in urban areas. Biodivers. Conserv. 6: 979–993.

Miotk P. 1996. The naturalized garden- a refuge for animals? – first results Zool. Anz. 235: 101–116.

Miyashita T., Shinkai A. and Chida T. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biol. Conserv. 86: 357–364.

Moran M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100: 403–405.

Ødegaard F. and Tømmerås B.Å. 2000. Compost heaps – refuges and stepping-stones for alien arthropod species in northern Europe. Divers. Distrib. 6: 45–59.

Owen J. 1991. The Ecology of a Garden: the first fifteen years. Cambridge University Press, Cambridge.

Owen J. 2002. My Romney Marsh garden. Atropos 17: 53–57.

Pyšek P. 1993. Factors affecting the diversity of flora and vegetation in central European settlements. Vegetatio 106: 89–100.

Roy D.B., Hill M.O. and Rothery P. 1999. Effects of urban land cover on the local species pool in Britain. Ecography 22: 507–515.

Saville B. 1997. The Secret Garden: Report of the Lothian Secret Garden Survey. Lothian Wildlife Information Centre, Edinburgh.

Smith C. 1989. Butterflies and moths in suburbia. Nature Cambridgeshire 31: 19–27.

Smith R.M., Gaston K.L., Warren P.H. and Thompson K. in press. Urban domestic gardens (V): relationships between landcover composition, housing and landscape. Landscape Ecology. in press.

Soulé M.E., Bolger D.T., Alberts A.C., Wright J., Sorice M. and Hill S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conserv. Biol. 2: 75–92.

Stace C. 1997. New Flora of the British Isles, 2nd ed. Cambridge University Press, Cambridge.

Sukopp H. and Starfinger U. 1999. Disturbance in urban ecosystems. In: Walker L.R. (ed.), Ecosystems of the World 16. Ecosystems of Disturbed Ground. Elsevier Science, Amsterdam, pp. 397–412.

Thompson K., Austin K.C., Smith R.M., Warren P.H., Angold P.G. and Gaston K.J. 2003. Urban domestic gardens (I): putting small-scale plant diversity in context. J. Veg. Sci. 14: 71–78.

Thompson K., Hodgson J.G., Smith R.M., Warren P.H. and Gaston K.J. 2004. Urban domestic gardens (III): composition and diversity of lawn floras. J. Veg. Sci. 15: 371–376.

Vickery M.L. 1995. Gardens: the neglected habitat. In: Pullin A.S. (ed.), Ecology and conservation of butterflies. Chapman and Hall, London, pp. 123–134.

Wright M. 1984. The Complete Handbook of Garden Plants. Michael Joseph, London.