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Species richness of Orthoptera along gradients of agricultural intensification and urbanisation

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Abstract

The relationship between species-richness of Orthoptera and remotely sensed land cover was investigated at a grain size of 100 km^2 within an area of 9,900 km^2 in central southern England, using species data extracted from county and national atlases. Gradients in landscape composition, identified using multivariate ordination, reflected agricultural intensification (associated with increasing acreage of arable crops) and urbanisation. The number of species declined as the area under arable crops increased, yet even in the most agriculturally intensive grid-squares there appeared to be sufficient non-arable land to support all species. A range of factors such as fragmentation and degradation of nonarable habitats may become more important as the area of cropped land increases. Investigation at greater spatial resolution is needed to confirm this hypothesis. No relationship was found between species richness and urbanisation, but it was concluded that the extent of urban development was too limited to enable detailed investigation of this phenomena. The study demonstrates that coarse-grained species data within county and national atlases, combined with remotely-sensed land cover data, can be useful in detecting and interpreting spatial variation in orthopteran species diversity at the regional scale. The relationship between species richness and land cover quantifies past human impacts and suggests the approach may be useful for monitoring and interpreting future changes.

Key words

species richness, biodiversity, land cover, landscape, agriculture, urbanisation, gradient analysis, atlas, remote sensing

Introduction

European landscapes are heavily modified by agriculture and urbanisation with consequences for biodiversity (Luck 2007, Firbank *et al.* 2008). A number of studies have investigated these effects by focusing on changes in biodiversity along gradients of landscape composition. For example, da Silva *et al.* (2008) studied changes in ground-beetle assemblages along a gradient of agricultural intensification, while other studies have focused on gradients from rural to urban landscapes (*e.g.*, Niemala & Kotze 2009). Intensification of agricultural management tends to reduce species richness (*e.g.*, Eggleton *et al.* 2005, Aavik & Liira 2009), but exceptions have been noted (*e.g.*, Batary *et al.* 2007, Burel *et al.* 1998). Patterns along urban-rural gradients are complex and scale-dependent (Luck 2007, Pautasso 2007). Moreover, relatively few studies utilizing a gradient-based approach have involved invertebrates (McDonnell & Hahs 2008).

The present study focuses on the Orthoptera within a study area centered on the three counties of Berkshire, Buckinghamshire and Oxfordshire within central southern England. The area was selected for several reasons. First, the region has been subject to more detailed field survey than many other areas (Paul 1989). Second, the latitudinal extent is also relatively small (110 km), such that the UK's major north-south climatic gradient will have a negligible effect on species' distributions. Third, the area supports a diversity of both orthopteran species and land covers which are representative of southern England.

There are a number of advantages to utilizing the Orthoptera to investigate the impact of landscape composition on species diversity in the UK. First, the ecology of the species is relatively well known (Marshall & Haes 1988). Second, there is a national atlas (Haes & Harding 1997) and a number of regional atlases of species' distribution (*e.g.*, Paul 1989, Haes 2004). Third, the Orthoptera includes both widespread habitat generalists and less common specialists, with individual species occupying a diversity of habitats including arable field margins, hedges, managed and unmanaged grasslands, marshy grassland, heath, scrub and woodland (Ragge 1965, Marshall & Haes 1988). Fourth, the Orthoptera have been used in a number of previous studies to assess the impacts of changes in landscape composition (Johannesen *et al.* 1999, Marini *et al.* 2008, With & Crist 1995) and climate (Cannon 1998, Wissmann *et al.* 2009, Gardiner 2009a). Fifth, a wealth of literature exists on the impacts of small-scale habitat management for conservation (*e.g.*, van Wingerden *et al.* 1991a, 1991b; van Wingerden *et al.* 1992; Jauregui *et al.* 2008; Gardiner 2009b). The Orthoptera, therefore, represent a candidate Order for use in monitoring the effects of large-scale changes in land use on British invertebrates.

The present study identifies major gradients in the land cover composition of the study area using data from a remote sensed map of Great Britain (Fuller *et al.* 1994). The principal gradients in landscape composition reflect variation in intensity of arable cropping, and the extent of urban development. Variation in the numbers of orthopteran species recorded within 100 km^2 grid-squares is related to these landscape gradients. The sensitivity of the analysis to data quality is explored by using species records from two atlases (Paul 1989, Haes & Harding 1997). The first had a cut-off date closely coincident with the remotely sensed land cover data, while the second incorporated a further eight years' data from field recording. Although, the Orthoptera are thought to be responsive to landscape change (Marshall 2001, 2010), the potential utility of this Order for describing and interpreting large-scale relationships between species richness and land cover in the United Kingdom has not been assessed previously.

Methods

Data on land cover and species richness were obtained from the 99 grid-squares included in the atlas of Berkshire, Buckinghamshire and Oxfordshire (Paul 1989). Each grid-square had sides of 10 km (area 100 km^2). For brevity these grid-squares are henceforth referred to as 10-km grid-squares (with reference to their linear dimensions). The grid-squares are arranged in a rectangular block measuring

90 km in longitude and 110 km in latitude. The coordinate of the SW corner of the study area is 420E 150N on the British National Grid.

Species data.—Data on the presence of 18 species in the Order Orthoptera within each of the 99 10-km grid-squares were extracted manually from two sources. Data from the orthopteran atlas of Berkshire, Buckinghamshire and Oxfordshire (Paul 1989) was supplemented by that within the atlas for Britain and Ireland (Haes & Harding 1997). Paul (1989) contained records up to 1989, while Haes & Harding (1997) included records up to 1997. Records in Paul (1989) were classified as being pre-1961 and 1961-onwards, while those in Harding & Haes (1997) were classified as pre-1970 and 1970-onwards. Only records from the more recent period in each atlas were accepted within this study. Two datasets summarising the number of species in each 10-km grid-square were produced. The first dataset contained only the eligible records from the Berkshire, Buckinghamshire and Oxfordshire atlas (1961-1989). The second dataset subsumed the first, but also included additional eligible records from the national atlas (1961-1997). The two datasets contained 595 and 810 records respectively and were maintained as separate dependent variables for analysis. The second combined dataset contained an additional 215 records. Some of these new records were the result of colonisations of new areas by species known to be expanding their range (Kleukers *et al.* 1996, Haes & Harding 1997, Marshall 2001, Gardiner 2009b), however many were probably populations that existed in the earlier period (1961-1989), but which had been overlooked (Dr J. Paul pers. com.).

Records of two species were omitted from the study. These species were the large marsh grasshopper, *Stethophyma grossum* (L.) and the house cricket, *Acheta domesticus* (L.). The former had been deliberately introduced within one 10-km square, while the latter (with 14 10-km records) is a pest of old hospital buildings and is also cultured as a laboratory animal (Paul 1989). Information on the habitats occupied by each was summarized from Ragge (1965), Marshall & Haes (1988), Paul (1989) and Evans & Edmonson (2007).

Land cover data.—Land cover information was obtained from the Countryside Information System (CIS) (Department of the Environment 1995) as the areas of 17 broad cover types within each of the 99 grid-squares. The land cover data were derived from Landsat Thematic Mapper imagery obtained between 1987 and 1990 with a final output pixel size of 25 m. Detailed descriptions of the 17 land cover types and their congruence with cover types observed in ground-based field surveys are reported elsewhere (Cherrill *et al.* 1995, Fuller *et al.* 1998). Studies have shown the land cover data to be a reliable representation of landscape composition and particularly when data from pixels are aggregated for larger areas (*e.g.*, 1-km or 10-km grid-squares) (Cherrill *et al.* 1994, Fuller *et al.* 1998).

The study area contained 13 of the 17 land cover types. Unclassified land averaged 1.2% (SD=0.95), with a maximum of 4.2%, within any one grid-square.

Five land covers were each found to represent <1% of the total study area. These covers were Bracken, Grass heath, Open dwarf shrub heath, Dense dwarf shrub heath, and Open water. With the exception of Open water, these land cover types are associated with unimproved heath-like vegetation. The four heath-like land cover types were combined into a single 'Heathland' cover type for analysis. Preliminary analyses, not reported here, found that this modification of the data led to greater explanatory power in the subsequent multivariate description of landscape gradients. Open water was absent from 29 grid-squares and, after the aggregation of the heath-like vegetation, was the only land cover type not present in all 99 grid-squares.

Land cover composition within each grid-square was summarised using Shannon's indices of diversity (H) and evenness (J) (also known as equitability) (Magurran 1988). The total area of classified land within each grid-square was standardised to 100% in these calculations. Shannon's H incorporates information on the number of land cover types per grid-square, but is also influenced by evenness (J) (Magurran 1988). There was little variation in the number of land covers per grid-square and consequently Shannon's H was highly correlated with evenness (J) (Pearson's correlation $r=0.99$, $P<0.001$, $n=99$). Only analyses using Shannon's J are therefore presented in this paper.

Statistical analyses.—Preliminary analyses focused on describing the gradient in orthopteran species richness. Examination of the frequency distribution of grid-squares containing different numbers of species was used to subjectively identify groups of grid-squares containing relatively low (0-4), medium (5-11), and relatively high (12-16) numbers of species per square. The frequency of occurrence of individual species and the areas of land cover types within these three groups of grid-squares was then explored. Preliminary analyses, not reported here, demonstrated that the patterns revealed were robust and replicated irrespective of the exact cut-off points in species richness used to group the grid-squares.

The dataset of ten land cover types was subjected to Principal Components Analysis to identify a reduced set of major axes of variation through the complex landscapes within the study area. These Principal Components were described in terms of the areas of the original land cover types and Shannon's J for land cover. Although not recommended for the analysis of species data, PCA is regarded as an effective method in the synthesis of environmental data as applied in this study (Kent & Coker 1992, p 186).

Correlations with the two estimates of orthopteran species richness were determined for a) the areas of each of the 10 individual land cover types, b) Shannon's J for land cover, and c) the Principal Components derived from the land cover type data. Spearman's nonparametric correlation test was applied where appropriate after testing for normality of the data.

Results

Orthopteran species richness.—In total 18 species were recorded in the study area (Table 1). The total number of records in 1989 was 595. This increased to 810 in 1997. The number of records increased for all but the least common species, *Gomphocerippus rufipes*. One species, *Conocephalus discolor*, was absent in 1989 but had colonised 17 grid-squares by 1997. This species, along with *Metrioptera roeselii* and *Chorthippus albomarginatus*, are known to be expanding their ranges nationally in response to climatic change (Haes & Harding 1997). The remaining new records probably reflect increased survey coverage rather than range expansions and many were likely to have been present, but undetected, at the earlier census date (Dr. J. Paul, pers. com.). Despite the increased number of records the relative frequency of the species changed little. The five most common species were the same at each date: *Meconema thalassinum*, *Leptophyes punctatissima*, *Omocestus viridulus*, *Chorthippus brunneus* and *C. parallelus* (Table 1).

The number of species recorded per square was 6.01 (SD=3.43) in 1989 and 8.18 (SD=3.72) in 1997. The frequency distribution of number of species per grid-square is broadly unimodal with few grid-squares containing few or many species (Fig. 1). The frequency of occurrence of individual species along the overall gradient of species richness is represented in Table 2 using the more complete

Table 1. The habitat and number of 100-km^2 grid-square records for each species in the study area. Habitat associations are based on Paul (1989), Marshall & Haes (1988) and Evans & Rogerson (2007). Records for 1961-1989 are from Paul (1989), while those for 1961-1997 include additional records post-1970 from Haes & Harding (1997).

Species	Number of records 1961-1989	Number of records 1961-1997	Dry grassland	Damp grassland	Dry heath	Wet heath	Bog / marsh	Woodland	Woodland edge	Hedgerow	Scrub	Field margins	Wasteland	Bare ground	Gardens
Meconema thalassinum (Degeer)	66	82						x		x	x				x
Tettigonia viridissima (L.)	9	13								x		x	x		x
Pholidoptera griseoaptera (Degeer)	53	64							x	x	x				x
Metrioptera brachyptera (L.)	11	13				x	x								
Metrioptera roeselii (Hagenbach)	5	30	x	x								x			
Conocephalus discolor (Thunberg)	0	17	x	x	x	x	x		x			x	x		
Conocephalus dorsalis (Latreille)	2	21		x			x								
Leptophyes punctatissima (Bosc)	62	80							x	x	x		x		x
Tetrix subulata (L.)	34	57												x	
Tetrix undulata Sowerby	46	64							x					x	
Omocestus rufipes Zett.	12	18						x	x						
Omocestus viridulus (L.)	67	81		x		x			x						
Myrmeleotettix maculatus (Thunberg)	24	28	x		x										
Gomphocerippus rufipes (L.)	2	2	x						x						
Chorthippus albomarginatus (Degeer)	23	33	x	x											
Chorthippus brunneus (Thunberg)	80	91	x		x							x	x		x
Chorthippus parallelus (Zetterstedt)	82	93	x	x								x	x		
Stenobothrus lineatus (Panzer)	17	23	x		x										

dataset from 1997. Grid-squares have been placed in three groups according to the number of species present. The grouping is subjective yet the frequency of occurrence of species within groups is relatively insensitive to the exact cut-off points applied. Similar frequencies were obtained using the 1989 dataset. Important observations common to both years' data are 1) the seven species recorded in the most species-poor grid-squares included the five which were most frequent overall, 2) no species were associated solely with species-poor grid-squares, 3) sixteen of the 18 species showed an increase in frequency as overall species-richness increased (i.e., moving left to right across Table 2), and 4) grid-squares containing the most species are relatively favorable to all species rather than just a subset of habitat specialists (Table 2).

Species richness and individual land cover types.—Over 70% of the study area comprised Tilled land and Managed grassland with Sub-

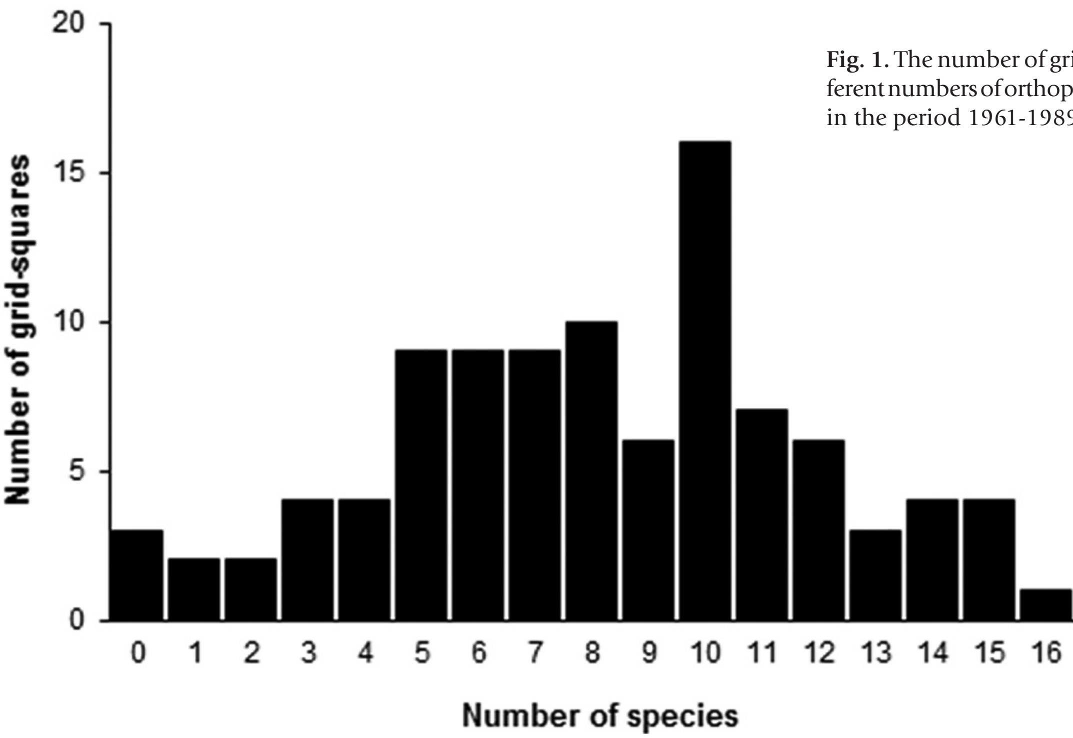

Fig. 1. The number of grid-squares from which different numbers of orthopteran species were recorded in the period 1961-1989 (n=99 grid-squares).

Table 2. The percent of grid-squares occupied by each species in the period 1961-1997. Grid-squares are grouped into those with low (0-4), medium (5-11), and high (12-16) numbers of species.

Species	Grid-square group based on species richness		
	Low	Medium	High
Meconema thalassinum (Degeer)	26.7	92.4	94.4
Tettigonia viridissima (L.)	0.0	12.1	27.8
Pholidoptera griseoaptera (Degeer)	26.7	63.6	100.0
Metrioptera brachyptera (L.)	0.0	4.6	55.6
Metrioptera roeselii (Hagenbach)	0.0	24.2	77.8
Conocephalus discolor (Thunberg)	0.0	4.6	77.8
Conocephalus dorsalis (Latreille)	0.0	7.6	88.9
Leptophyes punctatissima (Bosc)	26.7	87.9	100.0
Tetrix subulata (L.)	6.7	62.1	83.3
Tetrix undulata Sowerby	0.0	71.2	94.4
Omocestus rufipes Zett.	0.0	18.2	33.3
Omocestus viridulus (L.)	20.0	90.9	100.0
Myrmeleotettix maculatus (Thunberg)	0.0	19.7	83.3
Gomphocerippus rufipes (L.)	0.0	0.0	11.1
Chorthippus albomarginatus (Degeer)	6.7	31.8	61.1
Chorthippus brunneus (Thunberg)	46.7	100.0	100.0
Chorthippus parallelus (Zetterstedt)	66.7	98.5	100.0
Stenobothrus lineatus (Panzer)	0.0	18.2	61.1
Mean (SD) number of species per grid square	2.27 (1.53)	8.08 (2.00)	13.50 (1.34)
Number of grid squares	15	66	18

urban housing being the next most important cover type (Table 3). Variation in the areas of individual land cover types along the gradient of orthopteran species richness was explored in two ways. The mean areas of each land cover type within the groups of grid-squares, defined on the basis of numbers of species present area are shown in Table 4, while correlations between species richness and each land cover type are summarised in Table 5. The two analyses provide a complementary picture of the relationships between the variables. The areas of Urban, Suburban, Rough grassland, Deciduous woodland, Coniferous woodland and Open water were all positively correlated with species richness (Table 5), and were significantly greater in grid-squares containing the most species (Table 4). Conversely, the area of Tilled land was negatively correlated with species richness (Table 5), and was approximately 50% lower in the grid-squares containing the most species (Table 4). No relationships were detected between species richness and the areas of Managed grassland, Heathland, and Bare ground (Table 4, 5).

There were significant correlations between the areas of many pairs of land covers (Table 6). For example, as the area of Tilled land increased the areas of most other land cover types declined (Table 6). Positive correlations between species richness and the areas of individual land covers, for example Open water and Coniferous woodland (Table 5), cannot therefore not be interpreted as evidence that orthopteran species occur within these habitats [although, of course, some species are associated with wetlands and woodland edges (Table 1)]. The relationships are indicative of changes in species richness along complex multivariate gradients in landscape composition. These gradients can be explored further using Shannon's index and Principal Components Analysis (PCA) to reduce the land cover data to a smaller number of variables.

Table 3. The mean area (%) of land covers within grid-squares (n=99) within the study area (SD = Standard Deviation).

Land cover	Mean	SD
Urban	1.51	1.48
Suburban	11.20	5.34
Tilled	40.51	13.90
Managed grassland	32.58	9.15
Rough grassland	2.20	1.18
Deciduous woodland	6.77	5.10
Coniferous woodland	1.33	2.15
Heathland	1.27	1.04
Bare ground	1.02	0.92
Open water	0.38	1.11

Species richness and land cover diversity.—The diversity of land cover types within grid-squares was represented using Shannon's index for evenness (J). Evenness varied significantly between grid-squares grouped by the numbers of species recorded (Table 4) and was also positively correlated with the number of species recorded at both dates (Table 5). High evenness in land cover within species-rich grid-squares is associated with a relatively low dominance of Tilled land, and greater areas (and equitability) of other land cover types (Table 4).

Species richness and gradients in landscape composition.—Principal Component Analysis (PCA) identified three major composite axes of variation through the land cover data, explaining 70.4% of the total variation. Correlations between the principal components, the original land cover variables, Shannon's J, and the estimates of species richness are shown in Table 7.

The first axis explained 30.9% of the variation in land cover and represents a gradient from landscapes dominated by Tilled land (*i.e.*, arable cropping) to landscapes with a more equitable mixture of land cover types including Suburban, Urban, Managed grassland, Rough grassland, Woodland and Open water cover types (Fig. 2, Table 7). Orthopteran species richness was positively correlated with this gradient (Table 7). The gradient reflects closely that portrayed in Table 4, although here the area of Managed grassland also makes a significant contribution to landscape change (Table 7), perhaps because it is strongly negatively correlated with the area of Tilled land (Table 6).

The Suburban, Urban, Open water and Bare ground land cover types are clustered in ordination space (Fig. 2). The second axis,

Table 4. Mean and Standard Deviation (SD) for a) areas (%) of individual land covers, and b) Shannon's evenness index based on land cover data. Grid-squares are grouped into those with low (0-4), medium (5-11), and high (12-16) numbers of species. Comparisons between groups are based on the Kruskal-Wallis analysis of variance.

Land cover	Grid-square group based on species richness						Comparison between groups	
	Low		Medium		High			
	Mean	SD	Mean	SD	Mean	SD	H	P
a) Individual land cover types								
Urban	1.01	0.84	1.33	1.23	2.58	2.17	8.96	<0.02
Suburban	9.42	4.53	10.47	4.47	15.36	6.91	8.33	<0.02
Tilled	45.69	7.55	44.06	12.20	23.19	10.38	27.38	<0.001
Managed grassland	33.59	8.20	31.43	9.38	35.94	8.56	4.57	0.10
Rough grassland	2.03	1.32	1.91	1.00	3.41	0.90	22.66	<0.001
Deciduous woodland	4.29	3.96	6.04	4.60	11.48	4.98	18.57	<0.001
Coniferous woodland	0.54	0.79	0.89	1.25	3.61	3.64	24.61	<0.001
Heathland	1.23	0.77	1.26	1.02	1.35	1.36	0.16	0.92
Bare ground	0.68	0.77	1.05	0.88	1.17	1.14	4.26	0.12
Open water	0.11	0.29	0.20	0.45	1.22	2.31	20.10	<0.001
b) Land cover diversity								
Shannon's evenness J	0.57	0.07	0.59	0.07	0.71	0.07	30.35	<0.001
Number of grid-squares	15		66		18			

explaining 25.6% of variation, represents a gradient from landscapes characterised by these land cover types, and Tilled land, to landscapes with larger areas of Woodland and Managed grass (Fig. 2, Table 7). The evenness of land cover types did not vary along this axis (Table 7). There were no significant relationships with species richness, although that based on the 1997 species data set was barely non-significant and implies a trend of declining species richness with increasing urbanisation (Table 7).

The third axis explained 13.9% of the variation in land cover between grid-squares and represents a gradient from landscapes characterised by Managed grassland to landscapes characterised by Heath, Woodland and Bare ground (Table 7). Species richness was not related to this gradient (Table 7).

Discussion

A large number of studies have attempted to quantify the impacts of humans on biodiversity by investigating the numbers, and identities, of species along gradients of increasing agricultural intensification and urbanisation (Luck 2007, McDonnell & Hahs 2008). However, extrapolating from spatial patterns to interpreting changes in the past, and making predictions about the future, must be undertaken with caution. This is particularly true when working across areas of >10,000 km^2 with coarse grained data (resolution >1 km^2), because current land use patterns may be superimposed on older pre-existing gradients in biodiversity, thereby confusing interpretation of the relationship between the two (Luck *et al.* 2004). For example, a number of biogeographic studies (focusing mainly on birds) have shown that species richness and human density are positively related (Luck 2007). In these cases, productive environmental conditions favoring high biodiversity have also favored the development of dense human populations and intensive agriculture (Gaston 2005). Fine-grained ecological studies have tended to yield more intuitive results, namely that study plots (< 1 km^2) dominated by intensively farmed/urbanized land covers typically support fewer species than are found in plots with more natural vegetation (Pautasso 2007). The present study is intermediate in extent (9,900 km^2), but with a relatively coarse grain size (100

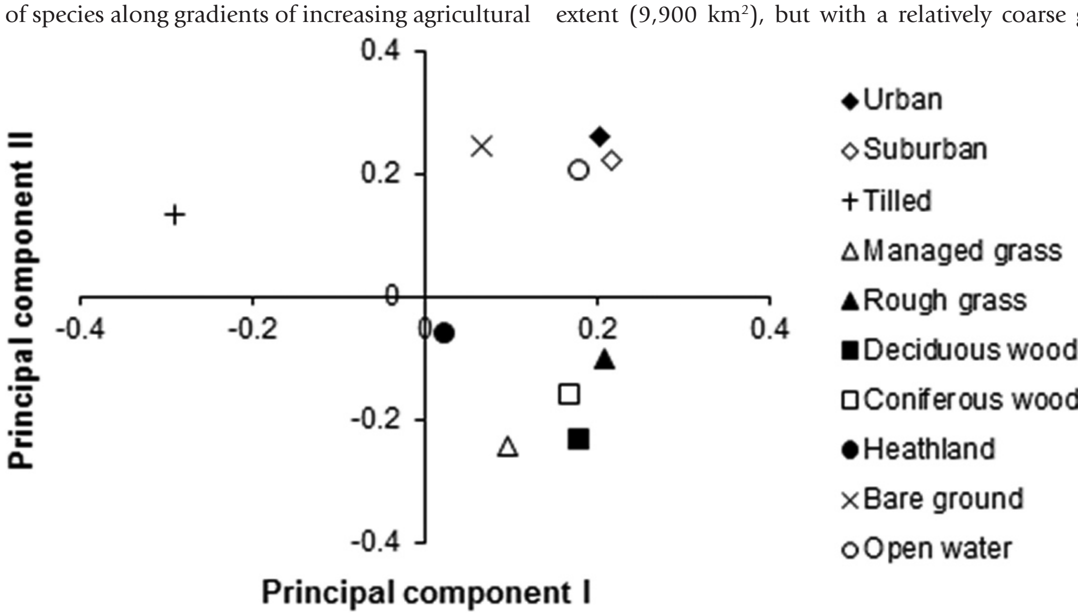

Fig. 2. Biplot for land cover variables on the first two Principal Components derived from PCA of remote-sensed land cover data from 99 10-km grid-squares.

Table 5. Correlations between the number of species in each grid-square and a) the area of each individual land cover type, and b) Shannon's evenness index based on land cover data (r_s = Spearman's correlation coefficient, n=99 in each case).

Variables correlated with species richness	Source of species richness data			
	1961-1989		1961-1997	
	r_s	P	r_s	P
a) Individual land cover types				
Urban	0.26	0.008	0.28	0.005
Suburban	0.28	0.005	0.28	0.005
Tilled	-0.31	0.002	-0.50	<0.001
Managed grassland	0.02	0.83	0.15	0.14
Rough grassland	0.34	0.001	0.45	<0.001
Deciduous woodland	0.33	0.001	0.51	<0.001
Coniferous woodland	0.41	<0.001	0.52	<0.001
Heathland	-0.04	0.70	-0.09	0.36
Bare ground	0.08	0.41	0.09	0.38
Open water	0.47	<0.001	0.51	<0.001
b) Land cover diversity indices				
Shannon's evenness J	0.40	<0.001	0.55	<0.001

km^2). At the outset of the study, the direction of relationships (if any) between species richness and land cover was therefore by no means certain.

Scale dependent patterns in biogeography present a challenge to the monitoring of the impact of land use on biodiversity at county and national levels. As the area studied increases, so the availability and resolution of both species and land cover data tend to fall. Thus, in the Orthoptera, detailed autecological studies have demonstrated close relationships between vegetation, land management and species distributions at the field-scale, yet such detailed data are available for only a small number of sites (*e.g.*, Cherrill & Brown 1990, Jauregui *et al.* 2008, Gardiner 2009b, Gardiner & Hassall 2009). At the county and national scales, species data are available widely only in the form of atlases recording the presence of species within 10-km grid-squares. A record may represent a single individual. Conversely, the absence of a record within a grid-square may reflect absence of survey, rather than true absence of the species (Haes & Harding 1997). The bulk of the orthopteran data was accumulated over several decades (Paul 1989) leading up to the production of the remotely sensed land cover data in 1988-1990, yet addition of further records from Haes & Harding (1997) did not alter the findings markedly (Table 5). The analysis suggests that both county and national species atlases provided a sound basis for analysis, despite the disparity in the number and dates of records contained.

The principal landscape gradient identified in Berkshire, Buckinghamshire and Oxfordshire reflected changes in the area of Tilled Land (arable) relative to the areas of other land cover types. Along the gradient, the area of Tilled Land fell, while the number of species increased, as did the areas of most other land cover types (Table 4, 7). As noted above, it was not a foregone conclusion that a negative relationship between agricultural intensification and species richness would emerge. Tilled Land averaged only 46% of the land surface in even the most species-poor grid-squares (Table 4) and small remnants of seminatural vegetation often support important numbers of species in agricultural landscapes (Hietala-Koivu *et al.*

Table 6. Correlations between the areas of pairs of land cover types. Figures are Spearman's rank correlation coefficients (bold font) and P for each pair of land cover types.

	Urban	Suburban	Tilled	Managed grassland	Rough grassland	Bracken	Deciduous woodland	Coniferous woodland	Heathland	Bare ground
Suburban	**0.79**									
	<0.001									
Tilled	**-0.24**	**-0.26**								
	0.02	0.01								
Managed grassland	**-0.21**	**-0.19**	**-0.71**							
	0.03	0.06	<0.001							
Rough grassland	**0.21**	**0.38**	**-0.52**	**0.24**						
	0.04	<0.001	<0.001	0.02						
Bracken	**0.09**	**-0.04**	**-0.03**	**-0.21**	**-0.06**					
	0.37	0.73	0.77	0.04	0.55					
Deciduous woodland	**-0.04**	**-0.05**	**-0.56**	**0.24**	**0.38**	**0.40**				
	0.73	0.65	<0.001	0.02	<0.001	<0.001				
Coniferous woodland	**-0.04**	**-0.16**	**-0.52**	**0.28**	**0.33**	**0.32**	**0.77**			
	0.71	0.11	<0.001	<0.01	<0.01	<0.01	<0.001			
Heathland	**-0.02**	**-0.09**	**-0.07**	**-0.12**	**-0.12**	**0.58**	**0.26**	**0.19**		
	0.83	0.36	0.50	0.24	0.25	<0.001	0.01	0.06		
Bare ground	**0.42**	**0.36**	**0.01**	**-0.37**	**-0.19**	**0.33**	**-0.01**	**-0.04**	**0.20**	
	<0.001	<0.001	0.91	<0.001	0.07	<0.01	0.89	0.72	0.05	
Open water	**0.37**	**0.37**	**-0.37**	**0.14**	**0.39**	**-0.16**	**0.08**	**0.23**	**-0.21**	**0.03**
	<0.001	<0.001	<0.001	0.16	<0.001	0.11	0.45	0.02	0.04	0.74

Table 7. Correlations between the Principal Components from PCA of land cover data and a) the area of each individual land cover type (r = Pearson's correlation coefficient derived from PCA), b) Shannon's evenness index based on land cover data, and c) species richness data (r_s = Spearman's correlation coefficient) (n=99 in each case).

	Principal Components					
	PC I		PC II		PC III	
a) Individual land cover types	r	P	r	P	r	P
Urban	0.63	<0.001	0.66	<0.001	-0.07	0.50
Suburban	0.67	<0.001	0.57	<0.001	-0.07	0.53
Tilled	-0.89	<0.001	0.34	<0.001	0.12	0.24
Managed grassland	0.30	<0.01	-0.63	<0.001	-0.52	<0.001
Rough grassland	0.65	<0.001	-0.26	<0.01	-0.14	0.16
Deciduous woodland	0.55	<0.001	-0.59	<0.001	0.33	<0.001
Coniferous woodland	0.52	<0.001	-0.41	<0.001	0.38	<0.001
Heathland	0.07	0.48	-0.16	0.13	0.82	<0.001
Bare ground	0.21	0.04	0.63	<0.001	0.36	<0.001
Open water	0.56	<0.001	0.52	<0.001	-0.13	0.20
b) Land cover diversity	r_s	P	r_s	P	r_s	P
Shannon's evenness J	0.90	<0.001	-0.12	0.25	0.23	0.02
c) Species richness data	r_s	P	r_s	P	r_s	P
1961-1989	0.44	<0.001	-0.07	0.49	-0.01	0.93
1961-1997	0.60	<0.001	-0.18	0.07	-0.06	0.56

2004, Aavik & Liira 2009, Gardiner *et al.* 2008). Many of the species in this study occur in field margins and other 'edge habitat' (Table 1). The most intensively farmed grid-squares therefore appear to contain untilled land sufficient to support a diverse assemblage of species. It is possible that the observed gradient in species richness existed prior to agricultural intensification, perhaps because areas used for intensive arable cropping were, in some other respect, less favorable for Orthoptera.

However, the most likely explanation for the observed decline in numbers of orthopteran species with increasing areas of Tilled land is that arable cropping is both directly, and indirectly, detrimental to the persistence of species at a landscape level. Direct impacts are likely to include loss of habitat through historical increases in the area of arable crops and field sizes (*e.g.*, resulting in loss of unimproved meadows and hedgerows) and current mortality of eggs, juveniles and adults within crops and managed field margins (*e.g.*, caused by ploughing and cutting) (Gardiner 2007, 2009a; Gardiner & Dover 2008). The indirect detrimental effects of arable intensification may include habitat fragmentation, landscape homogenisation, and eutrophication of adjacent areas (such as field margins) (Wilson *et al.* 1999, Benton *et al.* 2003, Eggleton *et al.* 2005, Baldi 2008, Firbank *et al.* 2008).

Habitat quality and habitat fragmentation are likely to be important unmeasured variables in the present study. The availability of remotely-sensed data, facilitates landscape-scale studies, but the ecological resolution of the land cover data is limited. A single land cover type, such as Managed Grassland, may encompass a range of ecologically distinct vegetation types which differ greatly in quality as potential habitat for Orthoptera (Cherrill *et al.* 1995). Grassland management, in terms of fertiliser application, grazing and cutting, is an important determinant of the orthopteran fauna (van Wingerden *et al*. 1991a, 1991b; van Wingerden *et al*. 1992; Gardiner 2009a), yet this information could not be deduced from the remote-sensed land cover. The quality of Managed grassland, and other, land cover types as a habitat for Orthoptera may change in parallel to the area under arable cropping (or indeed other unmeasured variables). The interpretation of the data is complicated because while the area of Managed grassland was not directly correlated with species richness (Table 5) it was correlated positively with the major axis derived from PCA (Table 7), and negatively with the area of Tilled land (Table 6). Managed grassland covered over 30% of the study area (Tables 3, 4) and its suitability as habitat for Orthoptera probably plays an important, but hidden, role in the present study. The importance of habitat quality has been demonstrated for a range of grassland invertebrates (including Orthoptera) and a related factor may be the spatial configuration of this habitat (With & Crist 1995, Hjermann & Ims 1996, Johannesen *et al.* 1999, Thomas *et al.* 2001, Honnay *et al.* 2003).

Burel *et al.* (1998) and Niemala & Kotze (2009) report that the characteristics of species vary along gradients of increasing agricultural intensification and urbanisation. Thus, even where species richness *per se* does not change, species may be replaced along gradients (*e.g.*, Baudry *et al.* 2000, Minor & Dean 2010). Assemblages of species found in less natural landscapes tend to include more nonnatives and species associated with open, disturbed and non-woodland habitats (*e.g.*, Baudry *et al.* 2000, Honnay *et al.* 2003, Wania *et al.* 2006). Niemala & Kotze (2009) reported that beetles in more urbanised landscapes have greater dispersal abilities compared to their more rural counterparts. In the present study, there was no evidence of 'species replacement' along landscape gradients. All species became more frequent as the percentage of tilled land decreased along the principal gradient (Table 2).

Species richness was not correlated with the second axis derived from PCA (Table 7). This gradient reflected increasing areas of Urban, Sub-urban and Tilled land (Fig. 2). Although many studies have reported correlations between species richness and urbanisation (Luck 2007), the study area contained no large cities. The most urbanised grid-square contained 36% of the Sub-urban and Urban land cover types combined. Only 7 grid-squares contained more than 25% of these cover types. Garaffa *et al.* (2009) report that the likelihood of finding a relationship between urbanisation and biodiversity increases with city size. Further investigation focusing on a major city would therefore be required to determine if a relationship existed between orthopteran diversity and urbanization in the UK.

Conclusions.—The present study has demonstrated landscape scale patterns in the occurrence of individual species and the total species richness of Orthoptera within an area of 9,900 km^2 in southern England at a resolution of 100 km^2. The principal factor correlated with species richness was the area of Tilled (arable) Land. The areas of other land cover types were broadly negatively related to the areas under arable cropping, and the evenness of land cover types also declined with increasing arable area. All species decreased in frequency as the area of Tilled Land increased, such that total orthopteran species richness was greatest in the least agriculturally intensive landscapes. However, even in the most species-poor grid-squares less than half of the land surface was tilled suggesting that there was potentially sufficient land to support all species in all grid-squares. A range of factors such as increasing fragmentation and degradation of non-arable habitats within intensively managed agricultural landscapes are likely to be important, but investigation at finer spatial resolution is needed to determine the contribution of these factors.

No relationship was found between species richness and urbanisation, but it was concluded that the extent of urban development was too limited to enable detailed investigation of this phenomena.

The study demonstrates negative impacts of agricultural intensification on the species richness of orthopteran assemblages at the landscape scale. It is established that coarse grained species data within atlases of Orthoptera, combined with remotely-sensed land cover data, are useful for detecting and interpreting current patterns in biodiversity. The approach provides a basis for interpretation of future patterns arising from changes in land-use change and climate.

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