Ecosystem services and biodiversity in urban environments

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Abstract

Here I consider the effect of land-use change by urbanisation on organic carbon (C) storage within three study areas in north-east England. I found that the contiguous urban extent of Darlington, Durham and Newcastle had increased by 67%, 229% and 65% respectively between 1945 and the present, and that the total C stored within the land occupied had decreased by around one-third. Decreases in C storage have occurred due to the replacement of agricultural land with urban land-uses of lower C storage value; notably, there have been large gains in low- to moderate-density residential areas and commercial land-uses. The greatest loss of C has been from the soil C pool, as the surface area occupied by soil, and soil depth, are greatly reduced in built urban land-uses compared to agriculture. Next, I investigated the spatial congruence between C storage and biodiversity in an urbanised area, using birds as a biodiversity indicator taxon. I found that land-uses with greatest C storage value per unit area also had the highest bird species richness and diversity, whilst land-uses with lowest C storage value had among the lowest bird species richness and diversity. However, the relationship was not straightforward; most notably, species richness and diversity were high in low- to moderate-density housing, despite these land-uses having low C storage value. Beta-diversity increased among land-uses, further highlighting the biodiversity value of some moderate to low C storage land-uses within the urban matrix. When not categorised by land-use, the overall spatial relationship between C storage and species richness and diversity was positive, and tree and woody vegetation C pools had the strongest positive relationship with bird species richness and diversity. I discuss the results with respect to UK urban planning options aimed at meeting both C emissions and biodiversity conservation targets, whilst also considering the continued well-being of increasing urban human populations.

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Abbreviations and acronyms

ANOVA	Analysis of variance
ARD	Afforestation, reforestation and deforestation
C	Carbon
CAP	Common Agricultural Policy
CBD	Convention on Biological Diversity
CO_2	Carbon dioxide
dbh	Diameter at breast height
df	Degrees of freedom
EIT	Economies in transition
GE	Google Earth
GHG	Greenhouse gas
GLM	Generalised linear model
GPS	Global positioning system
IPCC	Intergovernmental Panel on Climate Change
KML	Keyhole markup language
LOI	Loss on ignition
LULUCF	Land use, land-use change and forestry
MA	Millennium Ecosystem Assessment
NPPF	National Planning Policy Framework
OECD	Organisation for Economic Co-operation and Development
SOC	Soil organic carbon
UKNEA	United Kingdom National Ecosystem Assessment
UN	United Nations

UNFCCC United Nations Framework Convention on Climate Change

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Thesis structure

This thesis is presented in two parts covering two separate but complementary themes. Each part consists of an introductory chapter followed by a data chapter. The data chapters are written in scientific paper format and are intended to be read as stand-alone documents. There is therefore, some repetition of text from the introductory chapters within the introduction sections of the respective data chapters. The final chapter gathers the key results and findings from the previous chapters, and discusses them collectively with concluding remarks.

Part 1:

The effect of land-use change by urbanisation on carbon storage

Chapter 1:

Introduction

1.1 Ecosystem services: what, when and why?

Humanity has always been dependent upon the services provided by Earth's biosphere, and it has long been recognised that populations are limited by restrictions imposed upon them by nature. As long ago as 1798, Thomas Robert Malthus (1798, reprinted 2008) warned of an impending food shortage brought about by human population growth (Johnson, 2000), and one-hundred and sixty years later, Rachel Carson's *Silent Spring* (1962) epitomised the impairment to human psychological well-being as nature and the environment succumbed to humanity's endeavours to nourish a burgeoning population. A continued assault on ecosystems in a quest for food and fuel has damaged the public service functions of those systems (Ehrlich and Mooney, 1983). These functions are now widely referred to as ecosystem services, and simply put, are the outputs from ecosystems from which humans derive benefits (Costanza *et al*., 1997).

Gretchen Daily's (1997) *Nature's Services* is considered a landmark publication representing modern-day ecosystem service science, and its arrival coincided with increasing political concern for loss of global service delivery; concern that resulted in the production of the Millennium Ecosystem Assessment (MA; 2005a). The MA was requested in 2000 by the United Nations (UN) and completed in 2005 with input from over 1300 scientists worldwide. Its most powerful statement is that 60% of the ecosystem services it examined are being degraded or lost, largely at the expense of human activities. The MA provided a scientific basis for the necessary actions to encourage the conservation and sustainable use of ecosystems and their contributions to human well-being. Furthermore, by emphasising the importance of environmental accounting, the MA transported ecosystem service science into the field of economics (Barbier *et al*., 2009).

The MA distinguishes four broad headings under which ecosystem service contributions to human well-being might be ordered: provisioning services, supporting services, regulating services and cultural services. This categorisation has since been criticised for being overly generic and open to ambiguity, and as such, is of limited use to both economists (Boyd and Banzhaf, 2007) and landscape managers (Wallace, 2007) for providing assistance in placing value on ecosystem services. Fisher and Turner (2008) went on to separate the MA's headings into *intermediate* and *final* ecosystem services. This structure is adopted by the UK's response to the MA, the UK National Ecosystem Assessment (UKNEA; 2011), and is presented here in Table 1.1. Despite its potential shortcomings, the MA's categorisation emphasised, for the first time (Barbier *et al*., 2009), regulating services; services that regulate the earth's ability to react to environmental shock and stress.

Table 1.1 A classification system for ecosystem services derived from the Millennium Ecosystem Assessment (MA), with modifications by Fisher and Turner (2008) and the UK National Ecosystem Assessment (UKNEA; 2011). Final ecosystem services contribute directly to goods and services valued by people; intermediate services and ecosystem processes underpin final ecosystem services, but are not directly linked to goods and services. Provisioning and cultural services are always final ecosystem services, regulating services may be final or intermediate, and supporting services are always intermediate services/ecosystem processes (taken from UKNEA, 2011).

Intermediate services/ecosystem processes		Final ecosystem services (example of goods)	
Supporting services	Primary production	Provisioning services	Crops, livestock, fish (food)
	Soil formation		Trees, standing vegetation, peat (fibre, fuel, carbon sequestration)
	Nutrient cycling		
	Water cycling		Water supply (domestic and industrial)
			Wild species diversity (bioprospecting and medicines)
		Cultural services	Wild species diversity (recreation)
	Decomposition		Environmental settings (recreation, tourism, spiritual)
	Weathering		
	Climate regulation	Regulating services	Climate regulation (equable climate)
	Pollination		Pollination
	Disease and pest regulation		Purification in soils, air and water (pollution control)
	Ecological interactions		
	Evolutionary processes		Hazard regulation (erosion control, flood control)
	Wild species diversity		
			Noise regulation
			Disease and pest regulation

1.2 Carbon storage: a regulating ecosystem service

Human activities have contributed, and continue to contribute, to the increasing greenhouse gas (GHG) concentrations in the atmosphere. The Intergovernmental Panel on Climate Change (IPCC; 2013) states with *very high confidence* that anthropogenic GHG emissions have substantially increased radiative forcing, with effects on global temperatures and extreme weather and climate events, since the pre-industrial era. The majority of the increase in radiative forcing is due to increases in atmospheric carbon dioxide (CO_2). These changes to the earth's climate are intensifying the impact of various other stressors on ecological systems, such as habitat-loss and degradation, pollution, and invasive species. The combination of impacts is causing changes to ecosystem processes, with potentially adverse implications for people (IPCC, 2007; Grimm *et al*., 2013). Therefore, any natural process that alleviates or buffers the rate of climate change can be viewed as a regulating ecosystem service. Carbon (C) storage is one such service.

The most influential international agreement concerning mitigation against the ecological impacts of climate change is the Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC). This agreement is intended to reduce the pace of anthropogenic contributions to atmospheric CO_2 concentrations by committing its parties to set internationally binding emissions targets (Diaz *et al*., 2009). Aside from enhancement of energy efficiency and direct emissions reductions from industrial processes, agriculture and waste, the Kyoto Protocol calls for protection and enhancement of GHG sinks and reservoirs, making a provision for Annex I parties (i.e. industrialised countries that were members of the Organisation for Economic Co-operation and Development in 1992 [OECD parties], plus countries with economies in transition [EIT parties]) to account for afforestation, reforestation, and deforestation (ARD), and other land use, land-use change, and forestry (LULUCF) activities in meeting their commitments to the agreement (United Nations [UN], 1998; IPCC, 2000).

1.3 Land use, land-use change and forestry

The major natural mechanisms driving C release into the atmosphere in terrestrial ecosystems include plant respiration and decay of organic matter, and the major natural mechanism of C uptake from the atmosphere is photosynthesis by vegetation (Churkina, 2013). Perennial or woody vegetation may retain C within relatively long-lived sinks, thus, stalling its eventual release into the atmosphere, and the C within detritus may accumulate as an organic component of soils. The balance between C release and uptake within a given area of the earth's surface is therefore, dependent upon its land cover, as the function of a particular land-cover type depends upon the amount of C that it sequesters and stores, and the magnitude of its C exchange with the atmosphere (Churkina, 2013). By altering the balance and composition of land-cover types, humanity is changing the natural rate of exchange of atmospheric C with the terrestrial biosphere through land-use change (Meyer and Turner, 1992; Dale, 1997; Bolin and Sukumar, 2000; IPCC, 2000; Robinson *et al*., 2013).

Land use is defined by the Food and Agriculture Organization of the UN (2005) as *the arrangements, activities and inputs people undertake in a certain land-cover type to produce, change or maintain it*. Up until the 1950s, land-use change was the primary source of human-induced CO_2 (Houghton and Skole, 1990). Contributions made by fossil fuel burning increased rapidly after this period, but at the turn of the century, emissions attributable to land-use change activities remained responsible for approximately 20% of the 7.9 Gt of C released annually within global human-induced GHG emissions (IPCC, 2000; Schlamadinger *et al*., 2007). Of the total annual C emissions, it is estimated that nearly 30% is taken up by terrestrial ecosystems (IPCC, 2000). An equal amount is taken up by the earth's oceans, and the remainder remains stored in the atmosphere (IPCC, 2000), thus, contributing to radiative forcing and global climate change.

The potential for terrestrial photosynthesis and soil respiration to buffer C emissions release, and the importance of vegetation and soil C sinks in the regulation of global warming and climate change, are recognised in the Kyoto Protocol. Considering the influence that land-use activities have upon C emissions and removals, and in turn, their potential to be influenced by policy measures, it is vital to understand how C stocks fluctuate in response to land-use change activities (IPCC, 2000; Schlamadinger *et al*., 2007).

1.4 Land-use change by urbanisation

At present, urban areas occupy only a small proportion of the earth's total land surface area. Current estimates vary from less than 1% up to 3%, depending on the set of standards used for urban characterisation (Liu *et al*., 2014). However, global urban human populations have increased dramatically during the past 100 years (Alberti and Hutyra, 2013), and now more than half of the world's population live within towns, cities and urban agglomerations (UN, 2012). Consequently, in recent decades, the urban environment has become the fastest growing land-use type (Antrop, 2000; Hansen *et al*., 2005; Radford and James, 2013). Furthermore, because it results in changes to hydrology, biogeochemistry, climate and biodiversity (Grimm *et al*., 2008), and because of its level of permanence (Seto *et al*., 2012), urbanisation has become one of the most important land-use change processes in the world today (Berland, 2012), and next to climate change, the biggest environmental challenge of our time (United Nations Secretariat, 2012).

Despite their small area of land surface occupation, urban areas have high C footprints (Svirejeva-Hopkins *et al*., 2004; Trusilova and Churkina, 2008). Indeed, it is estimated that 70% of all anthropogenic C releases are attributable to urban environments (International Energy Agency [IEA], 2008; Churkina *et al*., 2010). The process of urbanisation also contributes to emissions release through loss or reduction of longer-term C stocks made by radical changes to land cover (Hutyra *et al*., 2011). This is particularly so in temperate forested regions (Imhoff *et al*., 2004; Pouyat *et al*., 2006), where the establishment or expansion of urban environments involves the replacement of natural vegetation or agricultural habitat with impervious artificial surfaces, turf, gardens and scattered trees (Churkina *et al*., 2010; Berland, 2012).

Until recently, urban areas have been omitted from estimates of emissions release by land-use change (Houghton, 2013). However, as urban human populations are set to continue rising into the foreseeable future, with a forecasted 67% of the world's estimated 9.6 billion people living in towns and cities by 2050 (United Nations [UN], 2012, 2013), and with global expansion of urban areas currently being twice as rapid as their population growth (Angel *et al*., 2011; Seto *et al*., 2011), understanding the impact of urban land-use and the process of urbanisation on global and regional C stocks and cycles is an increasingly important area of research.

1.5 Post-war urbanisation in the United Kingdom

The inter-war years experienced a dramatic 40% increase in urban extent in the UK (Ward, 1994), and this trend continued following the end of the Second World War. Inner-city housing was cleared and rebuilt at lower densities, and council estates were created at the periphery of towns and cities to accommodate the cleared dwellers (Couch and Karecha, 2006). This coincided with a surge in the development of privately occupied dwellings (Couch and Karecha, 2006), creating the sprawling housing estates of suburbia, which came largely at the expense of agricultural land (Best, 1981).

Estimates of the extent of urbanised area in England and Wales were assisted upon the introduction of the 1947 Town and Country Planning Act. Under the Act, planning authorities were required to produce a comprehensive account of existing and proposed acreages under various forms of land-use, including any significant urban areas, which were defined as cities and towns with populations of over 10,000 people (Best, 1981). Initial estimates of urban land area in the early 1950s were approximately 1,458,000 ha in England and Wales and 190,000 ha in Scotland (Best and Coppock, 1962; Best, 1981). In the ensuing decades, at least up until the early-1970s, the London region, the central urban region (notably, Lancashire and Cheshire) and outliers in Durham and parts of South Wales, maintained a relatively high rate of agricultural land conversion to urban uses (Best, 1981).

Although the inefficiencies of urban sprawl were recognised early, resulting in the Green Belt policy for England in 1955, it was not until the late-1980s that policy was reinforced in response to environmental concern over the loss of greenfield land (Couch and Karecha, 2006) and the belief that sprawling urban settlements promote fuel consumption and C emissions (Echenique *et al.*, 2012). By the mid-1990s, UK government had set targets stating that at least half of all new housing would be built on previously developed urban land (Couch and Karecha, 2006), the so-called brownfield sites. Hence, since 2000, UK policy has actively promoted the process of urban densification (Office of the Deputy Prime Minister [ODPM], 2005, 2010; Dallimer *et al*., 2011; UKNEA, 2011).

Today, the area under urban and developed land-use in the UK is estimated at 2,748,000 ha, and accounts for approximately 10% of the total land area (Khan *et al*., n.d.). The conversion of greenfield land to urban land-uses accounts for around 5,000 ha per year, which is about one-third that of the post-war years leading up to 1975 (Bibby, 2009; *cf*. Best, 1981). Furthermore, of the greenfield land developed between 2000 and 2006, approximately 20% was lost from within the urban matrix, and consisted mainly of recreation (Bibby, 2009). Indeed, in 2011, 68% of new residential dwellings within England were built on brownfield sites, and 53% of the land utilised was brownfield (Department for Communities and Local Government [DCLG], 2013). Consequently, growth in urban extent has slowed over the last two decades, and is now less than at any time in the inter-war years and the first three decades following the end of the Second World War (Bibby, 2009). However, concerns have been raised over the economic and technical feasibility of continued urban densification, as well as over its social acceptability (Breheny, 1997; Couch and Karecha, 2006; Echenique *et al*., 2012). Indeed, the introduction of the National Planning Policy Framework (NPPF; DCLG, 2012), which sets out UK government's revised planning policy for England, has initiated debate over policy protection of Green Belt land (Smith, 2014), and further raises concern over the sustainability of urban densification leading into the future.

1.6 Carbon storage in urban environments

The role of urban vegetation and soils as C sinks in global and regional C cycles has, until recently, remained largely neglected (Churkina, 2008), and urban areas have been recognised only as a source of emissions (Hutyra *et al*., 2011). Within early national inventories of C stored within the vegetation and soils of the UK, Milne and Brown (1997) reported a C density of zero tonnes per ha for urban and suburban land-use, and Bradley *et al*. (2005) assumed a soil C content of zero tonnes per ha for built-over urban areas, and that suburban soils store half that of adjacent pasture. However, these assumptions about urban C stores were made whilst mapping the land on a coarse-scale 1 km^2 grid, and further studies based upon finer-scale land-cover data in the United States (Nowak and Crane, 2002; Pouyat *et al*., 2006; Churkina *et al*., 2010; Hutyra *et al*., 2011), Germany (Strobach and Haase, 2012) and the United Kingdom (Davies *et al*., 2011; Edmondson *et al*., 2012; Edmondson *et al*., 2014a, 2014b), have produced estimates indicating that a substantial store of C exists within urban vegetation and soils. This contradiction arises because urbanisation typically results in a matrix of high- and low-density built-up areas, often mixed with patches of fragmented natural or semi-natural habitat and other greenspace (Cadenasso *et al*., 2007; Hutyra *et al*., 2011). Fine-scale studies produce greater C storage estimates, as they identify patches of high C storage within the urban matrix that coarse-scale studies are prone to overlook (Davies *et* *al*., 2013). However, comparisons between studies, and between their respective study sites, are rarely possible, because variation within factors such as climate, soil-type, population density, land management and history of urbanisation influence the C storage capacity of settlements (Davies *et al*., 2013), as will the author's definition of urban land-use (Raciti *et al*., 2012) and the classification in how they combine social, physical and biotic components (Davies *et al*., 2013).

Although the process of urbanisation may initially reduce the C storage of an area of land, the urban environment may regain C stocks over time as the vegetation recovers (Zhao *et al*., 2007; Berland, 2012), until eventually, stores within certain areas of the urban matrix may surpass those of the land cover they have replaced. This is said to be especially so of tree cover following urbanisation of former agricultural land (Berland, 2012); the latter has been reported to be both less productive in terms of primary productivity (Zhao *et al*., 2007; but see Imhoff *et al*., 2004) and to contain less soil organic carbon (SOC; Edmondson *et al*., 2014b) than some land-cover types within adjacent urban areas. Ultimately however, the outcome of such comparison may be dependent upon the scale of analysis, and the areal extent of patches of high C storage within the urban matrix. For example, although Edmondson *et al*. (2014b) found that urban greenspace soils in Leicester, UK contained greater SOC per unit area than adjacent agricultural land, when totalled across the full extent of the city, so as to incorporate the entire matrix of urban land-cover types, greenspace or otherwise, the area occupied by the city would in fact store less SOC than had the area remained in agricultural use[1]. As such, it remains unclear whether the C storage capacity of the entire area occupied by a matrix of urban land-use types is greater, or less, than had it remained in non-urban use.

[1]Edmondson *et al*. (2014b) estimated the average soil organic carbon (SOC) in the greenspace of Leicester, UK to be 9.9 kg m^{-2} (to 21 cm depth). When multiplied by the area of greenspace within the city reported by the study (41.5 km^2), this amounts to 410.8 million kg SOC across the city (soil capped by artificial surfaces was excluded from their estimate). The same study estimated SOC within arable land surrounding Leicester to be 7.1 kg m^{-2}. When multiplied by the total area of the city as reported by the study (73 km^2), this amounts to 518.3 million kg SOC.

With the extent of urban area set to continue increasing into the foreseeable future, understanding the historical impact of land-use change by urbanisation on C storage can help inform planning decisions and aid efforts to meet with UK climate change mitigation policy aimed at delivering an 80% reduction in GHG emissions (relative to the 1990 baseline) by 2050 (Climate Change Act 2008; Ostle *et al*., 2009).

1.7 Aims and objectives

In Part 1 of this thesis, I will estimate historical land-use change by urbanisation in three study areas in north-east England between 1945 and the present, and take this as a proxy for changes in the vegetation C and SOC storage of the study areas. This was a period of major expansion in the towns, cities and infrastructure of the country, which coincided with major reform in, and intensification of, agricultural practices (Robinson and Sutherland, 2002; UKNEA, 2011), leading to a loss of agriculture at the expense of urban land-use types. Few studies have attempted to map such long-term changes in C storage as a consequence of land-use change. A recent exception is provided by Jiang *et al*. (2013), who recorded changes in the extent and spatial pattern of C stores across the county of Dorset, UK between the 1930s and 2000. However, at a resolution of 1 ha, their study is too broad to detect the fine-scale changes caused by increases in the extent of urban land-use types. This present study therefore, is unique in this respect.

The aims of the study will be achieved under the following objectives:

1) Utilising high resolution satellite imagery and newly digitised historical photography, I will produce land-use maps of the contiguous urban extent of three representative urban study areas, Darlington, Durham and Newcastle, in north-east England, which

show the extent and distribution of assigned urban and non-urban land-use categories in 1945 and the present.

2) I will estimate the mean vegetation C and SOC storage per unit area of each of the assigned land-use categories from vegetation and soil samples collected from the field, and will estimate the total historical and contemporary C storage capacity of the study areas using the contemporary and historical land-use maps.
3) I will calculate the change in contiguous urban extent, and in the C storage capacity of the land within the historical and contemporary land-use maps of the study areas.
4) I will discuss the results and findings in terms of historical and current policy regarding land-use change by urbanisation, and their implications for the future.

Chapter 2:

Urbanisation and carbon storage in north-east England

ABSTRACT

Context: Human land-use change is affecting the rate of exchange of atmospheric carbon (C) with the terrestrial biosphere, with impacts on climate. Urbanisation is one of the most important land-use change processes worldwide today, and the urban environment is the fastest growing land-use type. As urban human populations are set to continue rising into the foreseeable future, understanding the impact of urban land-use and the process of urbanisation on C stocks is an increasingly important area of research.

Aims: I measured the areal change in *i*) contiguous urban extent, and *ii*) different urban land-use categories in three towns and cities in north-east England between 1945 and the present, a period of major expansion in the urbanised areas of the UK.

Methods: I combined contemporary satellite imagery with historical aerial photography to categorise urban and non-urban land-uses. C storage values were calculated from data collected in the field and applied to land-use categories. The effect of urban expansion and fine-scale land-use change within the urban matrices on the C storage value of the land occupied was then evaluated.

Results: The urban extent of Darlington, Durham and Newcastle increased by 67%, 229% and 65% respectively between 1945 and the present, and consequently, the C storage value of the land occupied decreased by 34%, 33% and 31% respectively. Decreases in the C storage of the study areas occurred through loss of surrounding agricultural land and replacement with urban land-uses of lower C storage value; notably, there were large gains in low- to moderate-density residential and commercial land-uses. Loss of soil organic carbon

(SOC) was the dominant driver of decreases in C storage, as the surface area occupied by soil, and soil depth, were reduced in many urban land-use categories compared to agriculture. Increases in the area of urban woodland off-set some C losses. Indeed, increases in urban tree cover more than compensated for loss of hedgerow trees in the former agricultural landcscape, emphasising the mitigation value of urban trees. However, gains from urban trees were small in comparison to SOC losses.

Conclusion: The contiguous extents of the three urban study areas increased dramatically between 1945 and the present, and the associated changes to land-cover reduced C storage within the vegetation and soils of the land occupied by approximately one-third. Modification to UK planning policy, implemented in recent decades, has promoted urban densification, which has succeeded in slowing the outward growth of towns and cities, with a potential incidental reduction in the rate of C storage loss. However, there are economic, technical and social concerns over continued densification. The way we choose to grow our cities leading into the future will have implications for national and international C emissions targets

2.1 INTRODUCTION

Anthropogenic processes, notably land-use change, are changing the natural rate of exchange of atmospheric carbon (C) with the terrestrial biosphere, with impacts on climate (Meyer and Turner, 1992; Dale, 1997; Bolin and Sukumar, 2000; Intergovernmental Panel on Climate Change [IPCC], 2000; Robinson *et al*., 2013). In 1945, land-use change was the primary source of human-induced carbon dioxide (CO_2) release (Houghton and Skole, 1990). Emissions by fossil fuel burning increased dramatically after this time, but at the turn of the century, emissions attributable to land-use change activities remained responsible for approximately 20% of the annual CO_2 within global human-induced greenhouse gas (GHG) emissions (IPCC, 2000; Schlamadinger *et al*., 2007). Land-use change also influences the spatial distribution of terrestrial C sources and sinks within the landscape (Canadell, 2002; Müller *et al*., 2007). The Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC) calls for protection and enhancement of GHG sinks and reservoirs, making a provision for Annex I parties (industrialised countries that were members of the Organisation for Economic Co-operation and Development in 1992 [OECD parties], plus countries with economies in transition [EIT parties]) to account for land use, land-use change, and forestry (LULUCF) activities in meeting their commitments to the agreement (United Nations [UN], 1998; IPCC, 2000; Dyson and Mobbs, 2009).

One of the most important land-use change processes worldwide today is urbanisation (Berland, 2012); a highly dynamic process causing rapid alteration of the landscape (Antrop, 2000) with a high degree of permanence (Seto *et al*., 2012). Globally, urban human populations have increased dramatically over the past 100 years (Alberti and Hutyra, 2013), and the urban environment has become the fastest growing land-use type (Antrop, 2000; Hansen *et al*., 2005; Radford and James, 2013). Urbanisation results in changes to local and regional hydrology, biochemistry, climate and biodiversity (Grimm *et al*., 2008), and despite a small area of land surface occupation, urban areas have disproportionately high C footprints (Svirejeva-Hopkins *et al*., 2004; Trusilova and Churkina, 2008). Indeed, it is estimated that 70% of all anthropogenic C releases are attributable to urban environments (International Energy Agency [IEA], 2008; Churkina *et al*., 2010). The process of urbanisation also contributes to emissions release through loss or reduction of longer-term C stocks made by radical changes to land cover (Hutyra *et al*., 2011), where the establishment or expansion of urban environments involves the replacement of natural vegetation or agricultural habitat with impervious artificial surfaces, turf, gardens and scattered trees (Churkina *et al*., 2010; Berland, 2012). As urban human populations are set to continue rising into the foreseeable future, with a forecasted 67% of the world's estimated 9.6 billion people living in towns and cities by 2050 (UN, 2012, 2013), and with global expansion of urban areas being twice as rapid as their population growth (Angel *et al*., 2011; Seto *et al*., 2011), understanding the impact of urban land use and the process of urbanisation on global and regional C stocks and cycles is an increasingly important area of research.

There was a period of major expansion in the towns, cities and infrastructure of the UK in the decades following the end of the Second World War. This coincided with major reform in, and intensification of, agricultural practices (Robinson and Sutherland, 2002; UK National Ecosystem Assessment [UKNEA], 2011), and led to loss of agricultural land at the expense of outwardly expanding urban areas. Early environmental concern over the loss of greenfield and rural landscapes led, in 1955, to the Green Belt policy for England. More recently, in the 1990s, UK government set targets stating that at least half of all new housing should be built on previously developed urban land (Couch and Karecha, 2006); so-called urban densification. These policies have served to slow the rate of urban expansion, especially in recent years, when conversion of greenfield into urban land-uses reduced to approximately one-third the annual rate of the post-war years leading up to 1975 (Bibby, 2009). However, concerns have been raised over the economic and technical feasibility of continued urban densification, as well as over its social acceptability (Breheny, 1997; Couch and Karecha, 2006; Echenique *et al*., 2012). Indeed, the introduction of the National Planning Policy Framework (NPPF; Department for Communities and Local Government [DCLG], 2012), which sets out UK government's revised planning policy for England, has initiated debate over policy protection of Green Belt (Smith, 2014), and raises further concerns over the sustainability of urban densification leading into the future. Little is known of the change to C stores within the vegetation and soils of urban and non-urban land-uses during phases of rapid outward urban growth. However, such information may influence decisions regarding potential reinforcement or relaxation of densification policy.

Early national inventories of biological C stored within the vegetation and soils of Great Britain report a C density of zero tonnes per hectare for urban areas (Milne and Brown, 1997), or assume a soil organic carbon (SOC) content of half that of adjacent pasture (Bradley *et al*., 2005). However, these assumptions about urban C stores were made using a coarse-scale 1 km^2 grid, and further studies based upon finer-scale land cover data in the United States (e.g. Nowak and Crane, 2002; Pouyat *et al*., 2006; Churkina *et al*., 2010; Hutyra *et al*., 2011), Germany (e.g. Strobach and Haase, 2012) and the United Kingdom (e.g. Davies *et al*., 2011; Edmondson *et al*., 2012, 2014a, 2014b), have produced estimates indicating that substantial C stores currently exist within urban areas. This is because urbanisation typically results in a matrix of high- and low-density built-over areas, often inter-mixed with patches of fragmented natural or semi-natural habitat and other greenspace (Cadenasso *et al*., 2007; Hutyra *et al*., 2011). Fine-scale studies produce greater C storage estimates, as they identify patches of high storage within the urban matrix that coarse-scale studies are prone to overlook (Davies *et al*., 2013). Moreover, the C storage value of some land covers within the urban matrix may surpass those of the land cover they have replaced. This is said to be especially so of tree cover following urbanisation of former agricultural land (Berland, 2012); the latter has been reported to be less productive in terms of primary productivity (Zhao *et al*., 2007; but see Imhoff *et al*., 2004) and to contain less SOC (Edmondson *et al*., 2014b) than some land-cover types within adjacent urban areas. However, when considering C storage within the entire urban area, one needs to account for impervious surfaces and buildings. These features are largely devoid of organic C-containing vegetation and topsoil, and comprise a considerable proportion of the urbanised area. Therefore, even if certain land covers within the urban matrix contain equal or greater vegetation C and/or SOC stores per unit area than some of the non-urban land covers they have replaced, when considered in its entirety, it is unclear whether the area occupied contains a greater or lesser C stock than had it remained in non-urban use.

Few studies have attempted to map long-term changes to C storage as a consequence of land-use change. A recent exception is provided by Jiang *et al*. (2013), who recorded changes in the extent and spatial pattern of C stores across the county of Dorset, UK between the 1930s and 2000. However, at a resolution of 1 ha, their study is too broad to detect the fine-scale changes caused by increases in the extent of urban areas. Here, I use high resolution satellite imagery and newly digitised historical aerial photography to recognise and categorise urban and non-urban land-uses. I aim, firstly, to measure the change in contiguous areal extent of three major towns and cities in north-east England between 1945 and the present, and, secondly, to determine the effect that this, and land-use change within the urban matrices, has had on the vegetation C and SOC stores of the land occupied.

2.2 METHODOLOGY

2.2.1 Study areas

To provide a reasonable representation of urban areas within the north-east region of England, three study areas were sampled: Darlington, Durham City (hereafter Durham) and Newcastle-upon-Tyne (hereafter Newcastle; Figure 2.1). The study area for Newcastle consisted of a 40.4 km^2 portion of the city to the west of the B1318 Great North Road, and accounted for approximately one quarter of the current total area of the city. This portion was selected to reflect the partial coverage of the city by historical imagery, and also provided a study area comparable in extent to Darlington and Durham. The entirety of the urban areas of both of the latter was considered.

Latitude, and climatic variables such as mean annual precipitation and temperature, have the potential to indirectly affect regional carbon (C) budgets by influencing the vegetation type and vegetation growth rates (Bachelet *et al*., 2001). In addition, mean annual precipitation, along with the clay content of soils, correlate positively with regional soil organic carbon (SOC) content, whilst, in general, mean annual temperature correlates negatively with SOC (Jobbagy and Jackson, 2000). Information on the location, current areal extent, population size and climate of the three study areas is presented in Table 2.1, and a description of soil types is presented in Table 2.2.

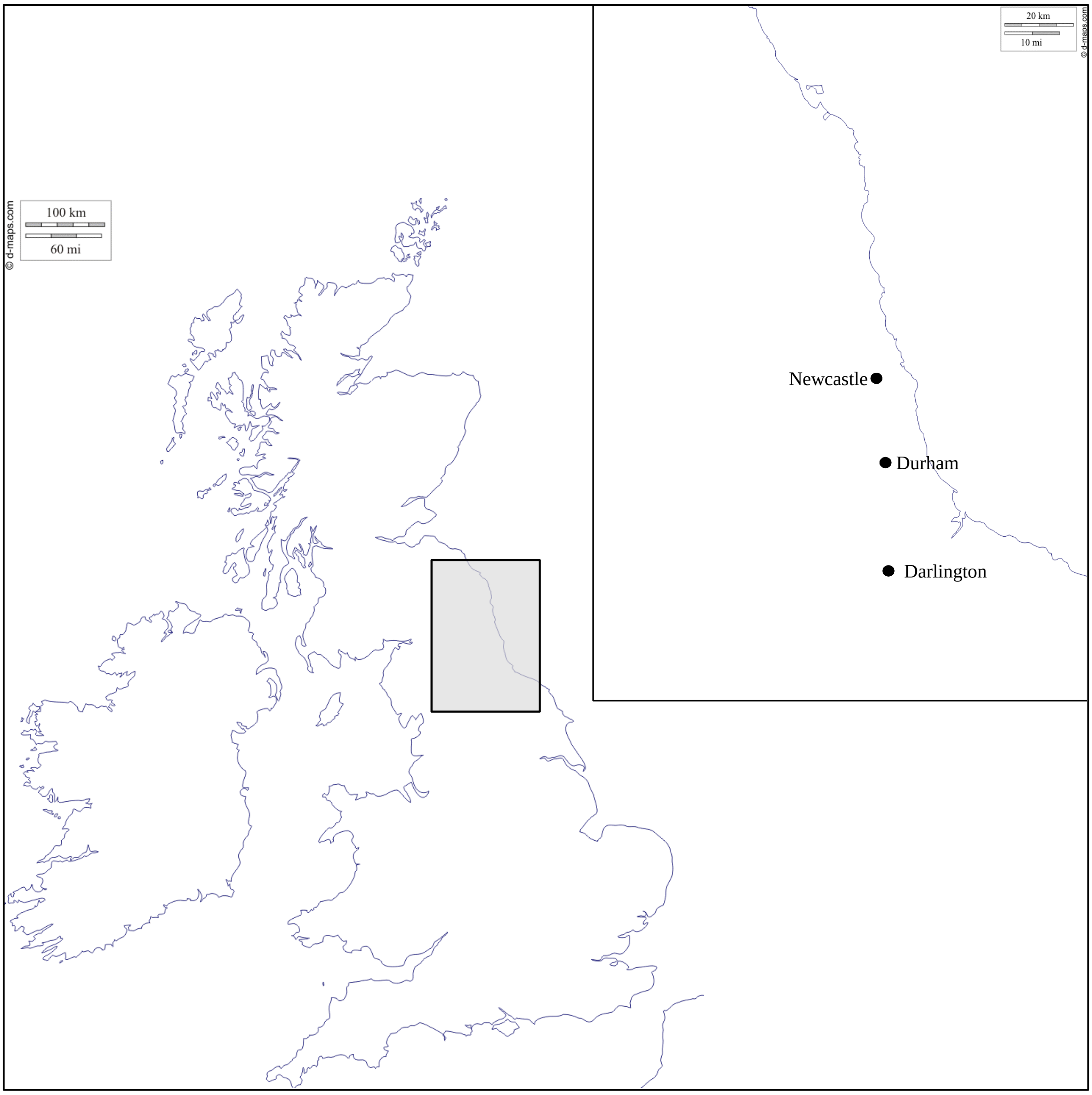

Figure 2.1 Outline map of the United Kingdom (excl. Shetland Isles) highlighting the north-east region of England and the location of the urban study areas of Darlington, Durham and Newcastle within this region (inset). Map outlines taken from d-maps.com.

Table 2.1 Selected attributes of the three study conurbations of Darlington, Durham and Newcastle. Study area extent is based upon boundaries defined by the present study. Mean annual precipitation and mean annual daily temperatures are based upon the period 1981-2010, as measured by the nearest climate station to the respective study area. Population estimates are for the entire conurbations, and are based on the parliamentary constituency population estimates for mid-2012.

Attribute	Study area		
	Darlington	Durham	Newcastle
Co-ordinates	54°31'25.66" N, 01°33'34.11" W	54°46'32.70" N, 01°35'06.23" W	54°59'21.20" N, 01°39'35.81" W
Study area extent (km^2)	24.6	15.3	40.4
Population[a]	91,100	95,000	282,500
Mean annual precipitation (mm)[b]	574	651	597
Mean annual daily temperature (°C)[b]:			
Minimum	5.2	5.4	6.7
Maximum	13.1	12.9	12.1

[a] Office for National Statistics (ONS; 2013)

[b] Met Office (n.d.)

Table 2.2 The soil characteristics of Darlington, Durham and Newcastle. Data taken from Cranfield Soil and Agrifood Institute (http://www.landis.org.uk).

Study area	Description of soil
Darlington	Freely draining, slightly acid loams in centre of urban area; slowly permeable, seasonally wet, slightly acidic but base-rich loams and clays elsewhere
Durham	Freely draining, slightly acid sandy soils through centre of urban area; slowly permeable, seasonally wet, acidic loams and clays to west; slowly permeable, seasonally wet, slightly acid but base-rich loams and clays to east
Newcastle	Slowly-permeable, seasonally wet, slightly acid, but base-rich loams and clays

2.2.2 Land-use mapping and categorisation

Contemporary land-use categorisation within the three study areas was determined using Google Earth (GE) v7.1.2 software (Google Inc., Mountain View, CA, USA), which combines high resolution contemporary satellite imagery and aerial photography to create a three-dimensional globe. GE also incorporates digitised historical aerial photography, making it possible to assess land-use change within an area at two points in history. GE included historical photography dating from 1945 for all three study areas. Contemporary satellite imagery was dated 2009 for Darlington and Durham, and 2012 for Newcastle.

Defining urban extent is ambiguous (Raciti *et al*., 2012), as urban areas invariably consist of a heterogenous mix of various land-cover types, and as such, are a matrix of small-scale vegetated and artificial surfaces (Cadenasso *et al*., 2007; Hutyra *et al*., 2011). In this study, the contemporary boundaries of the study areas were defined by the delineation between what was classified as an urban land-use category (see Table 2.3) and contiguous non-urban land-use (e.g. agriculture) or semi-natural land-cover (e.g. woodland or scrub). If these latter land-uses or land-covers were not contiguous, and were set within the matrix of urban land-use categories, the area was considered urban, and included within the boundary of the study area. For simplicity, the term *land-use* was applied to all categories, although strictly, *grassland, scrub, woodland* and *no vegetation* describe land cover.

Each study area was divided into urban land-use categories as defined in Table 2.3. The criteria distinctive to each category needed to be discernible within historical photography as well as in contemporary satellite imagery. Example satellite imagery of each of the land-use categories is provided in Figure 2.1. The extent of each category was defined using GE's polygon tool and each was colour-coded to produce a visual matrix of land use within the boundary of each study site. This process was repeated for contemporary and 1945 maps.

Contemporary land-use polygons were ground-truthed using GE street-view and by site visitation. Although this was not possible for the historical land-use polygons, all land-uses were categorised easily, and there were no areas omitted due to ambiguity. The land surface area of each polygon was calculated by importing the KML-encoded data from GE into KML Toolbox (Zonum Solutions, Tucson, AZ, USA, http://zonums.com/online/kmlArea/).

Table 2.3 The land-use categories of Darlington, Durham and Newcastle, and their qualifying criteria. The density of buildings within residential land-use categories was based upon figures obtained by Gill *et al*. (2008). School and university buildings were assigned to a land-use category best matched by their vegetative structure and building density.

Land-use category	Criteria
Agriculture	Land used for livestock grazing or for production of arable crop. Includes boundary hedgerows, field margins and farm buildings.
Allotment	Community garden areas; typically used for individual or non-commercial food production and horticulture.
Amenity grassland	Mown turf; typically sporting facilities (including those belonging to schools and universities) or parks without mature trees.
Commercial	Industry, commerce or retail including areas of greenspace and/or lawn within the infrastructure. Includes hospitals and fire stations.
Grassland	Semi-natural or rough grassland. Includes pasture for horses.
Parkland	Large (>4 m), sparsely distributed, mature trees within open grassy areas. Includes parks and cemeteries.
Residential:	
Urban no garden	High housing density (>45 buildings ha^{-1}). Typically terraced buildings with small backyards, an absence of vegetated garden areas, and often few or no trees.
Urban with garden	Moderate housing density (25-45 buildings ha^{-1}). Typically semi-detached or terraced buildings with front and/or rear vegetated gardens, and, in general, a significant number of trees.
Suburban	Low (<25 buildings ha^{-1}) to moderate housing density. Detached or semi-detached buildings, with front and/or rear vegetated gardens, and often many trees.
Scrub	Mixed semi-natural vegetation, dominated by shrubs, small trees (<4 m) and rough grassland. Often includes railway embankments and embankments to major through-roads (e.g. A1).
Woodland	Large (>4 m), mature trees in dense stands; typically with an understorey/shrub-layer and leaf litter.
No vegetation	Non-vegetated areas that do not fit the description of other land-use categories; typically construction sites, brownfield and substrate extraction. Also includes the surfaces of major through-roads (e.g. A1).

Figure 2.2 Examples of each of the land-use categories from contemporary satellite imagery: A) agriculture, B) allotment, C) Commercial, D) Grassland, E) Parkland, F) Recreation, G) Scrub, H) Urban no garden, I) Urban with garden, J) Suburban, K) Woodland, L) No vegetation. Imagery taken from Google Earth™.

2.2.3 Selection of sample-points for carbon storage data collection

Sample points for C storage data collection within urban land-uses were selected using a stratified random sampling design. The KML-encoded data generated by GE, describing the co-ordinates of polygons, was imported into Quantum GIS v2.4.0 (QGIS Development Team) software and the co-ordinates generated for random points within the polygons. The process was repeated for all sets of polygons pertaining to an urban land-use category within each study area, with the exception of *no vegetation*; which was assumed from the outset to possess zero C storage value. The number of samples within each land-use category reflected the area occupied by each within contemporary maps, and as such, the stratified random sampling design was only valid for the contemporary land cover. Quadrats of 50 x 50 m were centred upon the co-ordinates of the random points. This size was chosen as it provided sufficient area for a representative sample of surface cover, even in areas dominated by buildings or large trees (Butler, 1996), but was not so large as to repeatedly fall across more than one land-use category. If, on occasion, this did occur, the quadrat was classified according to the central co-ordinates, and its position adjusted manually until the entire quadrat was included within that land-use category. In total, 198 quadrats across the three study areas were selected in this way (Table 2.4). All quadrats were located in the field using a handheld global positioning system (GPS) device (Garmin e Trex 20, Olathe, US) and aided by maps printed from GE.

Agriculture sample points were selected manually by viewing the landscape on GE, and were limited to areas accessible by public rights of way. This prevented the selection of points with limited or prohibited access, which may have occurred using random-point generation. Quadrats were centred on the co-ordinates of the sample points as for the other land-use categories, and the number of samples taken provided a fair representation of the areas covered by different crop varieties within the north-east region of England, as reported in the provisional arable crop areas of England as at June 2013 (Department for the Environment

Food and Rural Affairs, 2013), as well as providing an arable/pasture mix. Hedgerows potentially constitute an important store of C within agricultural landscapes (Falloon *et al*., 2004). However, their small size relative to crop or pasture, and their linear rather than evenly-scattered distribution within the landscape, would have resulted in under-representation by randomly-selected points; whilst their value would have been over-estimated if they were included within every manually-selected point. Therefore crop/pasture and hedgerows were sampled separately in the field and later amalgamated to provide a single C storage value for *agriculture* (see section 2.2.4.5). Hedgerows were sampled as 50 m lengths, and were selected as those closest to the pre-selected crop/pasture quadrat. As points where chosen along rights of way, and therefore, along the boundaries of fields, hedgerows were usually, but not always, present.

Table 2.4 The number of 50 x 50 m quadrat samples (50 m linear samples for hedgerows) taken from each of the land-use categories across Darlington, Durham and Newcastle. Sample size (*n*) reflects the area occupied by the land-use categories in contemporary maps; *n* is low for pasture as this sub-category was rarely represented in the study areas.

Land-use category	Sample size (*n*)
Agriculture:	
Arable	15
Pasture	3
Hedgerow	14
Allotment	8
Amenity grassland	20
Commercial	25
Grassland	21
Parkland	19
Residential:	
Urban no garden	14
Urban with garden	20
Suburban	30
Scrub	20
Woodland	21
Total	230

2.2.4 Vegetation and soil survey, preparation and carbon analysis

2.2.4.1 Tree (4 m+) carbon pool

Above-ground vegetation C pools were categorised by minimum and maximum vegetation height. Prior studies typically define trees as woody vegetation >5 m tall (see Davies *et al*., 2013), but experience in the field during the present study revealed that trees in urban environments, particularly heavily-managed trees and ornamental trees in residential and commercial land-uses, are often shorter than free-growing native specimens in semi-natural environments. Therefore, a minimum height of 4 m was applied in this study. All trees present within each 50 x 50 m quadrat were identified to species- or genus-level, and the diameter at breast height (dbh) was measured at 1.3 m (following Bruce and Schumacher, 1950). Where close access to trees was not possible in the field (e.g. within residential or other privately-owned land-uses with no ability to request access), they could not always be identified to species- or genus-level, and instead, were identified as broadleaf or coniferous. Their dbh and height was estimated, based upon trained observations of accessible trees in the field. Such estimations were frequently applied to the residential land-use categories, and as such, may constitute a source of bias if they were regularly inaccurrate.

Tree dry-weight biomass was calculated using species-specific allometric equations from the literature (Appendix 1). These equations mathematically describe the relationship between the above-ground biomass of a tree and other variables that can be easily measured in the field, such as dbh and/or canopy height (Snorrason and Einarrson, 2006). For the majority of trees, dbh alone was sufficient to calculate biomass. However, equations for some species required that tree height was also recorded. If a species-specific equation was not found, an equation for the genus or family was substituted. For trees that were identified as broadleaf or coniferous, a broad equation for each, as derived by Davies *et al*. (2011; Appendix 1), was applied.

Tree biomass allometric equations are typically derived from individuals growing within natural stand conditions, and may not accurately represent open-grown, maintained trees within urban environments, which tend to have reduced above-ground biomass compared to woodland trees of the same dbh (Nowak, 1994; McHale *et al*., 2009). In light of this, the biomass of trees recorded within the human-dominated *agriculture*, *allotment*, *amenity grassland*, *commercial* and residential land-use categories were multiplied by a factor of 0.8 to correct for allometric overestimation (following Nowak and Crane, 2002; Hutyra *et* *al*., 2011; Strobach and Haase, 2012). The total above-ground biomass of each tree was then converted to C mass by applying a conversion factor of 0.46 for broadleaf species and 0.42 for coniferous species, which is the approximate fraction of wood mass that is C (following Milne and Brown, 1997). The total above-ground tree C storage was summed for each quadrat, and a mean value per unit area (Mg C ha^{-1}) across all quadrats within each land-use category was calculated.

Measurement of the below-ground biomass of trees was not possible within the field. Prior studies have estimated this by applying a conversion factor based upon root-to-shoot ratios (e.g. Jo and McPherson, 1996; Nowak and Crane, 2002; Mokany *et al*., 2006). However, there is considerable uncertainty in estimates provided by the application of such factors (Strobach and Haase, 2012), especially in urban areas, where roots may comprise anything between 16% and 41% of a tree's biomass (Johnson and Gerhold, 2003). Furthermore, there is uncertainty in estimating the volume of topsoil displaced by root systems, as an unknown proportion of the roots are likely to penetrate deeper than this layer. Considering these uncertainties, the approach taken by Hutyra *et al*. (2011) and Strobach and Haase (2012) was adopted, and below-ground tree biomass was omitted from the study, despite the potentially large C stores here.

2.2.4.2 Woody vegetation (1-4 m) carbon pool

Woody bushes, hedgerows, woodland understory and small trees with a height of 1-4 m were defined as woody vegetation. Difficulties in harvesting woody vegetation within the field meant that representative samples could not be collected. Therefore, the ground coverage of woody vegetation within each quadrat was measured by viewing the quadrats on GE, and using the polygon tool to outline the extent of woody vegetation before importing the KML-encoded data into KML Toolbox to calculate the area covered. This method was more objective and reliable than estimating by eye within the field, especially for residential land-use categories, where cover within private gardens was often obscured by housing. For *woodland* and *parkland* however, views of the woody understory were obscured on GE by the canopy, so the proportion of cover was estimated in the field.

Owing to the method used to collect woody vegetation data, the high diversity of species, and the often heavily maintained form of hedgerows, the use of species-specific allometric equations was not practicable. Therefore, a process similar to that used by Davies *et al*. (2011) was adopted. Specifically, a broad C value of 18 Mg C ha^{-1}, taken from a study by Patenaude *et al*. (2003), was applied. However, it should be noted that Patenaude *et al*. obtained this value by sampling woodland understory trees (>7 cm and <18 cm dbh) only, and therefore, may not so reliably represent C stores within woody bushes and hedgerows. The total woody vegetation C store was summed for each quadrat, and a mean value per unit area (Mg C ha^{-1}) across all quadrats within each land-use category was calculated.

2.2.4.3 Herbaceous vegetation carbon pool

Herbaceous vegetation, defined as grasses, non-woody plants and litterfall, was sampled during the months of June and July, when biomass was at a peak. All 50 x 50 m quadrats were visited, from which a 30 x 30 cm sample of herbaceous vegetation was selected whilst in the field. This sample was assumed to be representative of the herbaceous vegetation within the quadrat. If all the herbaceous vegetation within a quadrat was located within private gardens, an equivalent vegetation-type (e.g. mown grassland or perennial flower-bed) was sampled from an adjacent area. The standing crop within a 30 x 30 cm frame quadrat was cut at ground level, and the entire sample, including litterfall, was harvested and returned to the laboratory for further analysis.

Each sample underwent a 24-hour drying process at 80°C, before its dry-weight was recorded. A sub-sample of each was then taken and weighed. The sub-sample was placed in a muffle furnace at 550°C for four hours (following Christensen and Malmros, 1982), before being re-weighed and loss on ignition (LOI) calculated. The LOI value was applied to obtain the C mass within each 30 x 30 cm sample as follows:

$$x = \frac{(\frac{a}{2.05})}{(\frac{b}{c})} \qquad \text{(Equation 1)}$$

Where *x* is the C mass per 30 x 30 cm sample of herbaceous vegetation (g), *a* is the LOI value (g), 2.05 is a constant that converts LOI to C-content in herbaceous vegetation (including litterfall; following Christensen and Malmros, 1982), *b* is the dry-weight of the vegetation sub-sample (g), and *c* is the dry-weight of the 30 x 30 cm sample from which the sub-sample was taken (g).

To estimate the C mass within the herbaceous vegetation of each 50 x 50 m quadrat, the value obtained for the 30 x 30 cm sample was scaled-up before being multiplied by the proportion of the quadrat with herbaceous vegetation cover. This proportion was measured by viewing each quadrat on GE and using the polygon tool to outline the area of herbaceous cover. The KML-encoded data was imported into KML Toolbox, where the area of herbaceous cover was calculated. As explained by the methodology for estimating woody vegetation cover (see section 2.2.4.2), views of the herbaceous layer in *woodland* and *parkland* were obscured on GE by canopy-cover, so the proportion of herbaceous cover in these land-uses was estimated in the field. The mean herbaceous vegetation C mass per unit area (Mg C ha^{-1}) across all 50 x 50 m quadrats within each land-use category was then calculated.

2.2.4.4 Soil carbon pool

Much of the soil sampling and measurement of SOC within this study was carried out by a second researcher prior to this study's commencement. As such, to allow for comparison, the same methodology used prior was initially followed when collecting and analysing further samples. This involved estimating the depth of the organic layer within the sample soil cores, and using this depth in subsequent SOC density calculations, as it was considered that the organic layer included the major C-component of the soil. However, there is a level of practice required, and some ambiguity involved, in estimating the organic layer depth of soils. Therefore, it was decided to use a capped soil depth to ensure that SOC density measured within all soil core samples were directly comparable.

In their study of SOC within Leicester, UK, Edmondson *et al*. (2012) found that land-use effects on SOC concentrations are most important in the topsoil, which they defined as 0-21 cm depth. Beyond this depth, down to 1 m, they found that C concentrations decreased significantly, and those beneath different land-uses, including beneath impervious surfaces, converged. The view that the majority of land-use effects on SOC occurs within the topsoil is widespread. For example, Emmett *et al*. (2010) sampled soils within multiple land-uses to 15 cm depth, Smith *et al*. (1997, 1998, 2000) sampled agricultural soils to 30 cm depth, and Edmondson *et al*. (2014b) sampled urban soils to 21 cm depth, following the data obtained by Edmondson *et al*. (2012). Therefore, this present study concentrated on the topsoil of the study areas, defined as 0-22 cm depth. Capping at this depth is suggested if SOC densities were significantly reduced at depths below 22 cm. To show this, soil cores were extracted to a depth of 27.5 cm from within a sub-sample of quadrats, which were manually selected by viewing land-use maps of the study areas previously created (see section 2.2.2). It was considered that the quadrats chosen for this purpose were evenly distributed and represented a fair sub-sample of each land-use category. Cores were divided into the following depth intervals determined by the specifications of the coring equipment: 0-5.5 cm, 5-11 cm, 11-16.5 cm, 16.5-22 cm and 22-27.5 cm; the volume of each division measured 5.5 cm^3. All samples were returned to the laboratory to begin analysis on the day of collection.

Soil samples were dried in a drying oven at 80°C for 24 hours and their dry-weight recorded. Samples were then placed in a muffle furnace at 550°C for 4 hours (following Christensen and Malmros, 1982) before being re-weighed, and LOI calculated. The LOI value was then applied to obtain the SOC density per cm^3 of each sample as follows:

$$y = \frac{(\frac{a}{2.25})}{d} \qquad \text{(Equation 2)}$$

Where y is the SOC density per cm^3 of soil (g C cm^{-3}), a is the LOI value (g), 2.25 is a constant that converts LOI to C-content in soils to 20 cm depth (following Christensen and Malmros, 1982), and d is the volume of soil within the sample (cm^3).

To test whether SOC density decreases at depths below the topsoil (0-22 cm) of the study areas, SOC density values obtained by the above process were subjected to a two-way ANOVA, testing for difference in SOC density *i*) among land-use categories, and *ii*) among soil depth intervals. Results showed that *i*) SOC density did not differ among land-use categories (F_{10}=0.748, P=0.679), and *ii*) SOC density of the soil samples differed significantly between depth intervals (F_4=9.010, P<0.001). Tukey HSD tests showed that SOC density of soil samples taken from 22-27.5 cm depth intervals was significantly lower than that of samples taken from each of the shallower depth intervals (Table 2.5). All analyses were conducted using R v2.15.3 (R Development Core Team, 2008) software, and results suggested the use of 22 cm as a suitable capping depth for further SOC analyses of all land-use categories.

Table 2.5 Results of Tukey HSD *post-hoc* tests on ANOVA testing for difference in soil organic carbon (SOC) densities of soil cores taken from varying depth intervals in different urban and agricultural land use categories. Bold p-values denote significant differences.

Soil depth interval (cm)		Difference	P
0-5.5	5.5-11	0.0015	0.993
11-16.5	5.5-11	-0.0025	0.952
16.5-22	5.5-11	-0.0051	0.598
22-27.5	5.5-11	-0.0226	**<0.001**
0-5.5	11-16.5	0.0039	0.783
16.5-22	11-16.5	-0.0027	0.945
22-27.5	11-16.5	-0.0266	**<0.001**
0-5.5	16.5-22	0.0066	0.344
22-27.5	16.5-22	-0.1746	**0.001**
0-5.5	22-27.5	0.0241	**<0.001**

Following the above analysis on a sub-sample of quadrats across the land-use categories, the topsoil depth of the remaining 50 x 50 m quadrats was measured. Six soil cores were extracted from within each quadrat to a maximum depth of 27.5 cm, as determined by the specifications of the coring equipment, or to the depth at which rock or other impenetrable surface was reached. The locations of the soil cores were chosen to capture the potential range of soil depths, which may have fluctuated with microhabitat, within each quadrat. The mean depth of the six soil cores was calculated. An additional soil core was then taken from a representative area of each quadrat, and the top 0-5.5 cm division was extracted and returned to the laboratory to undergo the process of measuring SOC density cm^{-3} as detailed above. As prior analysis showed that SOC density cm^{-3} did not differ with depth to 22 cm, the SOC density cm^{-3} values of these 0-5.5 cm samples were multiplied by the mean soil depth of the quadrat from which they were taken, or to the capped depth of 22 cm if the mean exceeded this. This value was then multiplied by the area of the quadrat surface with topsoil cover. For this, it was assumed that topsoil occurred to the same depth as the core mean values for all areas of bare soil, and all areas of vegetation cover. It was assumed that there was no topsoil beneath buildings or impervious surfaces, as this would have been removed by excavation during the construction process, to a depth of at least 15 cm under pavements and 40 cm under roads (Edmondson *et al*., 2012). The mean SOC mass stored per unit area (Mg C ha^{-1}) to the capped depth of 22 cm across all 50 x 50 m quadrats for each land-use category was then calculated.

2.2.4.5 Agriculture land-use category

As mentioned within section 2.2.3, the agricultural components of crop/pasture and hedgerow were sampled separately within the field to provide a mean C storage value per unit area for each component. Consequently, the *agriculture* land-use category was processed differently to other land-uses. Initially, from the historical imagery on GE, all hedgerows within the boundary of each study area were outlined using the polygon tool, and their area measured by importing the KML-encoded data into KML Toolbox. The total area occupied by hedgerows was then calculated as a proportion of the historical area of the *agriculture* land-use category (defined as per Table 2.3). To obtain a single C storage value for each of the four C pools (trees, woody vegetation, herbaceous vegetation and soils) per unit area (Mg C ha^{-1}), the mean crop/pasture and hedgerow C storage values across the samples were amalgamated, consisting of data proportional to the area of each component within the boundary of the study site in historical maps. The amalgamated C storage values were applied to further analyses of changes to C storage due to urbanisation and land-use change.

2.2.5 Analysis of carbon storage among land-use categories

The C storage values obtained for each of the four C pools within each 50 x 50 m quadrat were summed to provide a total vegetation C and SOC storage value for each quadrat.

The quadrat C data did not meet the assumptions of parametric tests, and could not be transformed to do so. Therefore, Kruskal-Wallis non-parametric ANOVA was used on untransformed data to test for differences between the land-use categories in the C storage per unit area (Mg C ha^{-1}) of *i*) total vegetation and soils, *ii*) trees (4 m+), *iii*) woody vegetation (1-4 m), *iv*) herbaceous vegetation, and *v*) soils. For the purpose of these analyses, the two components of crop/pasture and hedgerow within *agriculture* were treated separately. All analyses were conducted using R v2.15.3 software.

The total C storage for each land-use category was calculated by multiplying the area occupied by each land-use category with the corresponding combined C storage value per unit area (Mg C ha^{-1}) for each C pool (trees + woody vegetation + herbaceous vegetation + soils). Total C storage values for land-use categories were then summed to provide a C storage value for the entire study area. This was repeated for contemporary and 1945 land-use maps.

2.3 RESULTS

2.3.1 Change in land use between 1945 and the present

The contiguous urban extent of Darlington, Durham and Newcastle (*i.e.* their boundaries as defined in section 2.2.1 of the methodology) increased by 987 ha (+67%), 1,049 ha (+229%) and 1,581 ha (+65%) respectively, between 1945 and the present. The majority of the increase in each study area was in low-density *suburban* residential land-use (Figure 2.1a). However, there were also notable increases in *commercial* land-use in all three study areas. In Newcastle, the increase in moderate-density *urban with garden* residential land-use was comparable with increases in *suburban* land-use, but was far lower in Darlington and Durham. Other land-use categories that increased in areal extent within all three study areas were *amenity grassland*, *scrub* and, to a lesser extent, *woodland*. The area of *no vegetation* increased most notably in Newcastle (Figure 2.1).

The increase in the urban extent of the three study areas came entirely at the expense of *agriculture*, which surrounded the urban boundaries of the study areas in 1945 (Figure 2.2). Within the expanding urban matrices of all three study areas, the area occupied by *allotment* decreased, as did the high-density *urban no garden* residential land-use in Darlington and, in particular, in Newcastle (Figure 2.1).

Percentage change in area of land-use categories between 1945 and the present may highlight trends not apparent from areal change; for example, although increases in *woodland* were small in areal extent (Figure 2.1a), *woodland* cover actually increased by 111%, 90% and 78% in Darlington, Durham, and Newcastle respectively (Figure 2.1b). In Durham, the percentage increases of many land-use categories were particularly high compared to those in Darlington and Newcastle. This was to be expected, owing to the far higher percentage increase in the contiguous urban extent of Durham. However, the percentage increase in *scrub* was far more pronounced in Darlington and Newcastle (Figure 2.1b), highlighting a particularly high rate of increase of this land-use category in these study areas. Figure 2.2 provides a spatial visualisation of the increases to contiguous urban extent, and changes to land use in the three study areas.

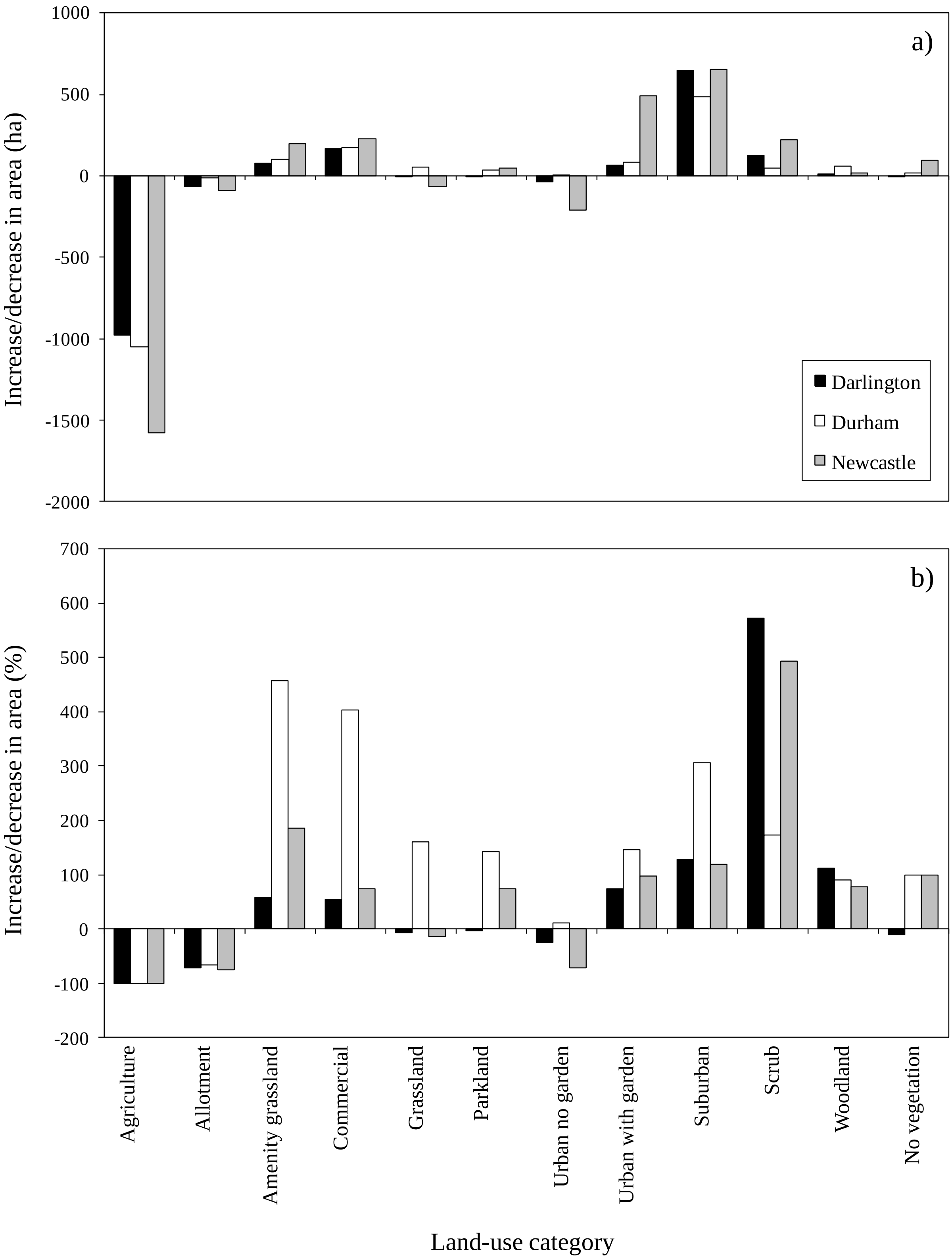

Figure 2.1 The a) change in area, and b) percentage change in area of land-use categories within Darlington and Durham between the years 1945 and 2009, and within Newcastle between the years 1945 and 2012. The total areal extent of each study area in both years is defined by its contemporary contiguous urban extent.

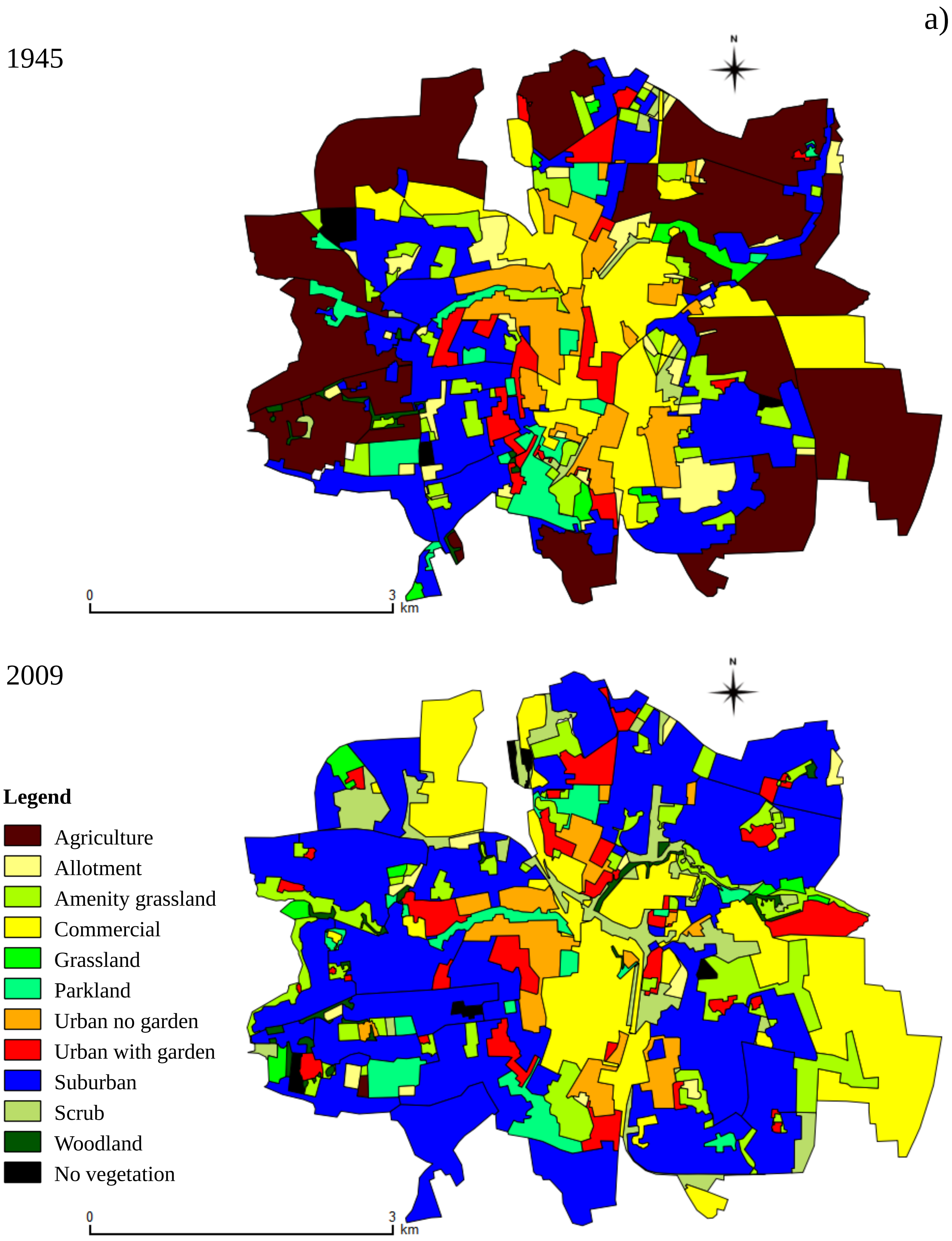

Figure 2.2 Continued overleaf

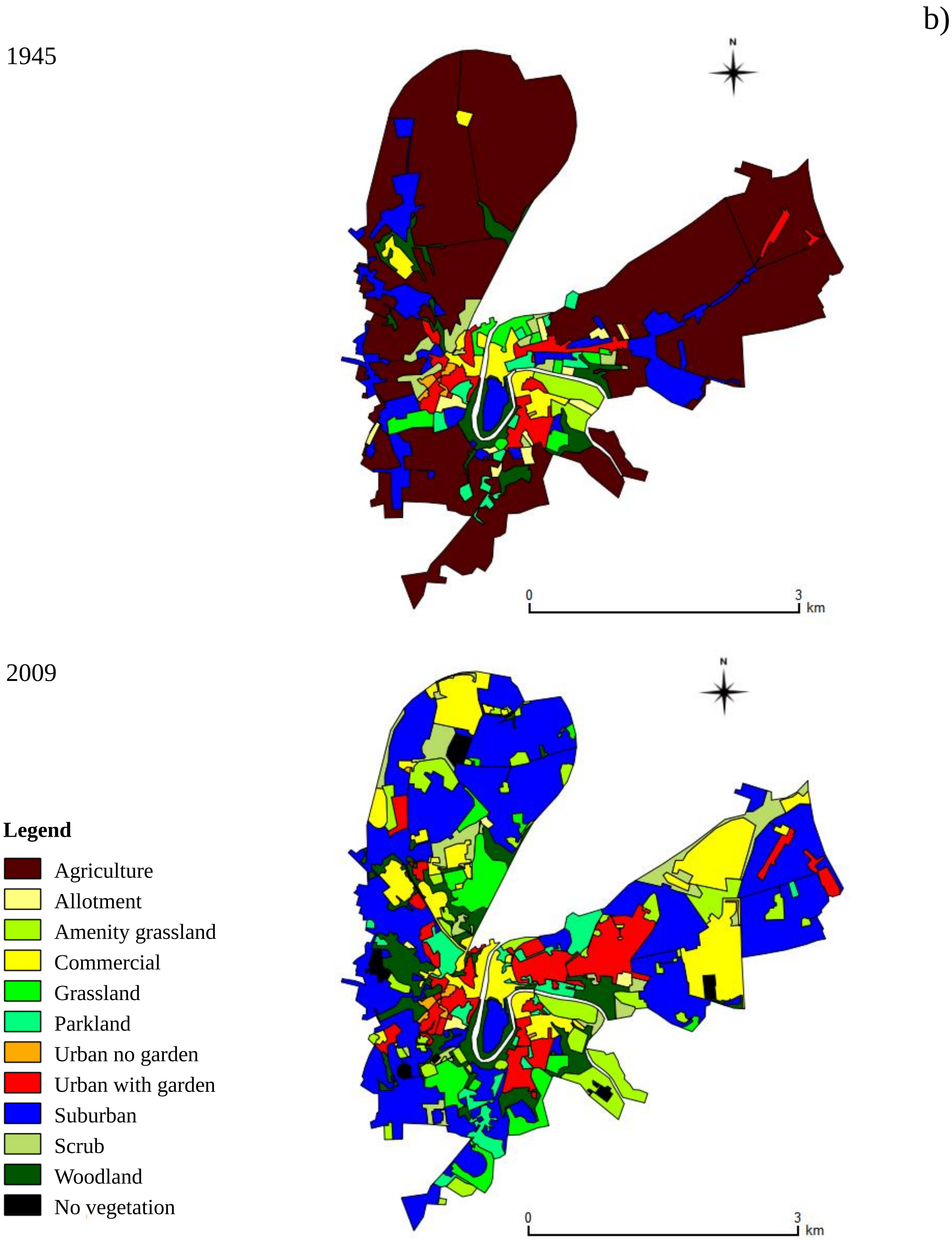

Figure 2.2 Continued overleaf

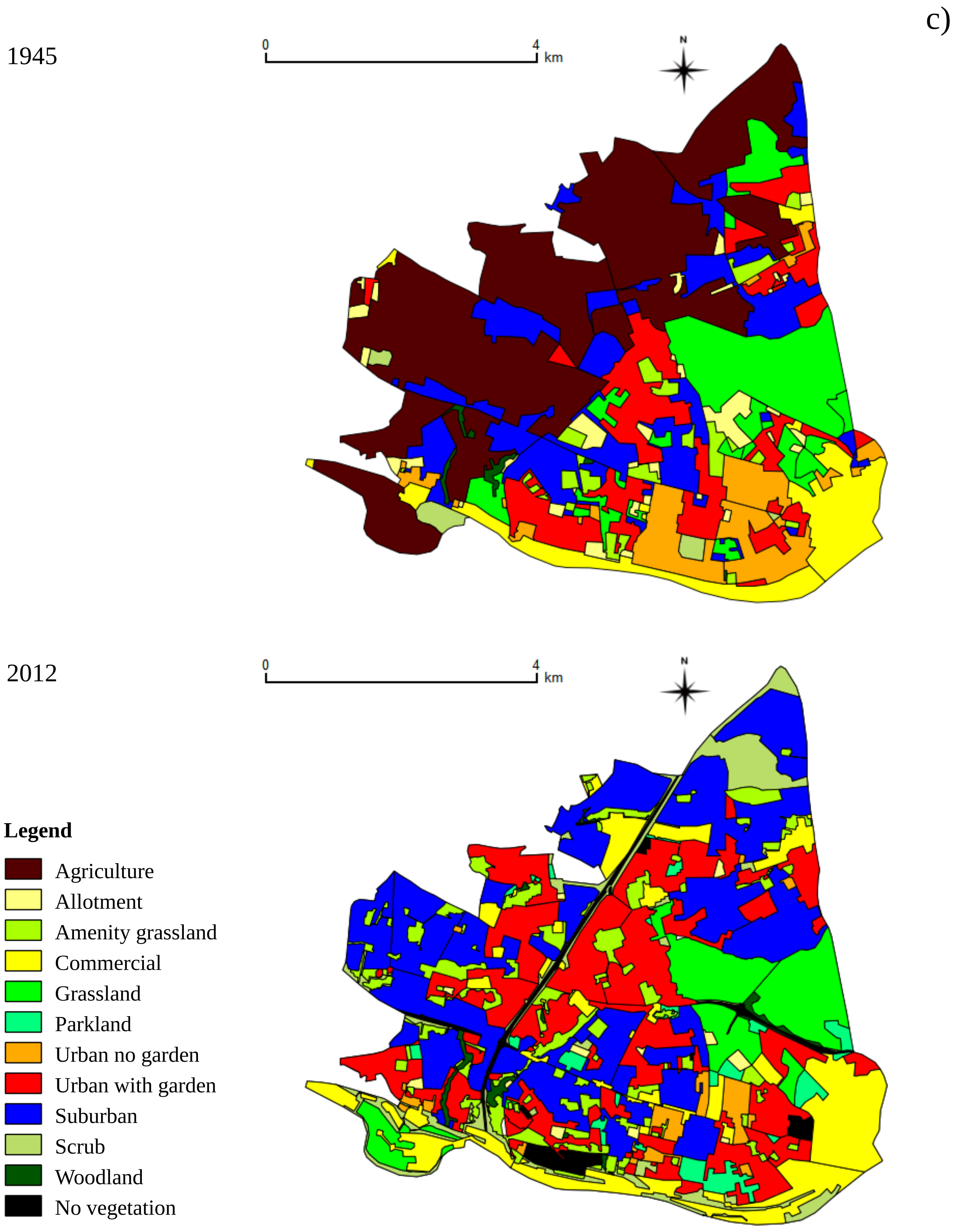

Figure 2.2 Land-use maps of a) Darlington and b) Durham, in 1945 and 2009, and c) Newcastle in 1945 and 2012, showing the change in land-use categories and expansion in urban extent between the two years.

2.3.2 Carbon storage per unit area of land-use categories

Carbon (C) storage per unit area within the vegetation and soils was significantly different among the contemporary land-use categories. This was the case for total vegetation C and soil organic carbon (SOC; $\chi^2_{11,220}$=195.56, p<0.001), and for the component C pools of trees (4 m+; $\chi^2_{11,220}$=168.28, p<0.001), woody vegetation (1-4 m; $\chi^2_{11,220}$=130.68, p<0.001), herbaceous vegetation ($\chi^2_{11,220}$=190.89, p<0.001) and soils ($\chi^2_{11,220}$=173.28, p<0.001; see Appendix 2 for *post-hoc* test results). *Woodland* contained the greatest mean total C store per unit area (296 Mg C ha^{-1}) and *urban no garden* contained the lowest (1.54 Mg C ha^{-1}). Indeed, three of the four lowest values for C storage were residential sub-categories; the fourth was *commercial* (Figure 2.3). When C pools were analysed separately (Figure 2.4), it was apparent that total vegetation C and SOC stores were heavily influenced by the tree and soil pools respectively, and as a result, the values of C per unit area for these pools closely matched that of the total stores (compare Figures 2.3 and 2.4). Tree C pools were largely determined by the number and size of trees within a land-use category, although species composition also played a role. *Woodland* had the greatest number of trees recorded per sample, as well as having greater proportions of trees within larger size classes than most other land-use categories; only *parkland* had a more even spread of trees across different size classes (Table 2.6).

When hedgerow and crop/pasture were combined according to their relative area within *agriculture*, a total vegetation C and SOC storage value of 134 Mg C ha^{-1} was attained. Only *woodland*, *parkland* (197 Mg C ha^{-1}) and *allotment* (158 Mg C ha^{-1}) had greater total C values per unit area.

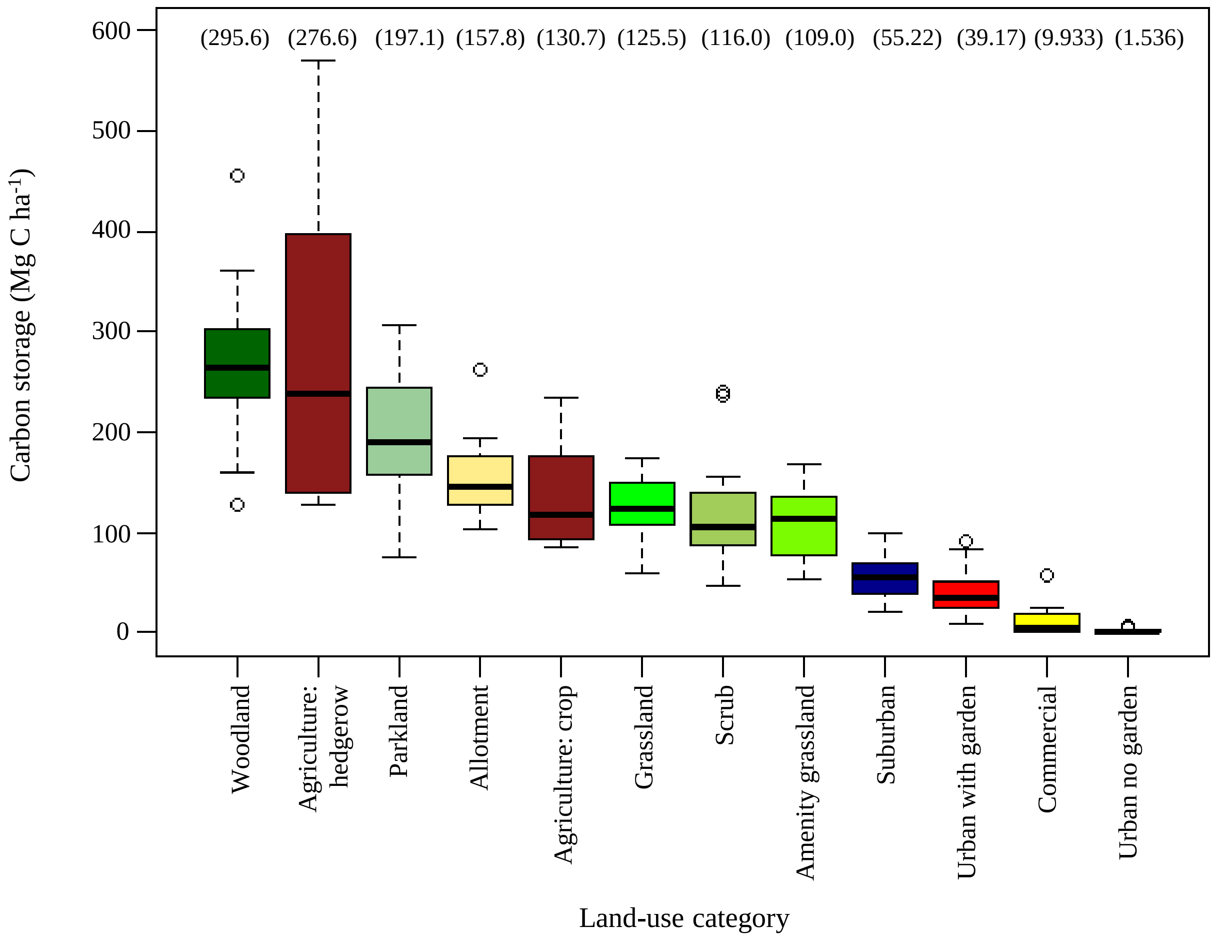

Figure 2.3 The median total vegetation carbon (C) and soil organic carbon (SOC) storage per unit area of land-use categories in Darlington, Durham and Newcastle, calculated from 50 x 50 m quadrat samples. Boxes show where the middle 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 2.2, and presented in order of decreasing mean C storage value per unit area (means shown in parentheses).

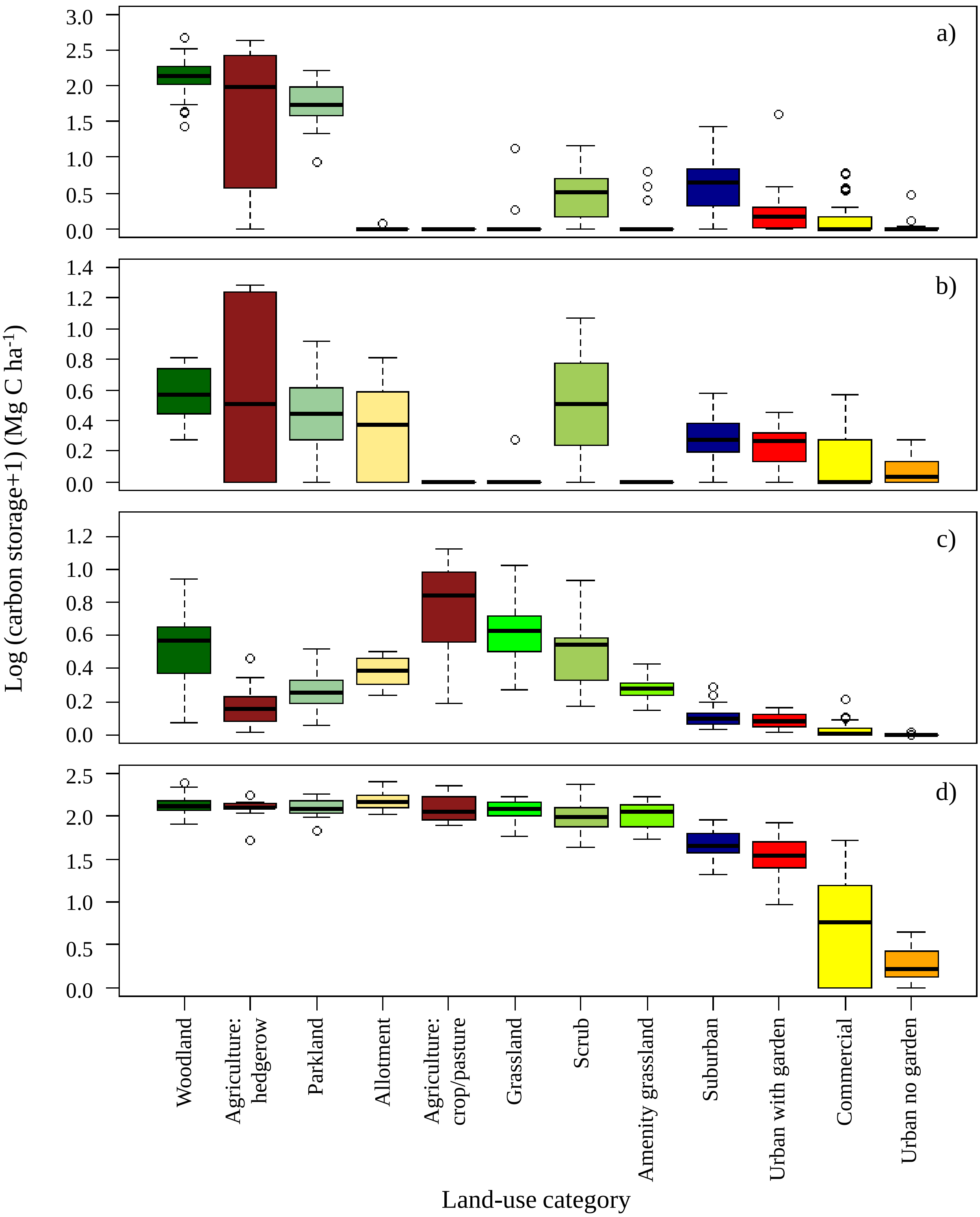

Figure 2.4 The median log carbon storage within a) trees (4 m+), b) woody vegetation (1-4 m), c) herbaceous vegetation, and d) soils per unit area of land-use categories in Darlington, Durham and Newcastle, calculated from 50 x 50 m quadrat samples and presented in order of the decreasing mean total vegetation and soil carbon storage value (see Figure 2.3). Boxes show where the middle 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 2.2. Log transformation of data applied to aid visualisation only. Note different scales on y-axes.

Table 2.6 The median number of trees (4 m+) and the inter-quartile range (Q1-Q3), recorded within 50 x 50 m quadrat samples of land-use categories within Darlington, Durham and Newcastle, and the proportion of the total number of trees within size classes according to their diameter at breast height (dbh). Land-use categories are presented in order of decreasing median number of trees per sample. Proportions are colour-coded in shades of green through yellow to red, with true green denoting highest proportions, yellow denoting moderate proportions, and true red denoting lowest proportions.

Land-use category	Median no. trees per sample (IQR)	Proportion of total number of trees within size class (dbh)					
		Up to 25 cm	>25 to 50 cm	>50 to 75 cm	>75 to 100 cm	>100 to 125 cm	>125 cm
Woodland	49 (35-89)	0.59	0.24	0.12	0.03	0.01	0.01
Parkland	18 (13-24.5)	0.39	0.33	0.18	0.08	0.02	0.01
Agriculture: hedgerow	18 (2.3-34.3)	0.90	0.06	0.01	0.02	0.01	0.00
Scrub	14 (3.5-33.3)	0.96	0.04	0.00	0.00	0.00	0.00
Suburban	9 (5.5-12.5)	0.74	0.23	0.03	0.00	0.00	0.00
Urban with garden	3 (1-6.3)	0.76	0.20	0.02	0.01	0.01	0.00
Commercial	0 (0-5.5)	0.91	0.09	0.00	0.00	0.00	0.00
Urban no garden	0 (0-1)	0.92	0.08	0.00	0.00	0.00	0.00
Amenity grassland	0 (0-0)	0.53	0.41	0.06	0.00	0.00	0.00
Grassland	0 (0-0)	0.93	0.00	0.00	0.07	0.00	0.00
Allotment	0 (0-0)	1.00	0.00	0.00	0.00	0.00	0.00
Agriculture: crop/pasture	0 (0-0)	n/a	n/a	n/a	n/a	n/a	n/a

2.3.3 Change in carbon storage between 1945 and the present

The total vegetation C and SOC storage of Darlington, Durham and Newcastle decreased by an estimated 75,615 Mg (-34%), 63,326 Mg (-33%) and 115,123 Mg (-31%) respectively, between 1945 and the present. These decreases were largely due to the loss of *agriculture* and its replacement by land-uses with lower mean C storage values per unit area; most notably, *suburban*, *commercial* and *urban with garden*. Loss of the moderately high C value *allotment* led to further C losses within the urban matrices. Losses were offset slightly by increases, however small, in high C storage value *woodland*, and in Durham and Newcastle, *parkland*. Increases in area of moderate C value *scrub* and *amenity grassland* also helped to offset some of the C losses caused by increases in low value residential and *commercial* land-uses. Loss of the lowest C value *urban no garden* category in Darlington and Newcastle (Figure 2.1) benefitted C storage, as its replacement with any other land-use category would have increased the C value of that parcel of land. Of the four C pools, the largest C loss was made from the soil pool in all study areas, which decreased by an estimated 73,585 Mg (-63%) 69,640 Mg (-58%) and 113,515 Mg (-67%) within Darlington, Durham and Newcastle, respectively. There were also large percentage losses in the herbaceous vegetation C pools of the three study sites, largely owing to the loss of crop from *agriculture*. However, gains were made in the C stores of trees and woody vegetation, as increases in the area of *woodland*, *parkland*, *suburban* and *scrub* land-uses more than compensated for loss of hedgerows and hedgerow trees from *agriculture*. A detailed analysis of the estimated changes to C storage within all land-use categories and C pools between 1945 and the present is provided in Appendix 3.

2.4 DISCUSSION

A requirement of the Kyoto Protocol is that Annex I countries must consider carbon (C) emissions and sequestration pertaining to land use, land-use change and forestry (LULUCF) activities in meeting their commitments to the agreement. This includes land-use change through the process of urbanisation. Although detailed inventories of C storage within contemporary urban areas exist, there remains scant information on the effect of urbanisation on the C storage of the area of newly occupied land. Mapping C storage at a reference point in the past can provide an understanding of how it has changed over time and can indicate where action might be targeted. In this study, I measured the change in land use and contiguous urban extent of three towns and cities in north-east England over a period of major urban expansion between 1945 and the present, and analysed the subsequent effect on the vegetation C and soil organic carbon (SOC) storage of the study areas. The major finding was that the contiguous urban extent of Darlington, Durham and Newcastle increased by 67%, 229%, and 65% respectively, which decreased the C storage value of the areas occupied by 34%, 33% and 31% respectively. Here I discuss the results in relation to three broad themes: 1) the change in land use between 1945 and the present, 2) C storage per unit area of land-use categories, and 3) the change in C storage between 1945 and the present.

2.4.1 Change in land use between 1945 and the present

The three study areas increased in contiguous urban extent between 1945 and the present, reflecting post-war national trends, whereby inner-city housing was cleared and rebuilt at lower densities, whilst the creation of council estates at the periphery of towns and cities accommodated the cleared dwellers (Couch and Karecha, 2006). This coincided with a surge in the development of privately-owned dwellings, and the creation of the sprawling housing estates of suburbia (Best, 1981), ultimately resulting in outward urban growth and increasing urban populations residing within lower-density housing (Antrop, 2000; Couch and Karecha, 2006).

Other land-use categories that increased notably within all three study areas were *commercial*, *amenity grassland* and *scrub*. The area of central commercial districts remained reasonably unchanged; rather, new agglomerations of commerce and industry towards the urban fringes were responsible for increases. This has been a characteristic of towns and cities in the UK and Europe in recent decades, and has arisen as a consequence of retailer demand for greater floorspace and improved transport links (Monheim, 1992). Like the increase in *suburban* land-use, much of the *commercial* gain replaced *agriculture*. The area occupied by *amenity grassland*, relative to its historical extent, increased markedly. This is surprising, as amenity grasslands for recreation and sports are reported to have decreased considerably in recent decades, as enforcement of UK urban densification policy has resulted in the loss of this land-use type in particular, to residential development within the urban matrix (Bibby, 2009). The exceptionally large percentage increase in Durham however, was sustained by increased provision of sports facilities for university students, and as such, should not be considered typical in this respect for UK towns and cities. Increases in *scrub* were largely confined to the urban fringes (Figure 2.2). This could be the result of succession within redundant arable fields claimed by urban expansion. Succession may also account for some losses of *grassland*, especially in Newcastle, where historical tracts have become *scrub* or *woodland* within the contemporary urban matrix (Figure 2.2c). Alternative areas where *scrub* had increased, within Darlington and Newcastle in particular, are the embankments of railways and major roads. For example, alongside the A1, which dissects the entire contemporary Newcastle study area, but which was absent in 1945.

In terms of areal extent, the increases in *woodland* within Darlington and Newcastle were minor (Figure 2.1a). However, the area of *woodland* in these study areas was small in 1945, so small increases in extent have still produced reasonably high percentage increases (Figure 2.1b). Percentage increases may reflect a shift in societal and political demand for increased urban woodland and greenspace (Moffat, 2001; Koninendijk, 2003). Indeed, forestry and woodland have more than doubled in area in the UK from 1.4 million ha in 1947 to 3.1 million ha in 2014 (Forestry Commission, 2014), although the majority of this has been established within agricultural holdings rather than in urban areas (Bibby, 2009). The area of *woodland* in Durham doubled from what was already a relatively high cover in 1945. Durham's topography, World Heritage Site designation and level of university ownership have undoubtedly aided the protection of existing wooded areas in the centre and to the east of the city. However, much of the increase in *woodland* occurred in the west of the study area (Figure 2.2b).

Aside from losses in *agriculture*, the other land-use loss common to all three study areas was in *allotment*. This is logical, as following peak allotment provision during the Second World War (Martin and Marsden, 1999), the requirement for self-sustainability fell throughout the ensuing decades. A recent resurgence in allotment demand in the UK (Edmondson *et al*., 2014a), may have prevented further loss in the extent of this land-use category.

2.4.2 Carbon storage per unit area of land-use categories

The total vegetation C and SOC storage per unit area (Mg C ha^{-1}) differed significantly between land-use categories, as did the constituent C pools of trees (4 m+), woody vegetation (1-4 m), herbaceous vegetation, and soils. Soils contributed the greatest proportion towards the total C storage per unit area in all land-use categories with the exception of *woodland*, where trees contributed a little over half (52%). As there were no differences in SOC density (g C cm^{-3} soil) between any of the land-use categories (Table 2.5), differences in SOC per unit area (Mg C ha^{-1}; Figure 2.4d) reflected the proportion of impervious surface among land-use categories, whereby artificial surfaces and buildings have replaced the topsoil excavated during the construction process (Edmondson *et al*., 2012). It also reflected soil depth, as some samples did not reach the capped sampling depth of 22 cm. The woody vegetation and herbaceous vegetation C pools contributed somewhat less (*cf*. Davies *et al*., 2011); this is not to say that these are unimportant, as their contribution may determine whether a land-use acts as a C source or sink. These smaller pools were also of relative importance in *agriculture*, and the semi-natural land-use categories of *grassland* and *scrub*, where lack of impervious surfaces and low-level management increase the surface cover and biomass of vegetation.

Woodland C values were high, relative to other land-use categories, within all four C pools (Figure 2.4), reflecting the three-dimensional vegetation structure and relatively deep topsoil; which often, but not always, reached the capped sampling depth of 22 cm. There were also relatively high C stores in all pools within *parkland* (Figure 2.4), although herbaceous vegetation within many of the sample quadrats (most notably within cemeteries) was managed. *Parkland* trees were sparsely distributed compared to those of *woodland*, but *parkland* contained over a quarter (26%) of all trees sampled with a diameter at breast height (dbh) of 100 cm or more, and contained a greater proportion of trees in larger size classes than any other land-use category (Table 2.6). Hedgerows within *agriculture* also had high total vegetation C and SOC storage value per unit area. However, there was much variation in the C stores of hedgerows (Figure 2.4), because their form and structure ranged from contiguous runs of trees (with relatively high C value), to hedges that completely lacked trees, and were highly managed rectilinear strips of homogenous woody vegetation. Just two or three large trees within a 50 m length of hedgerow were sufficient to increase considerably its overall C storage value. These results differ from those of Strobach and Haase (2012), who report an above-ground C store of zero for agricultural land in their study of Leipzig, Germany. It is assumed therefore, that hedgerow trees were either not present within their sampling area, or were omitted by their sampling design. The methodology used in this present study, which produced a detailed quantification of the area of land covered by hedgerows within the historical landscape (see Methodology section 2.2.4.5), ensured that hedgerow loss due to land-use change was captured within C loss estimates for the three study areas. The C mitigation potential of hedgerows and other boundary features of arable fields have been recognised previously (e.g. Falloon *et al*., 2004).

Agricultural land, especially arable crop fields, has previously been found to be depleted in SOC when compared to other land-use types, including urban land-uses. This applies to both C storage density per unit area (Edmondson *et al*., 2012; Edmondson *et al*., 2014b) and C concentration (g C g^{-1} soil; Lal, 2010; Edmondson *et al*., 2014b). Several factors contribute to this depletion, including removal of potential inputs of C with harvested products, and tillage practices, which expose otherwise protected C to weathering and microbial breakdown, as well as modifying the temperature regime of the soil (Post and Kwon, 2000; Smith, 2007). However, this study did not detect depletion in SOC density per unit area of agricultural soils compared to other land-use categories (Table 2.5). As such, the SOC storage of 124 (interquartile range, 89-163) Mg C ha^{-1} (0-22 cm) recorded by this study (Figure 2.4d) is greater than figures reported by prior studies; for example, 84 Mg C ha^{-1} (UK, 0-30 cm; Smith *et al*., 2000), 73 Mg C ha^{-1} (Leicester, 0-21 cm; Edmondson *et al*., 2014b), 70 Mg C ha^{-1} (England, 0-30 cm; Bradley *et al*., 2005), and 47 Mg C ha^{-1} (Great Britain, 0-15 cm; Emmett *et al*., 2010).

Commercial and *urban no garden* land-uses had relatively low C storage values per unit area across all four C pools (Figure 2.4), reflecting the high proportion of impervious surface cover, a scarcity of large trees, and, where it existed, shallow topsoil. Of the residential land-use categories, *suburban* had the greatest total C storage value per unit area. This arose largely due to C stored within a greater number of trees than *urban with garden*, and was not due to a greater size-class of trees (Table 2.6). It is recognised that the approach taken by this study, to define land-use categories, in part, based upon vegetation and tree cover, especially in residential categories, introduces some circularity into the claims made by the study, as greater vegetation and tree cover should inherently lead to greater C storage within these C pools. In addition, any comparison concerning residential land-use categories should be viewed with some caution, as many of the tree dimensions reported were estimated from distance, due to prohibited access to domestic gardens (see Methodology, section 2.2.4). Nevertheless, results contrast with a national survey of England's urban trees (Britt and Johnston, 2008), which stated that low-density residential areas have a greater proportion of larger trees than moderate-density areas. However, the national report also served to highlight variability, not only between urban areas in England, but also between regions of England.

Differences in methodology and urban land-use categorisation often make direct comparison with prior studies unfeasible. This is especially so of herbaceous vegetation C and SOC in the highly-modified residential and *commercial* land-use categories, as the values per unit area reported in this study are a function of the proportion of impervious surface within the category. Where comparison can be attempted, conformity with prior studies is mixed. For example, the tree C pool per unit area of residential and *commercial* land-uses is considerably less than values reported for equivalent land-use categories in Seattle, US (Hutyra *et al*., 2011), and Leipzig, Germany (Strobach and Haase, 2012). The opposite is true for *woodland* and *parkland* trees: the present study recorded approximately 50% and 100% greater C storage per unit area than the equivalent land-uses in Seattle and Leipzig respectively. However, the figure of 121 Mg SOC ha^{-1} (0-22 cm) recorded within *grassland* accords with 120 Mg SOC ha^{-1} (0-30 cm) obtained by Bradley *et al*. (2005). Variability between studies emphasises the differing interactions that respective study areas have with biotic and abiotic factors, including prevailing climate, geology, history of urbanisation, human population, land management (Davies *et al*., 2013) and vegetation-type (Jobbagy and Jackson, 2000). This suggests further studies are necessary to better understand variation in urban C storage, and that adaptation of a uniform methodology to facilitate comparisons would be beneficial (Davies *et al*., 2013).

2.4.3 Change in carbon storage between 1945 and the present

Changes in the extent of land-use categories due to urbanisation within the three study areas between 1945 and the present resulted in decreases in total vegetation C and SOC of around one-third within all three study areas (see Appendix 3 for a detailed analysis among land-uses and C pools). Overall decreases were very similar among the three study areas despite the very different growth rate of Durham, which is due to the different combination of land-use changes that took place here. With the exception of *allotment*, all urban land-use categories with moderate to high C storage value increased in area within Durham, most notably, *woodland* and *parkland*. Whereas Darlington and Newcastle experienced greater increases in low C storage value residential land-uses. Decreases in all three study areas were largely due to the loss of *agriculture* and its replacement with urban land-use categories of lower mean C storage value per unit area. Largest C losses were from the SOC pools of the study areas, caused by increases in impervious surface cover and reductions in soil depth when *suburban*, *urban with garden* and *commercial* land-uses replaced *agriculture*.

Agricultural hedgerows, specifically those with large trees, held significant and important stores of C (Figures 2.3 and 2.4), and their above-ground biomass presents significant opportunity for mitigation against C loss in arable fields and pasture (Falloon *et al*., 2004), and should be preserved within the landscape. However, their sparse distribution meant that their C value was diluted when considered, as they were, as a component of the wider, and largely treeless, agricultural landscape. Their loss therefore, was compensated for by relatively small gains in *woodland* and/or *parkland* within the expanding urban matrices. In Darlington, although *woodland* increased only slightly and *parkland* decreased, there was still an overall increase in the tree and woody vegetation C pools, emphasising the potential for urban woodland to mitigate C emissions through land-use change by urbanisation. Indeed, the tree and woody vegetation C pools increased overall across all three study areas. Increases in *scrub* also contributed to the increase in the woody vegetation C pool. Although scrub that has formed alongside road and railway embankments may be relatively safe from further development, patches at the urban fringe are perhaps more likely to be lost to future development than to experience succession through to woodland, as around a third of developed greenfield is within such areas (Bibby, 2009).

The herbaceous vegetation C pool experienced greater proportional loss than the soil pool within all three study areas between 1945 and the present. The large proportional decrease in this C pool was due to the loss of *agriculture* and the area occupied by crop. However, the inclusion of crop within C storage estimates is arguable, as it will be removed from the system at harvest (Post and Kwon, 2000), and its C store quickly released back into the atmosphere (Gitz and Ciais, 2004). Whilst some studies may include crops within C storage estimates (e.g. Milne and Brown, 1997) others omit them entirely (e.g. Strobach and Haase, 2012). Nonetheless, the herbaceous vegetation C pool was small compared to that of trees and soils, and if crop were omitted from the C storage estimate for *agriculture*, it would have made little difference to the overall loss of stored C between 1945 and the present, and the decreases in contemporary C stores stated above would have been reduced by a mean of just 1.7% across the three study areas.

An important assumption of this study is that the C storage value of the land-use categories was the same in the past as it is today, since the C storage value per unit area of each C pool within each land-use category was calculated from contemporary field data. As such, C values reported may not accurately represent the land-use categories as they were in 1945. For example, intensification of farming methods since 1945 (Robinson and Sutherland, 2002) has led to depletion of SOC stocks in agricultural soils (Matson *et al*., 1997; Stoate *et al*., 2001; Edmondson *et al*., 2014a), and Emmett *et al*. (2010) report that the mean SOC density of arable soils in Great Britain decreased by 3.8 Mg ha^{-1} between 1978 and 2007 (2.2 Mg ha^{-1} in England over the same period), equivalent to losses of 0.13 Mg SOC ha^{-1} yr^{-1}. Therefore, the value of 124 Mg SOC ha^{-1} reported for arable fields is likely to be an underestimate of its 1945 value, and consequently, the estimated losses of SOC from *agriculture* are somewhat conservative. In another example, Díaz-Porras *et al*. (2014) estimate that tree C stocks at locations within Sheffield, UK have doubled between the 1950s and 2010, due to significant increases in the number and size of trees during the period. This is likely to be a result of maturation of existing trees and recent urban tree planting and management schemes. Further, major afforestation from 1950 to the late-1980s resulted in an overall change to the species composition of UK woodland, from one of even deciduous-coniferous mix, to one dominated by conifers (Mason, 2007), which, individually, tend to have less biomass and store less C for a given tree diameter than deciduous species (see Zianis *et al*., 2005). However, C losses caused by the introduction of coniferous species may have been countered somewhat, by an almost complete cessation of deciduous coppice management over the same period (Mason, 2007). This has allowed for the development of regularly-structured, closed-canopy woodland (Rackham, 1986) with potentially greater C storage value than the coppice it replaced. Nevertheless, these changes to woodland management may have led to over-estimation of *woodland*, *parkland* and other tree-containing land-use categories in 1945. However, within urban areas, any changes to tree C stocks during this period would largely be applicable to mature development closer to the urban core (*cf*. Berland, 2012). The process of urbanisation results in immediate vegetation loss when the land is initially cleared (Berland, 2012), and as such, areas of new development will have particularly low vegetation cover. As 1945 pre-dates the post-war surge in urban development, one would expect a greater extent of new development within the contemporary urban matrices than in the historical ones; and given the stratified-random sampling design of this study, the inclusion of sample-points that have increased in vegetation cover between 1945 and the present would have been countered, to some degree, by selection of sample-points within new development of particularly low vegetation cover.

2.4.4 Conclusions

The contiguous urban extent of Darlington, Durham and Newcastle increased considerably between 1945 and the present, and reflected the national trend towards outward urban expansion during this period. When used as a proxy for C storage change, this land-use change had considerable negative effect on the C storage of the areas occupied, as surrounding agricultural land was replaced by urban land-uses of lower C storage value. Loss of soils was the dominant driver of C loss in these urbanising areas, with 113,515 Mg C lost from soils in Newcastle alone between 1945 and the present. Although C gains were made through small increases in the extent of woodland and trees within the urban matrices (e.g. +5,279 Mg C in Newcastle), these were far too small to mitigate effectively against losses made from soils. Modification to UK planning policy has encouraged the development of brownfield sites and slowed the outward growth of towns and cities in recent decades, but with urban human populations set to increase into the foreseeable future, the viability of continued urban densification has been called into question. The choices made now on how towns and cities are developed in the future will have implications for national and international emissions obligations and for provision of other ecosystem services in urban environments, including those relating to the well-being of human urban dwellers and conservation of urban biodiversity. This study has shown that choices made in the past can serve as our guide.

Part 2:

Carbon storage and biodiversity in the urban environment

Chapter 3:
Introduction

3.1 Biodiversity and ecosystem services: trade-offs and opportunities

Biodiversity is being lost worldwide through a combination of factors, including climate change, habitat loss and fragmentation, spread of invasive alien species and diseases, pollution and over-exploitation (Pullin, 2002; MA, 2005b; Butchart *et al*., 2010; Bellard *et al*., 2012). In response, by 2010, world leaders committed to achieving a significant reduction in the rate of biodiversity-loss at global, regional and national scales through the Convention on Biological Diversity (CBD; Secretariat of the CBD, 2003). These targets were not met (Butchart *et al*., 2010; Mace *et al*., 2010; Perrings *et al*., 2010; Secretariat of the CBD, 2010; Jones *et al*., 2011).

The collective failure to meet the CBD 2010 biodiversity targets can principally be attributed to limited funding, policy inaction and a lack of appreciation of biodiversity by governments (Adenle, 2012). In turn, this was fuelled by a general lack of incentive, as the short-term opportunity costs of biodiversity conservation are often seen to be too high (Balvanera *et al*., 2001; Balmford *et al*., 2003; Chan *et al*., 2007; Balmford *et al*., 2011). With this in mind, the revised targets set out within the Strategic Plan for Biodiversity 2011-2020, including the Aichi Biodiversity Targets (CBD, https://www.cbd.int/sp/), incorporate a requirement that, by 2020, the financial resources for effectively implementing the plan are made available, and that evaluation of biodiversity within national accounting and reporting systems is made. As such, the revised strategic plan encourages an approach to biodiversity conservation centred upon socio-economics and the benefits that biodiversity provides for people (Perrings *et al*., 2011). There are fears however, that this approach could lead to the elements of biodiversity that deliver the services that society desires most being conserved at the expense of functionally redundant species, or those with intrinsic value only (Chan *et al*., 2007; Perrings *et al*., 2011). Indeed, some authors challenge the ecosystem services approach to conservation by emphasising the trade-offs between this rationale and what they believe to be the conservationist's primary objective, which is to conserve biological diversity for its intrinsic value (McCauley, 2006; Chan *et al*., 2007; Ghazoul, 2007; Redford and Adams, 2009). Therefore, it is vital that the trade-offs and opportunities that stem from the inclusion of ecosystem services in biodiversity conservation efforts are realised (Cimon-Morin *et al*., 2013).

Identifying spatial congruence between habitats important for biodiversity and provision of ecosystem services is critical to conservation and land-management strategies under the revised global and regional biodiversity policies (Chan *et al*., 2006; Nelson *et al*., 2009). To date however, scientific guidance on how to proceed has been challenged by a difficulty in mapping many ecosystem services (Egoh *et al*., 2009). Despite several reports of positive relationships between biodiversity and selected ecosystem services (e.g. Balvanera *et al*., 2006; Turner *et al*., 2007; Strassburg *et al*., 2010; Bai *et al*., 2011; Larsen *et al*., 2011, 2012; Maes *et al*., 2012; Polasky *et al*., 2012), synergies may not apply in every region and at every scale. Whereas large- or global-scale analyses might suggest spatial unity, fine- or local-scale analyses may reveal weaker associations, or indeed, trade-offs (Naidoo *et al*., 2008; Cimon-Morin *et al*., 2013). If the potential for spatial congruence between biodiversity and ecosystem service delivery can be addressed, the ecosystem service approach to conservation could provide benefits to biodiversity by broadening the funding base and increasing the diversity of support (Chan *et al*., 2006; Goldman *et al*., 2008; Skroch and López-Hoffman, 2010).

Studies investigating multiple ecosystem service delivery have shown that no single habitat or biome performs optimally for all services under investigation (e.g. Rodriguez *et al*., 2006; Maskell *et al*., 2013), not least because provisioning services (e.g. crop and livestock production) often create trade-offs with regulating services (Maes *et al*., 2012). Carbon (C) storage is a regulating service commonly considered within such studies. However, although organic C stores in nature are well understood and C-rich biomes and habitats can be mapped (e.g. Reusch and Gibbs, 2008), their level of spatial congruence with biodiversity can be dependent upon the proxy used for biodiversity. Many globally- or internationally-based studies have used biodiversity priority areas as their biodiversity metric (e.g. Turner *et al*., 2007; Larson *et al*., 2012; Maes *et al*., 2012), whereas others have used species distributions (e.g. Strassburg *et al*., 2010). Likewise, national- and regional-scale studies have used protected area networks (e.g. Eigenbrod *et al*., 2009), biomes, habitats (e.g. Egoh *et al*., 2009; Bai *et al*., 2011), or the distribution of threatened or declining species (e.g. Anderson *et al*., 2009) as a biodiversity measure. As a result, there is ambiguity in the conclusions of existing studies, with reports of both positive and negative relationships between C storage and biodiversity. Furthermore, there remains a lack of spatially explicit assessments on a scale at which land is typically managed, or at which conservation investments usually occur (MA, 2005a; Naidoo *et al*., 2008; Nelson *et al*., 2009; Izquierdo and Clark, 2012). In this respect, urban areas offer small-scale and unique insights into how organisms react with their environment, and whether, or how, they can co-habit with people (Gil and Brumm, 2014). Those organisms that can, may offer cultural ecosystem services (see Part 1, Table 1.1), and make a vital contribution to the continued well-being of increasing urban human populations.

3.2 Biodiversity in urban environments

Of the various anthropogenic origins of habitat-loss and degradation, land-use change by urbanisation is responsible for some of the highest local extinction rates, and often results in eradication of a large majority of native species within numerous taxa (Vitousek *et al*., 1997; McKinney, 2002, 2006). It is the degree of habitat transformation, its permanence, and the density of human occupation that makes urbanisation so detrimental to local biodiversity (McKinney, 2006). The removal or simplification of natural vegetation through landscaping and maintenance of residential and commercial areas in particular, and its replacement with impervious surfaces, turf, and non-native species (Fahrig, 1999 cited by Marzluff and Ewing, 2001; Er *et al*., 2005; Burghardt *et al*., 2009) results in reduction and fragmentation of habitat available for native species (McKinney, 2008). Consequently, urban environments typically comprise of a highly modified, scattered matrix of habitats, with some small patches of remnant natural vegetation or other natural features mixed with built-up areas (Breuste *et al*., 2008).

The complex nature of urban land-use can have complicated influence on local biodiversity (McKinney, 2008). Urban-rural gradients are commonly adopted to uncover the effects of increasing urbanisation on biodiversity from the surrounding landscape through the urban matrix and into the urban core (McDonnell and Pickett, 1990). Several such studies have revealed a hump-shaped curve rather than a linear relationship between the intensity of urbanisation and diversity within animal taxonomic groups (e.g. Blair, 1996; Blair and Launer, 1997; Blair, 1999; Germaine and Wakeling, 2001), implying that species richness is favoured by low to moderate levels of urbanisation over the surrounding landscape, although this may be dependent upon the habitat that lies at the rural end of the gradient (see Verboven *et al*., 2014). However, such patterns are more commonly observed in plants (McKinney, 2008), which has been attributed to the introduction of exotic species (McKinney, 2002; Tait *et al*., 2005; McKinney, 2006; Wania *et al*., 2006; McCune and Velland, 2013) and high spatial habitat heterogeneity within urban areas, whereby species communities vary between habitat patches, resulting in high beta-diversity (Rebele, 1994; Niemelä, 1999; Kühn *et al*., 2004; Wania *et al*., 2006; but see McCune and Velland, 2013). These patterns have also been linked to relationships with the intermediate disturbance hypothesis (Niemelä, 1999; Porter *et al*., 2001; McKinney, 2008), or as a consequence of human settlement being prone towards areas of naturally high geological and biological diversity (Marzluff *et al*., 1998; Kühn *et al*., 2004; Pautasso, 2007). In a meta-analysis of urban-rural gradient studies, McKinney (2008) found that non-avian animal groups, vertebrates in particular, are less likely to show increasing species richness and diversity with moderate levels of urbanisation than are plants, and Marzluff (2001) found that 61% of avian studies indicate a linear decline in species richness with increasing urban intensity; other reviews support these findings (e.g. Chase and Walsh, 2006; Faeth *et al*., 2011). In fact, even low levels of urbanisation may eliminate many animal species found in rural habitats. It has been argued that this is because humans maintain direct control over much of the urban plant community, including the introduction of alien species, but that ecological and evolutionary drivers remain dominant in the response of native consumer communities to urbanisation (Faeth *et al*., 2011). Nonetheless, species richness in all taxa, whether plant or animal, declines when an urban-intensity threshold is exceeded (McKinney, 2008). Consequently, within the bounds of the urban matrix, biodiversity tends to be highest in suburban areas, or at the urban fringes, and lowest at the urban core. This has been reported for invertebrates (Blair and Launer, 1997; Sadler *et al*., 2006; Clark *et al*., 2007), amphibians (Beebee, 1979), reptiles (Germaine and Wakeling, 2001), birds (Blair, 1996; Savard *et al*., 2000; Sandström *et al*., 2006), and mammals (Isaac *et al*., 2014; Łopucki *et al*., 2013; Luck *et al*., 2013).

The local gradient of disturbance produced by urban areas as they accrete outwards also produces a gradient of biotic homogenisation (Knight, 1999; McKinney, 2006; Isaac *et al*., 2014). Despite the heterogeneity within urban areas, there is a degree of uniformity between urban areas in the set of physical conditions, functions and constraints that they create (Savard *et al*., 2000; McKinney, 2006), and as such, a simplified and cosmopolitan community of *urban exploiters* (*sensu* Blair and Launer, 1997) emerges that have become adapted to intense urbanisation (McKinney, 2006). The landscape surrounding the urban area will greatly influence the supplement of additional species found at the urban-rural interface and within land-use types of low to moderate levels of urbanisation (Blair and Launer, 1997; Savard *et al*., 2000); such species have been referred to as *suburban adaptors* (e.g. Blair and Launer, 1997). Those species that can adapt, often achieve higher population densities than conspecifics in natural or semi-natural habitats (Marzluff, 2001; Chace and Walsh, 2006; Rodewald and Shustack, 2008; Shochat *et al*., 2010; Møller *et al*., 2012), whilst those that cannot, often specialist or rare species, are progressively filtered from the community as urbanisation intensifies (Blair 1996; Blair and Launer, 1997; Deichsel, 2006; Clark *et al*., 2007; DeVictor *et al*., 2008). As unique roles and traits are lost over space and time, there becomes high redundancy in those of the remaining species, and functional, as well as biotic, homogenisation occurs within the community (Olden and Rooney, 2006).

3.3 Meeting carbon emissions and biodiversity targets in urban environments

The dramatic shift towards urbanisation is set to continue into the foreseeable future, both globally and nationally, and the environmental impact of expanding urban areas will become ever more severe. The harmful effect that this will have on emissions and biodiversity conservation obligations will be of great concern to governments and decision-makers. Therefore, there is a responsibility to implement policy that controls urban development in a way that it provides environmental needs whilst maintaining human well-being under increasing land-use constraints (Grimm *et al*., 2008; Seto *et al*., 2012). One strategy to reduce the impact of further urbanisation is to adopt planning policy that increases the compaction, or density, of existing settlements (Pauleit *et al*., 2005; Tratalos *et al*., 2007). This contrasts with the *sprawl* scenario, whereby low-density urban development extends beyond the urban periphery. The contrast has been likened to the land-sharing *versus* land-sparing debate in relation to agriculture (e.g. Lin and Fuller, 2013), whereby land-sharing, analogous to urban sprawl, favours species populations on farmland, but decreases agricultural yield per unit area; and land-sparing, in parallel with urban densification, minimises demand for farmland by increasing yield and leaving more intact habitat for species (Green *et al*., 2005). The densification approach may be preferable when considering regional C storage (Eigenbrod *et al*., 2011; but see Churkina *et al*., 2010) and biodiversity (Seto *et al*., 2012), as urban disturbance will be confined to small, explicit areas, but it may come at a cost to local ecosystem services within the urban environment itself, as well as to urban greenspace, urban biodiversity and ultimately, the well-being of urban human populations (Pauleit *et al*., 2005; Tratalos *et al*., 2007; Davies *et al*., 2009; Dallimer *et al*., 2011; Echenique *et al*., 2012).

Many of the factors that are detrimental to urban biodiversity also impact negatively upon urban C storage capacity. This is because there is often strong correlation between species richness and the productivity and structure of native vegetation (Emlen, 1974; Mills *et al*., 1989; Chace & Walsh, 2006; Savard *et al*., 2000). Increasing productivity increases biodiversity (Shochat *et al*., 2006) and C sequestration and storage, at least up until a point. Additionally, the loss of vegetation to impervious surfaces will reduce species richness and diversity by the loss of habitable area (McKinney, 2008), which may remain as isolated *islands* within the urban matrix (*sensu* MacArthur and Wilson, 1967). The construction of impervious surfaces and buildings also facilitates removal of soil organic carbon (SOC), and once in place, may hinder or prevent further accumulation of organic C, depending on the type and extent of the impervious cover (Edmondson *et al*., 2012). However, if the areas of highest biodiversity within the urban matrix are spatially congruent with areas of high C storage, there could be potential for urban areas to off-set some of the emissions and biodiversity-loss from elsewhere within the urban matrix by maintaining or increasing the extent of the most valuable land-use types, although it is appreciated that the effect of increasing tree cover would be minimal relative to the magnitude of emissions from urban areas (Nowak, 1994).

The UK experienced a period of urban sprawl following the end of the Second World War (Best, 1981; Williams, 2004; Couch and Karecha, 2006), and although current policy promotes urban densification (Office of the Deputy Prime Minister [ODPM], 2005, 2010; UK National Ecosystem Assessment [UKNEA], 2011), towns and cities, as they stand today, bear the influence of earlier policies that produced new peripheral estates, expanded towns and new towns (Couch and Karecha, 2006). Could there be an argument in favour this planning design if the matrix of urban land-uses that it creates optimises urban C storage and biodiversity? Or should the trend towards urban densification proceed, thus, sacrificing the C stores and modified biological communities in urban areas in favour of greater opportunities within the surrounding landscape?

3.4 Aims and objectives

In Part 1 of this thesis, I discovered that the urban extent of Durham, like many urban areas in the north-east region of England, has increased rapidly over the past six to seven decades, and that the city now exhibits the large expanse of low- to moderate-density residential and commercial land-uses typical of urban sprawl. I also explored the variation in C storage among the different urban land-uses within the city. In Part 2, I go on to investigate whether there is variation in biodiversity among the urban land-use categories, and then test for co-variation between biodiversity and C storage. If land-uses with greater C storage capacity are also those with greater biodiversity, then this spatial congruence may have positive implications when addressing C emissions reduction and biodiversity conservation targets within urban areas. I will employ birds as a biodiversity indicator taxon, as they respond both positively and negatively to human disturbances (Clucas and Marzluff, 2012), they frequently colonise urban areas throughout the world, and are commonly used to assess the conservation value of semi-natural habitats within urbanised landscapes (Chiari *et al*., 2010). Indeed, Blair (1999) concludes that birds meet the criteria of useful biological indicators (*cf*. Noss, 1991), and that responses of bird communities to urbanisation are similar to those of other animal groups.

The study will address the following questions:

1) What is the wintering and breeding bird species richness and diversity (as assessed by applying the Shannon-Wiener Diversity Index [H']) within each of the urban land-use categories identified within the city of Durham? To answer this, I will sample bird communities by carrying out point-count surveys at all sample points within which prior vegetation C and SOC samples were collected (see methodology Part 1, Chapter 2).
2) Is there a spatial relationship between bird *i*) species richness and *ii*) diversity and C storage within the city? I will use the C storage values per unit area from prior C sampling surveys of Durham, and data from the bird point-counts to model these relationships.
3) Are there differences in bird species richness and diversity among the different land-use categories, each with a varying C storage value per unit area.

4) Are there differences in the occurrence and abundance of species within the bird communities of the different urban land-use categories, and if so, does the matrix of land-uses contribute towards the overall species diversity within the city? I will use Principal Components Analysis (PCA) to show the similarity/dissimilarity among land-uses.

Chapter 4:
Spatial relationships between carbon storage and bird species richness and diversity in an urban environment

ABSTRACT

Context: Both major land-use change and human-induced climate change have been implicated in recent global biodiversity declines. Nowhere is this more evident than in urban areas, where patches of remnant habitat have become enclosed within a matrix of urban land-uses, many of which are unsuitable for the persistence of species. With urban human populations continuing to increase, there is a specific call for urban areas to increase their role in the implementation of the Convention on Biological Diversity (CBD) and the Kyoto Protocol for emissions reduction.

Aim: I aim to assess the relationship between carbon (C) storage and bird species richness and diversity in an urban matrix.

Methods: I used satellite imagery to categorise urban land-uses within the city of Durham, north-east England. C storage and bird species richness and diversity data were collected from the field for the different urban land-uses.

Results: Total C storage value per unit area differed significantly between different urban land-use categories, as did wintering and breeding bird species richness and diversity. The highest C storage value land-uses in woodland and parkland were associated with highest species richness and diversity, while land-uses with lowest C storage value (commercial and high-density housing without gardens) had among the lowest species richness and diversity.

However, the relationship was not straightforward between these two extremes. Beta-diversity among land-use categories highlighted the importance of some moderate- to low-C value land-uses to biodiversity throughout the urban matrix, although there was also some redundancy amongst certain land-uses in the assemblage of species that they supported. The overall relationship between C storage and species richness and diversity was positive, and the tree and woody vegetation C pools had stronger positive relationships with species richness and diversity than did the herbaceous vegetation and soil C pools.

Conclusions: Despite the generally positive relationships detected, this study also highlights difficulties in maximising C storage and biodiversity within urban environments, as a mix of both higher and lower C-containing land-uses are required to maintain biodiversity across the entire city**.** The study considers these results with reference to future planning strategies under continuing urban human population growth, warning that compromises are inevitable given the spatial restrictions within the bounds of existing urban areas.

4.1 INTRODUCTION

Identifying spatial congruence between habitats important for biodiversity and for the provision of ecosystem services is critical to conservation and land-management strategies under the revised biodiversity targets set out within the Convention on Biological Diversity's (CBD) Strategic Plan for Biodiversity for the period 2011-2020 (https://www.cbd.int/sp/; Chan *et al*., 2006; Nelson *et al*., 2009). To date however, scientific guidance on how to identify sites of dual importance has been challenged by difficulties in mapping many ecosystem services (Egoh *et al*., 2009). Despite reports of positive relationships between biodiversity and selected services (e.g. Balvanera *et al*., 2006; Turner *et al*., 2007; Strassburg *et al*., 2010; Bai *et al*., 2011; Larsen *et al*., 2011; Larsen *et al*., 2012; Maes *et al*., 2012; Polasky *et al*., 2012), synergies may not apply in every region and at every scale. Whereas large- or global-scale analyses might suggest spatial unity, fine- or local-scale analyses may reveal weaker associations, or indeed, trade-offs (Naidoo *et al*., 2008; Cimon-Morin *et al*., 2013). If the potential for spatial congruence between biodiversity and ecosystem service delivery can be addressed, the ecosystem service approach to conservation could benefit biodiversity by broadening the funding base and increasing the diversity of support (Chan *et al*., 2006; Goldman *et al*., 2008; Skroch and López-Hoffman, 2010).

Studies investigating multiple ecosystem service delivery have shown that no single habitat or biome performs optimally for all services under investigation (e.g. Rodriguez *et al*., 2006; Maskell *et al*., 2013), not least because provisioning services often create trade-offs with regulating services (Maes *et al*., 2012). Carbon (C) storage is a regulating service commonly considered within such studies. However, although organic C stores in nature are well understood and C-rich biomes and habitats can be mapped (e.g. Reusch and Gibbs, 2008), their level of spatial congruence with biodiversity can be dependent upon the proxy used for biodiversity. Many globally- and internationally-focused studies have used biodiversity priority areas as their biodiversity metric (e.g. Turner *et al*., 2007; Larson *et al*., 2012; Maes *et al*., 2012), though others have used species distributions (e.g. Strassburg *et al*., 2010). Likewise, national- and regional-scale studies have used protected area networks (e.g. Eigenbrod *et al*., 2009), biomes, habitats (e.g. Egoh *et al*., 2009; Bai *et al*., 2012), or the distribution of threatened or declining species (e.g. Anderson *et al*., 2009) as a biodiversity measure. As a result, there is ambiguity in the conclusions of existing studies, with reports of both positive and negative relationships between C storage and biodiversity. Furthermore, there remains a lack of assessments on a scale at which land is typically managed, or at which conservation investments usually occur (MA, 2005b; Naidoo *et al*., 2008; Nelson *et al*., 2009; Izquierdo and Clark, 2012).

A dramatic shift towards urbanisation in recent decades has led to more than 50% of the world's human population living within towns and cities (United Nations [UN], 2012). As a consequence, despite their small area of land surface occupation, urban areas have disproportionately high C footprints (Svirejeva-Hopkins *et al*., 2004; Trusilova and Churkina, 2008). Aside from direct emissions release through energy consumption, urban areas and the process of urbanisation can reduce the C storage value of a parcel of land when compared to its former land-use. However, the urban environment may regain C stocks over time as vegetation recovers, until eventually, stores within certain parts of the urban matrix may surpass those of the land-use they have replaced (Zhao *et al*., 2007; Berland, 2012). Urban areas may also retain patches of remnant semi-natural habitat, such as woodland, which can make a vital contribution to the C storage value of towns and cities. Indeed, studies based upon fine-scale land-use data have produced estimates indicating a substantial C store exists within urban vegetation and soils (e.g. Nowak and Crane, 2002; Pouyat *et al*., 2006; Churkina *et al*., 2010; Davies *et al*., 2011; Hutyra *et al*., 2011; Edmondson *et al*., 2012; Strobach and Haase, 2012; Edmondson *et al*., 2014b).

Urbanisation is responsible for severe local biodiversity loss, and often results in elimination of a majority of native species across numerous taxa (Vitousek *et al*., 1997; McKinney, 2002, 2006). As such, urban areas offer small-scale and unique insights into how organisms react with their environment, and whether, or how, they can live alongside people (Gil and Brumm, 2014). The complex nature of urban land-use however, can complicate its influence on local biodiversity (McKinney, 2008). Urban-rural gradients are commonly studied to uncover the effects of increasing urbanisation on biodiversity (McDonnell and Pickett, 1990). In a meta-analysis of such studies, McKinney (2008) found that plants may show increased species richness and diversity with moderate levels of urbanisation, but that animal groups, vertebrates in particular, are less likely to respond in such a manner. Indeed, Marzluff (2001) found that 61% of avian studies reviewed, showed a decline in species richness with increasing urban intensity; other reviews have revealed similar declines (e.g. Chase and Walsh, 2006; Faeth *et al*., 2011). In fact, even low levels of urbanisation can eliminate many animal species found in rural habitats. It has been argued that this is because humans directly control much of the urban plant community, including the introduction of alien species, but that ecological and evolutionary drivers remain dominant in the response of native consumer communities to urbanisation (Faeth *et al*., 2011). Nonetheless, species richness in all taxa, whether plant or animal, declines when an urban-intensity threshold is exceeded (McKinney, 2008). Consequently, within the bounds of the urban matrix, diversity within taxonomic groups tends to be highest in suburban areas, or at the urban fringes, and lowest at the urban core (e.g. Blair and Launer, 1997; Sadler *et al*., 2006; Clark *et al*., 2007; Beebee, 1979; Germaine and Wakeling, 2001; Blair, 1996; Savard *et al*., 2000; Sandström *et al*., 2006; Isaac *et al*., 2014; Lopucki *et al*., 2013; Luck *et al*., 2013).

The gradient of disturbance produced by urban areas as they accrete outwards also produces a gradient of biotic homogenisation (Knight, 1999; McKinney, 2006; Isaac *et al*., 2014). Despite the inconsistent mix of land-uses within different urban areas, there is a degree of uniformity between urban areas in the set of physical conditions, functions and constraints that they create (Savard *et al*., 2000; McKinney, 2006), and consequently, a simplified and cosmopolitan community of *urban exploiters* (*sensu* Blair and Launer, 1997) emerges, that has become adapted to intense urbanisation (McKinney, 2006). The landscape surrounding the urban area will greatly influence the supplement of additional species found at the urban-rural interface and within land-uses of low to moderate levels of urbanisation (Blair and Launer, 1997; Savard *et al*., 2000). Those species that can adapt, often achieve higher population densities than conspecifics in natural or semi-natural habitats (Marzluff, 2001; Chace and Walsh, 2006; Rodewald and Shustack, 2008; Shochat *et al*., 2010; Møller *et al*., 2012), whilst those that cannot, often specialist and rare species, are progressively filtered from the community as urbanisation intensifies (Blair, 1996; Blair and Launer, 1997; Deichsel, 2006; Clark *et al*., 2007; DeVictor *et al*., 2008).

Many of the factors that are detrimental to urban biodiversity also impact negatively upon urban C storage. This is because there is often strong correlation between species richness and the productivity and structure of native vegetation (Emlen, 1974; Mills *et al*., 1989; Chace & Walsh, 2006; Savard *et al*., 2000). Increasing productivity increases biodiversity (Shochat *et al*., 2006) and C sequestration and storage, at least up until a point. Additionally, the loss of vegetation to impervious surfaces will reduce species richness and diversity by the loss of habitable area (McKinney, 2008); isolated areas of the latter perhaps remaining as *islands* within the urban matrix (*sensu* MacArthur and Wilson, 1967). The construction of impervious surfaces and buildings also results in the removal of soil organic carbon (SOC), and once in place, further C sequestration may be impeded or prevented, depending upon the type and extent of the impervious cover (Edmondson *et al*., 2012).

The UK experienced decades of urban sprawl following the end of the Second World War (Williams, 2004), and although current policy promotes urban densification (Office of the Deputy Prime Minister [ODPM], 2005, 2010; UK National Ecosystem Assessment [UKNEA], 2011), towns and cities, as they stand today, bear the influence of earlier policies that produced new peripheral estates, expanded towns and new towns (Couch and Karecha, 2006). Here, I question whether there is an argument in favour this sprawl if the matrix of urban land-uses that it creates optimises urban C storage and biodiversity conservation. Or should the trend towards urban densification proceed at the expense of C storage and biological communities in urban areas, addressing emissions and biodiversity targets in the surrounding landscape? This contrast has been likened to the land-sharing *versus* land-sparing debate in relation to agriculture (e.g. Lin and Fuller, 2013), whereby land-sharing, analogous to urban sprawl, favours species populations on farmland, but decreases agricultural yield per unit area; and land-sparing, in parallel with urban densification, minimises demand for farmland by increasing yield and leaving more intact habitat for species (Green *et al*., 2005).

I use birds as an indicator taxon as they are considered particularly suited to studies concerning urban biodiversity. Birds are ubiquitous to urban environments worldwide, and they respond both positively and negatively to human disturbances (Clucas and Marzluff, 2012). Additionally, the presence of birds enhances the well-being of people living in towns and cities (Fuller *et al*., 2007; Clucas *et al*., 2011).

Using empirical data collected in the field, I explore C storage and biodiversity amongst urban land-use types, and test for co-variation between C storage and biodiversity. Knowing the features of urban environments that are important to a wide set of species can assist planning decisions in an increasingly urbanised world (Richter and Weiland, 2011; Gil and Brumm, 2014).

4.2 METHODOLOGY

4.2.1 Study area

Durham City (hereafter Durham) is a relatively small UK city situated within north-east England, UK (54°46'32.70" N, 01°35'06.23" W). It has a human population of 95,000 within the city limits (Office for National Statistics [ONS], 2013). The mean annual precipitation is 651 mm, and the mean minimum and maximum daily temperatures are 5.4°C and 12.9°C respectively. This study focused on the urbanised area of the city, defined by the delineation between what was classified as an urban land-use category (see Chapter Two, Table 2.3) and contiguous non-urban land-use (e.g. agriculture) or semi-natural land-cover (e.g. woodland or scrub). If the latter two land-use or land-cover categories were not contiguous, and were set within the matrix of urban land-use categories, they were considered urban, and included within the boundary of the study area. For simplicity, the term *land-use* was applied to all land-use categories, although strictly, *grassland*, *scrub, woodland* and *no vegetation* describe land cover.

4.2.2 Land-use mapping and categorisation

Land-use categorisation was determined using Google Earth (GE) v7.1.2 software (Google Inc., Mountain View, CA, USA) as described in Chapter Two of this thesis, where the reader should refer to the methodology concerning contemporary land-use mapping in section 2.2.2. The study area was divided into the urban land-use categories as defined in

Chapter Two, Table 2.3; with the exception of agricultural land-use, which was not applicable to the research within this chapter.

4.2.3 Sample-point selection

Sample points within urban land-uses were selected using the stratified random sampling process described in Chapter Two, and the reader should refer to section 2.2.3 for a detailed methodology. In total, 93 quadrats across the study area were selected in this way (Table 4.1). All quadrats were located in the field using a handheld global positioning system (GPS) device (Garmin e Trex 20, Olathe, US) and aided by maps printed from GE.

Table 4.1 The number of 50 x 50 m quadrat samples taken from each urban land-use category within Durham, UK.

Land-use category	Sample size (*n*)
Allotment	6
Amenity grassland	11
Commercial	10
Grassland	12
Parkland	10
Residential:	
Urban no garden	4
Urban with garden	10
Suburban	12
Scrub	8
Woodland	10
Total	93

4.2.4 Vegetation and soil survey, preparation and analysis

C storage data were collected from the following four C pools within each 50 x 50 m quadrat: *i*) trees (4 m+), *ii*) woody vegetation (1-4 m), *iii*) herbaceous vegetation, and *iv*) soils. The methodology for collecting this data, and for preparing and analysing vegetation and soil samples, is described in detail in Chapter Two, where the reader should refer to section *2.2.4.1* through to *2.2.4.4*. It should be noted however, that the research covered in this chapter is concerned only with C data collected from quadrats in Durham, and therefore, the two-way analysis-of-variance (ANOVA) within section *2.2.4.4*, that was applied to justify the use of 22 cm as a cut-off depth for further soil organic carbon (SOC) analysis, was repeated here omitting any soil sub-samples collected in Darlington and Newcastle. This did not alter the significance of the test, and the use of 22 cm as a cut-off depth for further SOC analysis within this chapter was justified. The results of the two-way ANOVA and Tukey HSD tests carried out on soil sub-samples collected within Durham quadrats are included in Appendix 4.

4.2.5 Bird survey

Bird point-count surveys involved standing at, or as close as possible to, the same stratified random sample co-ordinates generated for C data collection, and following a two-minute settling-down period, recording all birds seen and heard over a ten-minute period (following Fuller and Langslow, 1984) in the land-use category within which the sample point co-ordinates were situated. Birds flying over and not seen to alight were excluded from the survey. All individuals were recorded to species level. Additional parameters recorded in the field were *i*) the estimated distance, to the nearest 5 m, and *ii*) the bearing of the bird from the observer where it was initially located. If a bird was initially seen flying but was then observed to alight within the focal land-use category, the distance and bearing of the landing point from the observer was recorded. All sample points were surveyed in winter (December and January) 2013/14, and repeated in spring (April and May) 2014, and all point-counts were carried out within a two-hour period following sunrise. It is appreciated that bias introduced by detectability interactions with habitat is potentially serious (Bibby *et al*., 2000), especially as the effects of habitat within different land-use categories was an objective of this study. As such, although it is considered that the majority of all species present within all point-count samples, regardless of land-use, were duly recorded, it is possible that, on occasion, the exact abundance of indiviuals within species was not clear in land-uses with dense vegetation (e.g. woodland and parkland) or tall buildings (e.g. residential and commercial land-uses). On these occasions, only the individuals seen were recorded, or, if unseen birds were vocalising, abundance was estimated based upon vocalisations. Following a set of point-counts, the observer's position was located on the map of land-use polygons created in GE (see section 4.2.2), and using the information obtained in *i)* and *ii)* above, the location of each bird sighting and its position within the land-use category was verified. The species richness within each survey was recorded, and species diversity was calculated using the Shannon-Wiener Diversity Index (H'; Equation 3).

$$H' = -\sum (p\mathrm{i}) (\ln p\mathrm{i}) \qquad \text{(Equation 3)}$$

Where: pi = the proportion of the total sample belonging to the ith species.

4.2.6 Statistics and further analysis

4.2.6.1 Analysis of carbon storage among land-use categories

For further analysis, the C storage values obtained for each of the C pools within each 50 x 50 m quadrat were summed to provide a total vegetation C and SOC storage value for each quadrat. The quadrat C data did not meet the assumptions of parametric tests, and could not be transformed to do so; therefore, Kruskal-Wallis non-parametric ANOVA was used on untransformed data to test for differences between the land-use categories in the C storage per unit area (Mg C ha^{-1}) of the *i*) total vegetation and soils, *ii*) trees (4 m+), *iii*) woody vegetation (1-4 m), *iv*) herbaceous vegetation, and *v*) soils.

4.2.6.2 Analysis of bird species richness and diversity among land-use categories

Data collected from the point-count surveys for *i*) wintering, *ii*) breeding, and *iii*) aggregated total (wintering plus breeding) bird species richness by land-use category did not meet the assumptions of parametric tests, and therefore, differences between the land-use categories were tested using Kruskal-Wallis non-parametric ANOVA. Likewise, bird diversity data by land-use category, calculated from the point-count survey data, did not meet the assumptions of parametric tests and differences between the land-use categories for *iv*) wintering, and *v*) breeding bird diversity was tested using Kruskal-Wallis non-parametric ANOVA.

4.2.6.3 Relationships between carbon storage and bird species richness and diversity

The relationships between total vegetation C and SOC storage per unit area and *i*) bird species richness, and *ii*) bird diversity, were tested using generalised linear models (GLMs). GLMs were run with species richness and diversity as response variables, and C storage per unit area and land-use category as continuous and categorical explanatory variables respectively. The GLMs were then repeated using C storage per unit area for each of the four constituent C pools in turn (herbaceous vegetation, woody vegetation, trees and soils). However, there was no significance in the slopes of any of these models, and no significant interactions were found between C storage and land-use category. Therefore, the data were pooled and GLMs were re-run omitting land-use as an explanatory variable. Models containing response variables using count data (i.e. bird species richness) were fitted with a quasipoisson distribution. All of the above analyses were conducted using R v2.15.3 (R Development Core Team, 2008) software.

4.2.6.4 Multi-variate statistical analysis of bird communities

Similarity in the occurrence and abundance of bird species within land-use categories was evaluated using Principal Components Analysis (PCA), which was performed on $\log_{10}+1$ transformed point-count data to a maximum of five principal components (PCs). Logging of data assisted in the interpretation of results by increasing the dispersal of clustered data in the PCA plots. Cluster Analysis (CA) of the samples using the Group Averaging fusion strategy was then performed on a Euclidean Distance (ED) dissimilarity matrix calculated from the $\log_{10}+1$ data matrix. The resultant clusters were then imposed on the PCA plots with a dissimilarity distance of 1.35. PRIMER (v6.1.5) software (Clark and Gorley, 2006) was used for all PCA and CA analyses.

4.3 RESULTS

4.3.1 Carbon storage per unit area of land-use categories

The spatial extent of each land-use category is shown by the urban land-use map of Durham in Figure 4.1. Carbon (C) storage per unit area, as calculated from 50 x 50 m quadrat samples, within the vegetation and soils of Durham was significantly different between land-use categories. This was so of the total vegetation C and soil organic carbon (SOC; $\chi^2_{9,83}$=81.46, p<0.001), and of the component C pools of trees (4 m+; $\chi^2_{9,83}$=72.51, p<0.001), woody vegetation (1-4 m; $\chi^2_{9,83}$=59.18, p<0.001), herbaceous vegetation ($\chi^2_{9,83}$=79.79, p<0.001), and soils ($\chi^2_{9,83}$=70.42, p<0.001; see Appendix 5 for *post-hoc* test results). *Woodland* contained the greatest total C (vegetation and SOC) storage per unit area (253.20 Mg C ha^{-1}) and *urban no garden* contained the lowest (1.74 Mg C ha^{-1}; Figure 4.2). Indeed, three of the four lowest figures for total C storage were associated with residential sub-categories; the fourth was *commercial* (Figure 4.2). *Woodland* had high C storage value in all pools, relative to other land-use categories, whilst *commercial* and *urban no garden* land-uses had low C storage value in all pools (Figure 4.3). The soil pool held the greatest C store within all land-use categories (Figure 4.3), although in *woodland*, this was only slightly greater than the tree C pool. The tree C pool was also important in *parkland*, *scrub* and *suburban* land-uses. The woody vegetation and herbaceous vegetation C pools were of relatively high importance in *scrub* and *grassland* respectively (Figure 4.3).

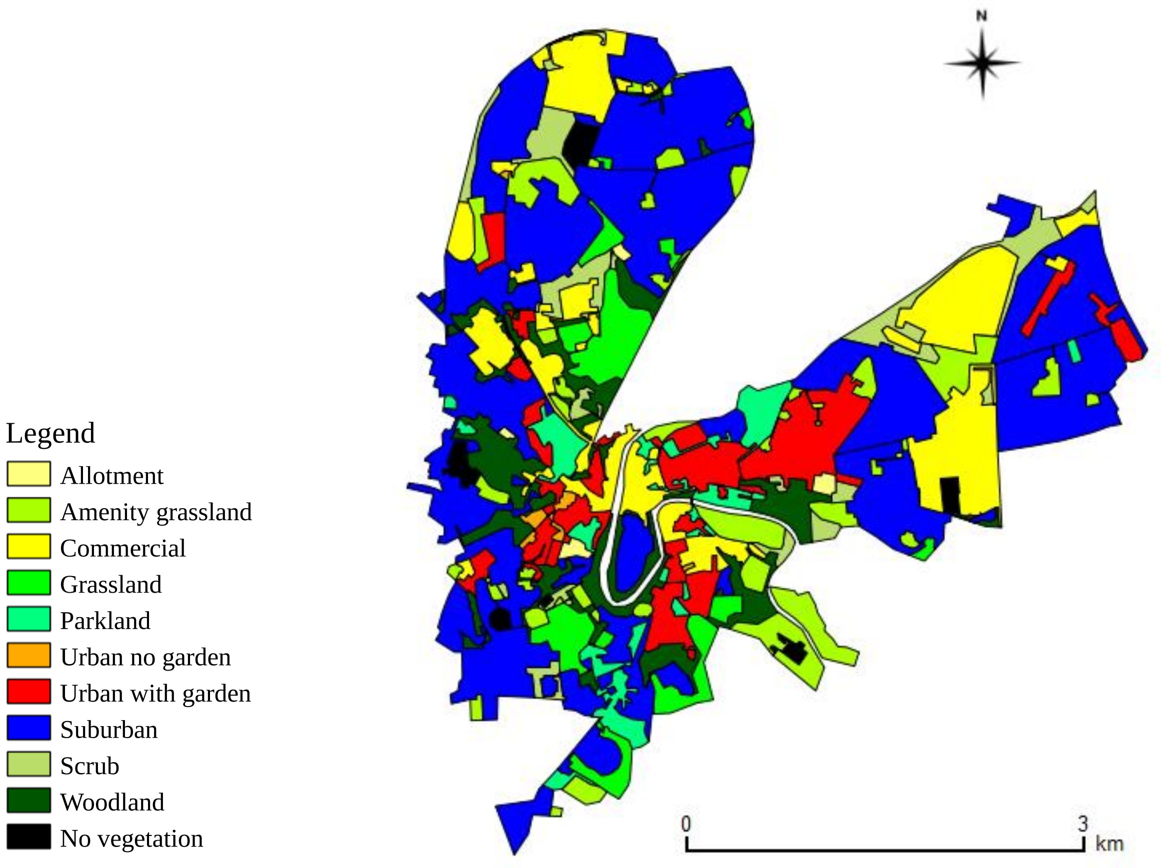

Figure 4.1 Land-use map of the urbanised area of Durham, UK as at 2009. Each colour-coded urban land-use category has an associated carbon (C) storage value (see Figure 4.2), and as such, the map also shows the distribution of C stored throughout the city. The land-use category *no vegetation* was assumed to have no C storage value.

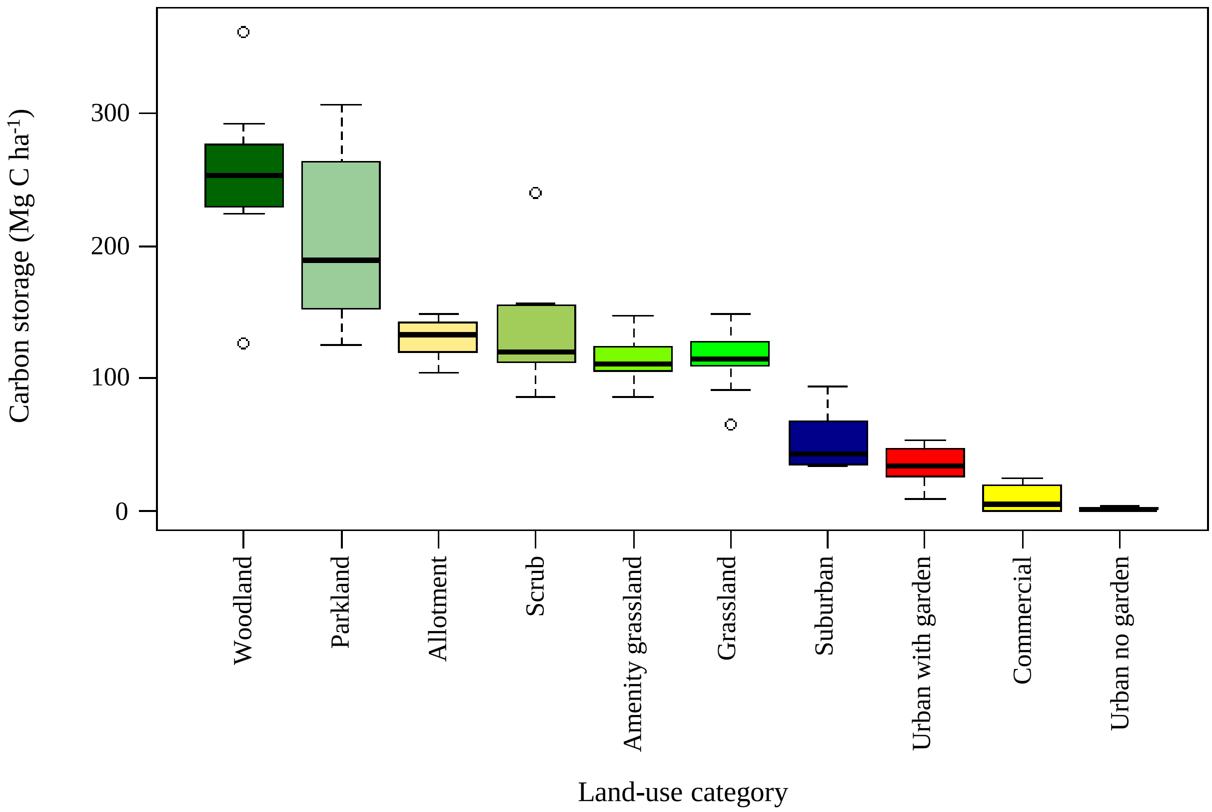

Figure 4.2 The median total vegetation carbon (C) and soil organic carbon (SOC) storage per unit area of urban land-use categories in Durham, UK. Boxes show where the central 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 4.1, and are presented in order of decreasing median C storage value per unit area.

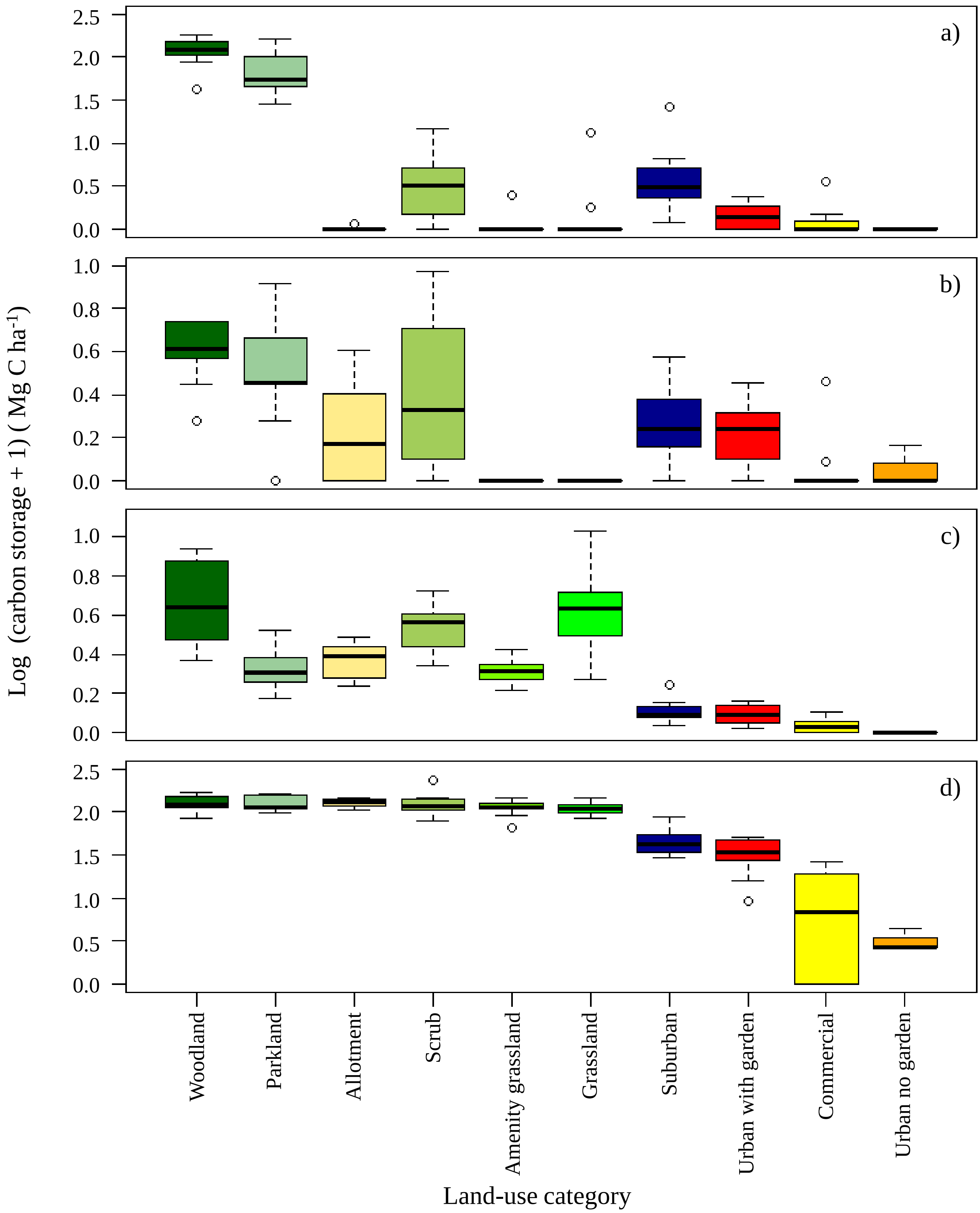

Figure 4.3 The median log carbon (C) storage within a) trees (4 m+), b) woody vegetation (1-4 m), c) herbaceous vegetation, and d) soils per unit area of urban land-use categories in Durham, UK. Boxes show where the central 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 4.1, and presented in order of decreasing median total vegetation C and soil organic carbon value (see Figure 4.2). Log transformation applied to data to aid visualisation only. Note differing scales on y-axes.

4.3.2 Bird species richness and the spatial relationship with carbon storage

The number of wintering, breeding and aggregated total (wintering plus breeding) bird species recorded throughout the urban matrix of Durham was 37, 46 and 51 respectively (see Appendix 7 for species lists). Mean species richness per point census differed significantly among land-use categories. This was the case for both the wintering ($\chi^2_{9,83}$=50.50, p<0.001) and breeding ($\chi^2_{9,83}$=53.42, p<0.001) bird communities, and also for the aggregated total species richness ($\chi^2_{9,83}$=46.92, p<0.001). Figure 4.4 shows the median bird species richness per point census within each land-use category arranged in order of decreasing total vegetation C and SOC storage value per unit area (see Figure 4.2). *Woodland* and *parkland* had highest wintering, breeding and aggregated total bird species richness per point census, and were also those with the two highest total C storage values per unit area (see section 4.3.1). The land-use categories with lowest aggregated total bird species richness, *commercial* and *urban no garden*, had lowest total C storage values per unit area (see section 4.3.1). Between these extremes, the relationship between bird species richness and C storage was less clear. For example, *suburban* and *urban no garden* had relatively high wintering and breeding bird species richness, but low total vegetation C and SOC storage value per unit area; and *amenity grassland* and *grassland* had low wintering and breeding bird species richness but moderate total C storage values per unit area. Further, *allotment* and in particular, *scrub* had relatively high bird species richness, but had moderate total C storage value per unit area only.

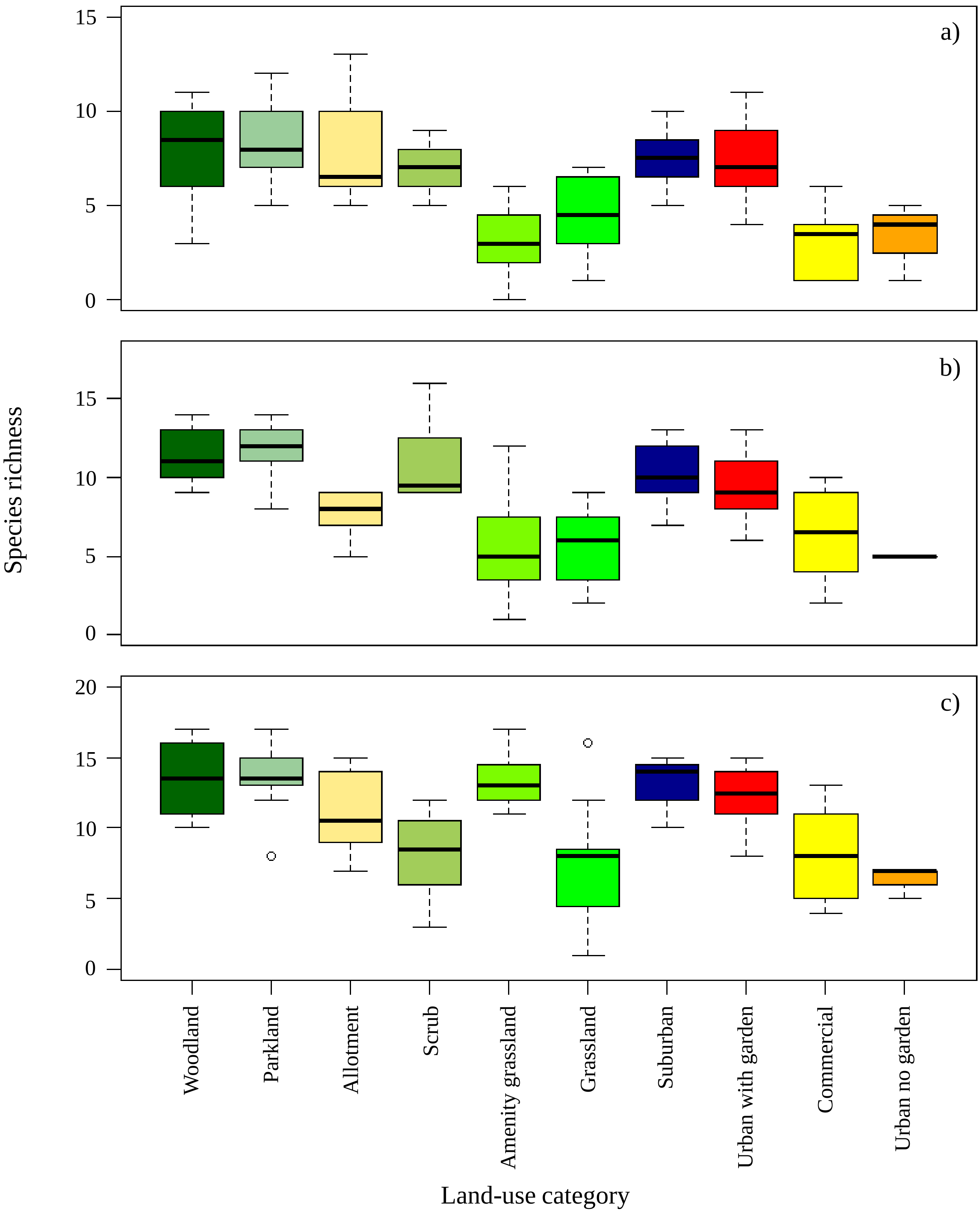

Figure 4.4 The median a) wintering, b) breeding, and c) aggregated total bird species richness of urban land-use categories in Durham, UK. Boxes show where the central 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 4.1, and presented in order of decreasing total vegetation carbon and soil organic carbon storage value per unit area (see Figure 4.2). Note differing scales on y-axes.

Figure 4.5 shows that, up to a point, the addition of progressively lower total C storage value categories continued to increase overall bird species richness (i.e. beta-diversity increased). Of note, a number of wintering and breeding bird species were recorded exclusively in *grassland* and, in particular, in *scrub*, although these land-use categories had only moderate C storage value per unit area, and two breeding species were recorded exclusively in the low C storage value *commercial* land-use (see Appendix 7 for species lists). On the other hand, not only was *urban no garden* land-use of particularly low C storage value, there were also no species unique to this land-use category, and it did not contribute towards beta-diversity.

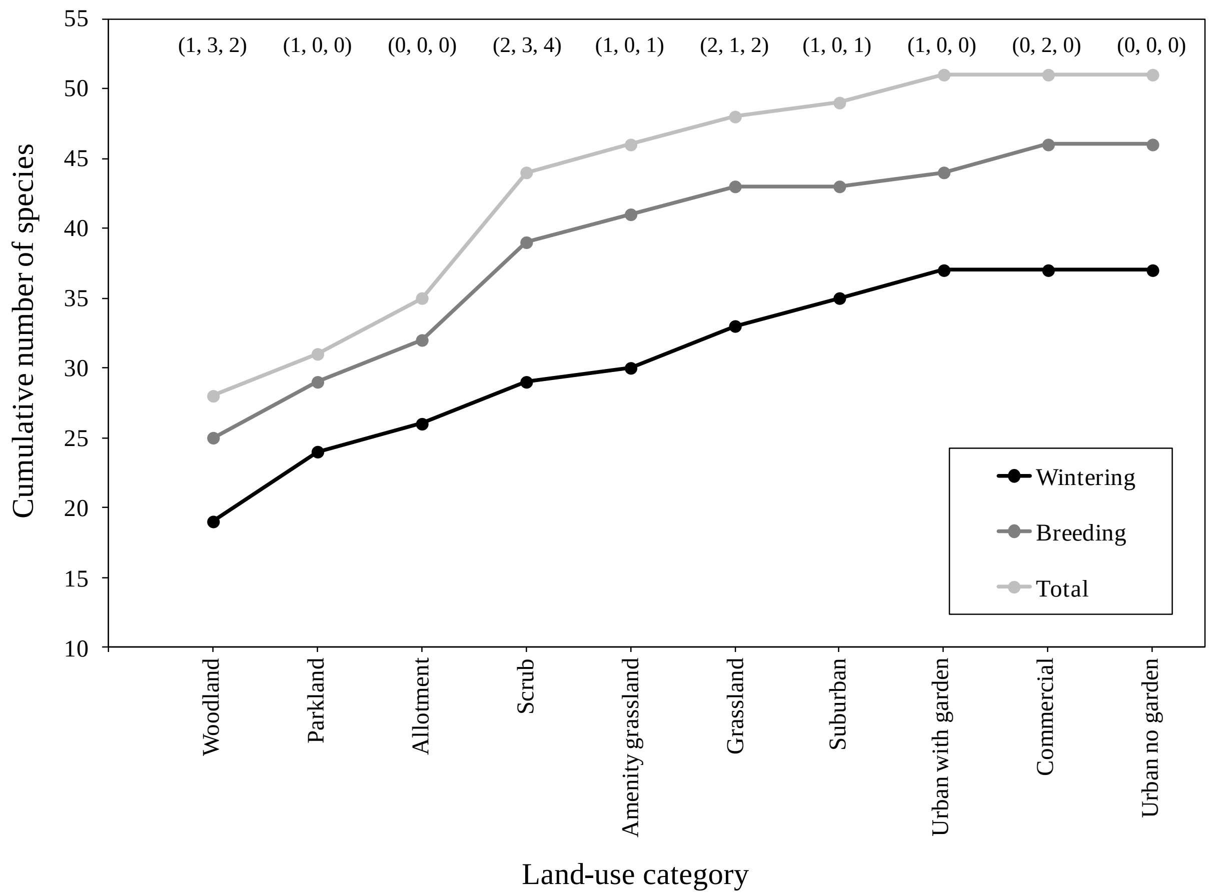

Figure 4.5 The cumulative number of *i*) wintering, *ii*) breeding, and *iii*) aggregated total bird species recorded in point-counts with each additional urban land-use category in Durham, UK. Land-use categories are presented in order of decreasing median total vegetation carbon and soil organic carbon storage value per unit area (see Figure 4.2). Figures in parentheses are the number of wintering, breeding and aggregated total bird species exclusive to the respective land-use category.

When C storage and bird species richness data were pooled, ignoring land-use, there was a significant positive relationship between total vegetation C and SOC storage per unit area and *i*) wintering, *ii*) breeding, and *iii*) aggregated total bird species richness (Table 4.2; Figure 4.6). Winter, breeding and total species richness also correlated positively and significantly with C storage of each of the tree and woody vegetation C pools; with species richness responding most rapidly to increases of C within the woody vegetation pool. However, the relationship with the herbaceous vegetation C pool was not significant, and the soil C pool had a significant relationship with breeding bird species richness only (Table 4.2;

Figure 4.7). Colour-coding of the plotted points in Figures 4.6 and 4.7 emphasises the absence of correlation between C storage and species richness within land-use categories.

Table 4.2 Results of generalised linear models (GLMs) with Poisson errors testing the relationship between *i*) wintering, *ii*) breeding, and *iii*) aggregated total bird species richness and carbon (C) storage per unit area (Mg C ha^{-1}) in different C pools in Durham, UK. Parameter estimates and predictions of the GLM are in logs. Bold p-values denote significant effects at $p<0.05$.

Bird community/carbon pool	Intercept	t (91)	p	Slope	t (91)	p	R^2
Wintering birds							
Total vegetation and soils	1.6241	20.368	**<0.001**	0.0015	2.812	**0.006**	0.0695
Trees (4 m+)	1.7345	32.304	**<0.001**	0.0025	2.711	**0.008**	0.0624
Woody vegetation (1-4 m)	1.6806	29.398	**<0.001**	0.0922	3.841	**<0.001**	0.1164
Herbaceous vegetation	1.7597	27.854	**<0.001**	0.0236	0.945	0.347	0.0084
Soils	1.6407	17.211	**<0.001**	0.0018	1.946	0.055	0.0355
Breeding birds							
Total vegetation and soils	1.9406	29.805	**<0.001**	0.0017	3.974	**<0.001**	0.1292
Trees (4 m+)	2.0605	46.883	**<0.001**	0.0031	4.192	**<0.001**	0.1375
Woody vegetation (1-4 m)	2.0059	44.006	**<0.001**	0.1040	5.563	**<0.001**	0.2151
Herbaceous vegetation	2.0963	39.547	**<0.001**	0.0271	1.303	0.196	0.0157
Soils	1.9809	24.997	**<0.001**	0.0018	2.374	**0.020**	0.0516
Total birds							
Total vegetation and soils	2.2636	38.683	**<0.001**	0.0011	2.802	**0.006**	0.0682
Trees (4 m+)	2.3415	59.355	**<0.001**	0.0020	2.909	**0.005**	0.0711
Woody vegetation (1-4 m)	2.2923	55.391	**<0.001**	0.0794	4.456	**<0.001**	0.1501
Herbaceous vegetation	2.3595	50.504	**<0.001**	0.0200	1.074	0.286	0.0106
Soils	2.2886	32.843	**<0.001**	0.0012	1.737	0.086	0.0279

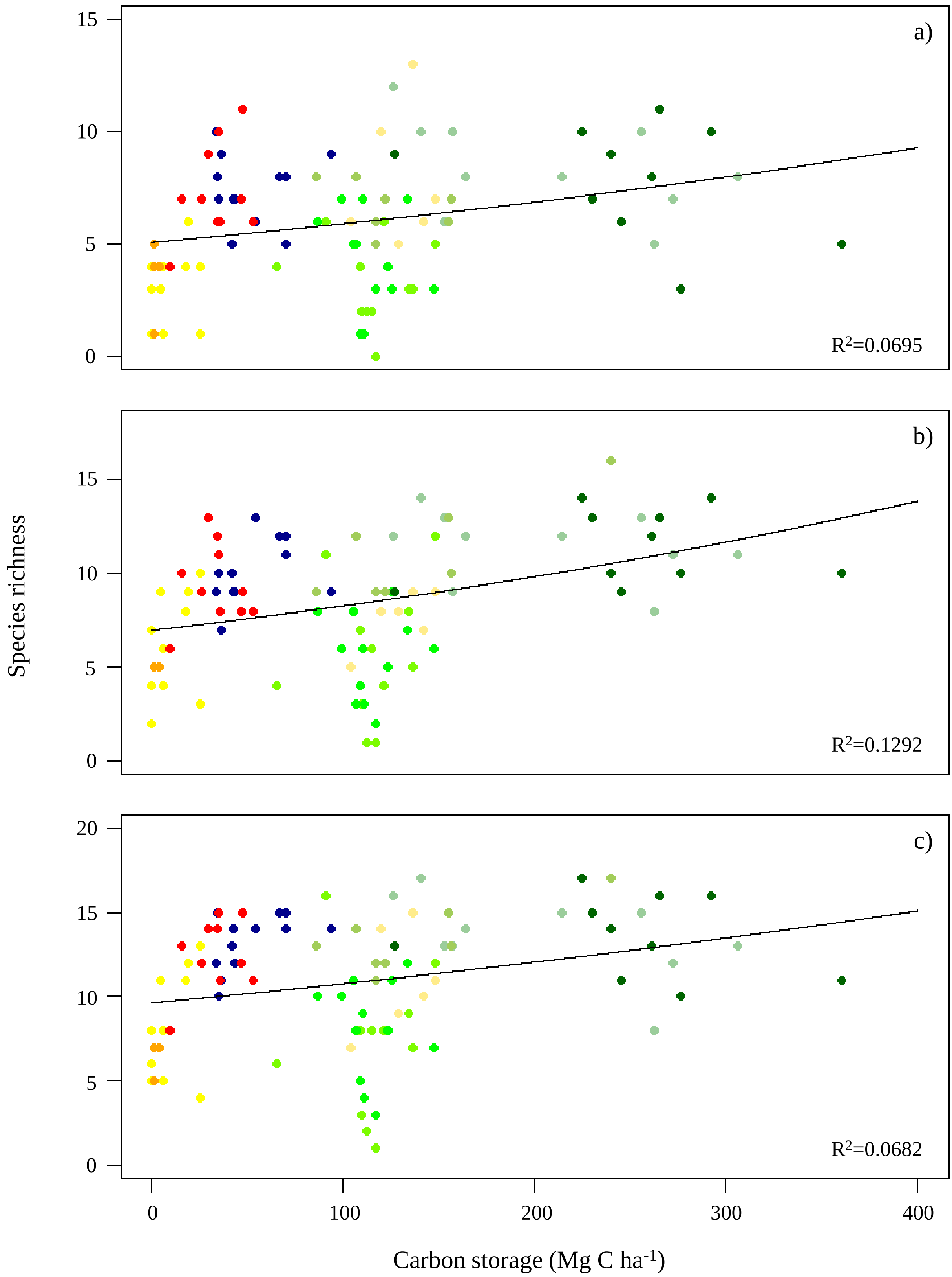

Figure 4.6 The relationship between a) wintering b) breeding, and c) aggregated total bird species richness and total carbon (vegetation plus soil organic carbon) storage per unit area. Plot points are colour-coded by land-use category as Figure 4.1. Lines show the fit of the model to the data points. Note differing scales on y-axes.

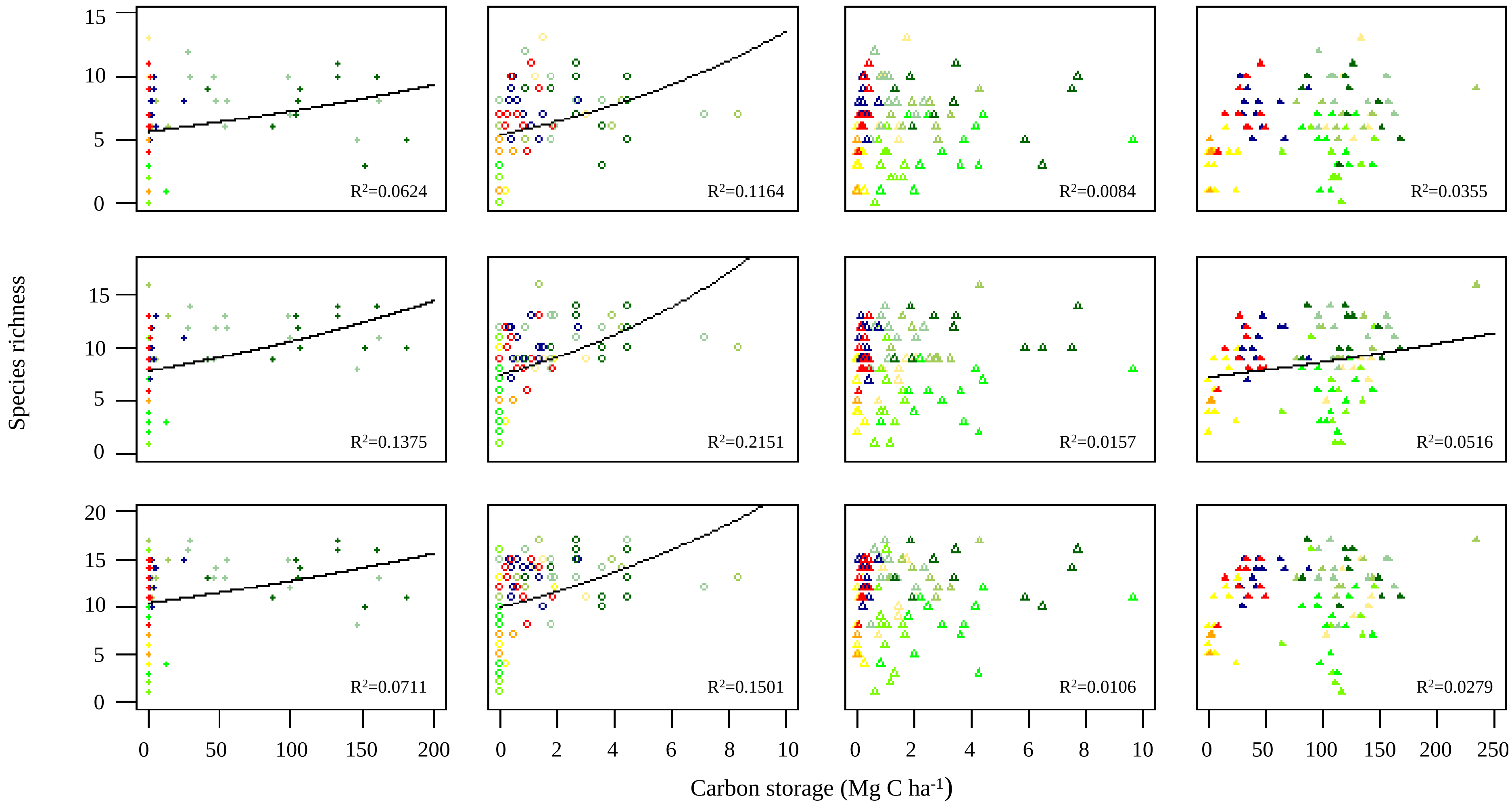

Figure 4.7 The relationship between bird species richness and tree (4 m+; filled circle, left plots), woody vegetation (1-4 m; open circle, centre-left plots), herbaceous vegetation (open triangle, centre-right plots), and soil organic (filled triangle, right plots) carbon storage. Top row shows results for wintering species richness, middle row for breeding species richness and bottom row for aggregated total species richness. Plot points are colour-coded to show land-use categories (as Figure 4.1). Model best fit lines are included for significant interactions only. Note differing scales on axes.

4.3.3 Bird diversity and the spatial relationship with carbon storage

Wintering ($\chi^2_{9,83}$=48.44, $p<0.001$) and breeding ($\chi^2_{9,83}$=47.46, $p<0.001$) bird diversity differed significantly between land-use categories. Figure 4.8 shows the median bird species diversity within each land-use category, with land-use categories presented in order of decreasing total C and SOC storage value per unit area (see Figure 4.2). As with bird species richness, the highest total C storage value land-use categories of *woodland* and *parkland* also had highest wintering and breeding bird diversity (although this was comparable in *scrub* and *allotment*), and the low total C storage land-use categories *commercial* and *urban no garden* land-use categories had relatively low winter bird diversity. However, the moderate C storage *amenity grassland* had the lowest winter bird diversity, which was significantly lower than all but *urban no garden* (see Appendix 9 for *post-hoc* test results). Along with *grassland*, *commercial* and *urban no garden*, *amenity grassland* also had one of the lowest breeding bird diversity values, but these were significantly less than *woodland* and *parkland* only. As with bird species richness, *suburban* and *urban with garden* residential land-uses had relatively high bird diversity, despite having relatively low total C storage value per unit area.

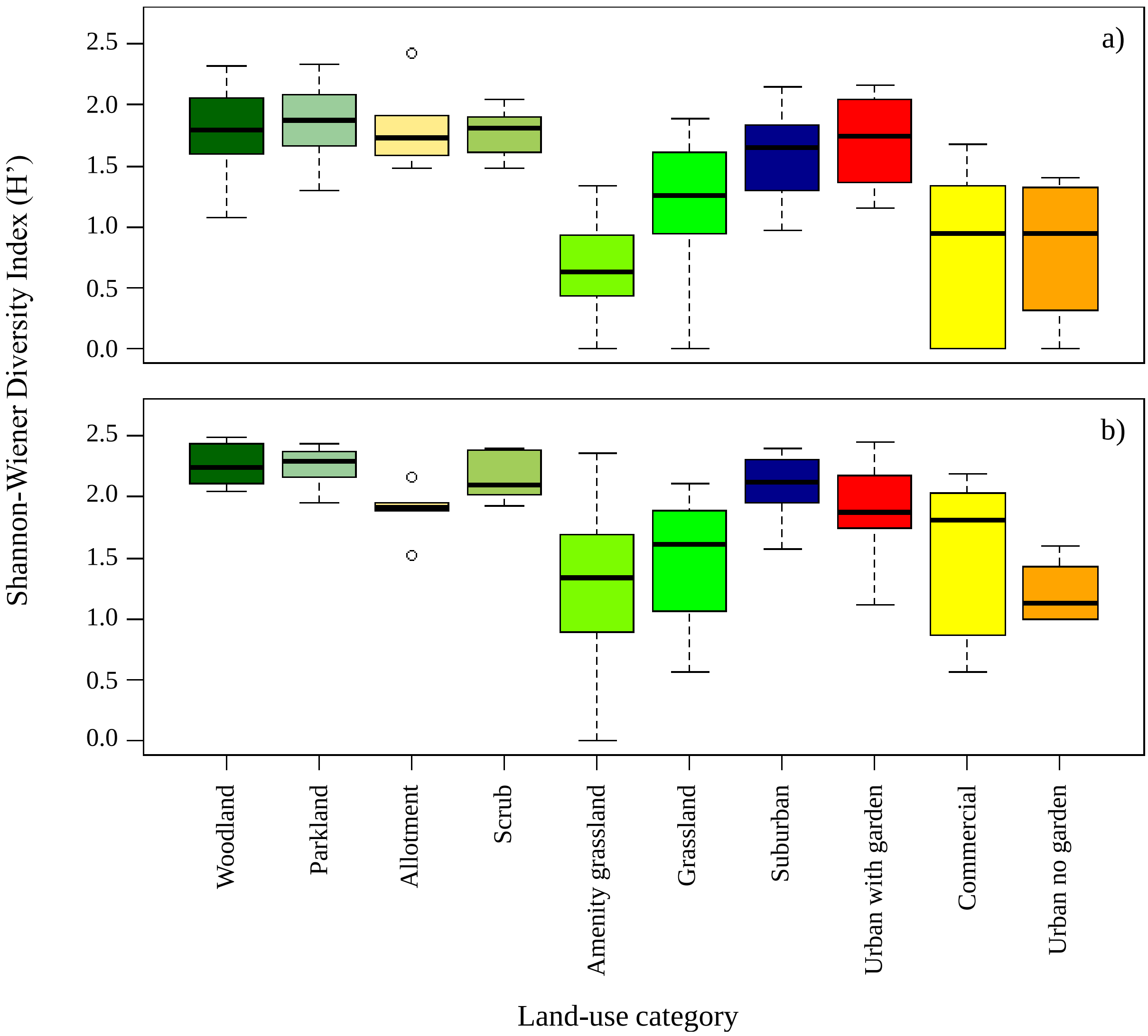

Figure 4.8 The median a) wintering, and b) breeding bird diversity, assessed by applying the Shannon-Wiener Diversity Index (H'), of urban land-use categories within Durham, UK. Boxes show where the central 50% of data lie, black bars show the median value, whiskers show maximum and minimum values, and open circles represent outliers. Land-use categories are colour-coded as Figure 4.1, and presented in order of decreasing total vegetation carbon and soil organic carbon storage value per unit area (see Figure 4.2).

There was a significant positive relationship between total vegetation C and SOC and *i*) wintering, and *ii*) breeding bird species richness (Table 4.3; Figure 4.9). Wintering and breeding bird diversity correlated positively with C storage in all four individual C pools (trees, woody vegetation, herbaceous vegetation and soils). However, the relationship with the herbaceous vegetation C pool was not significant, and the soil C pool had a significant relationship with wintering bird species richness only. Bird diversity responded most rapidly to increases in C within the woody vegetation C pool (Table 4.3; Figure 4.10). Colour-coding of the plotted points in Figures 4.9 and 4.10 emphasises an absence of correlation between C storage and bird diversity within land-use categories.

Table 4.3 Results of generalised linear models testing the relationship between *i*) wintering, and *ii*) breeding bird diversity, assessed by applying the Shannon-Wiener Diversity Index (H'), and carbon (C) storage per unit area (Mg C ha^{-1}) in different C pools in Durham, UK. Bold p-values denote significant effects at $p<0.05$.

Bird community/carbon pool	Intercept	t (91)	p	Slope	t (91)	p	R^2
Wintering birds							
Total vegetation and soils	1.1828	11.824	**<0.001**	0.0020	2.739	**0.007**	0.0762
Trees (4 m+)	1.3265	19.511	**<0.001**	0.0033	2.484	**0.015**	0.0635
Woody vegetation (1-4 m)	1.2370	17.610	**<0.001**	0.1453	4.121	**<0.001**	0.1573
Herbaceous vegetation	1.3210	16.272	**<0.001**	0.0515	1.529	0.130	0.0251
Soils	1.1991	10.127	**<0.001**	0.0024	1.996	**0.049**	0.0419
Breeding birds							
Total vegetation and soils	1.5969	17.691	**<0.001**	0.0021	3.247	**0.002**	0.1038
Trees (4 m+)	1.7310	28.910	**<0.001**	0.0044	3.760	**<0.001**	0.1345
Woody vegetation (1-4 m)	1.6642	26.412	**<0.001**	0.1471	4.652	**<0.001**	0.1921
Herbaceous vegetation	1.7673	23.682	**<0.001**	0.0405	1.307	0.194	0.0184
Soils	1.6698	15.310	**<0.001**	0.0019	1.720	0.089	0.0315

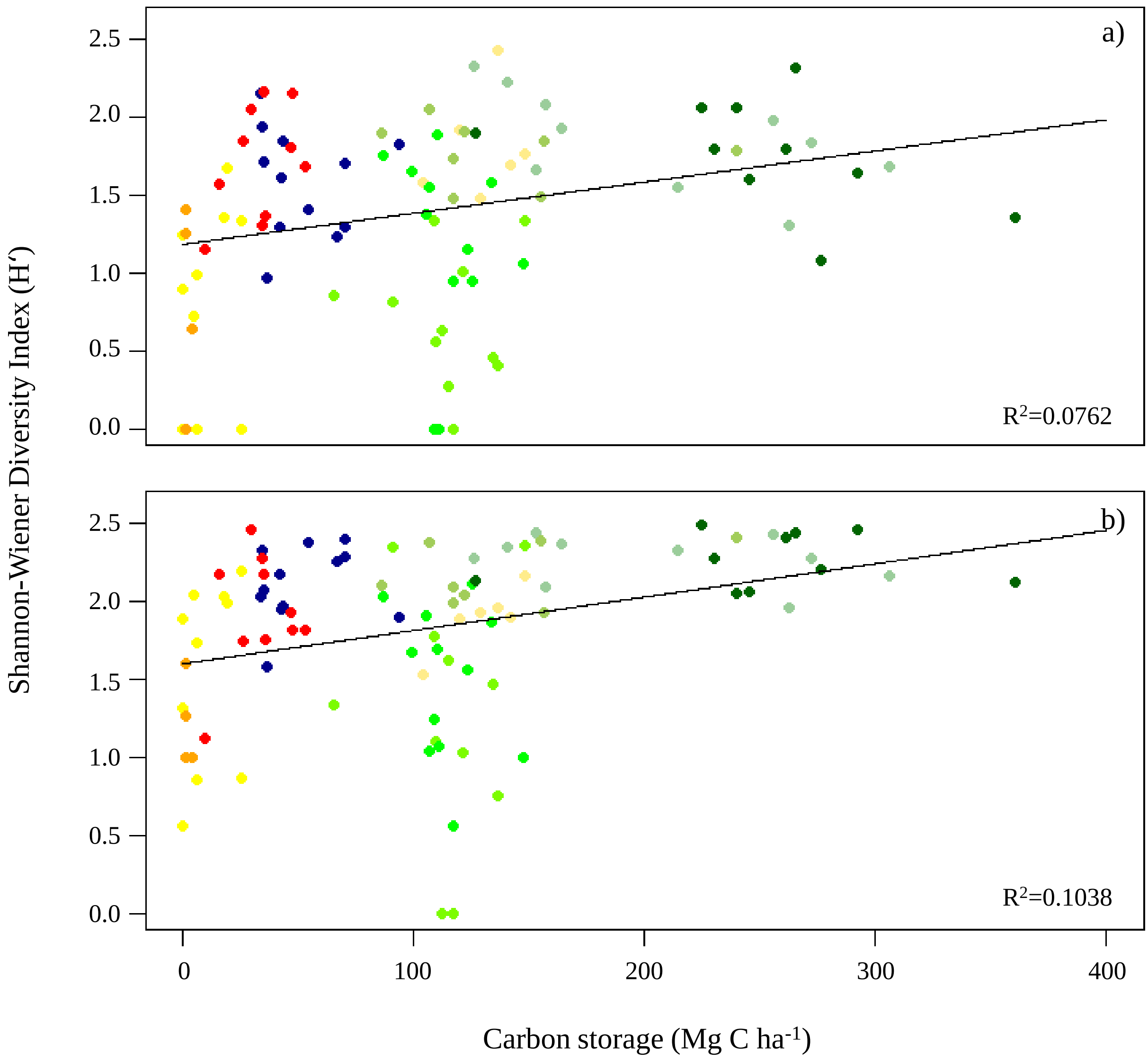

Figure 4.9 The relationship between a) wintering, and b) breeding bird diversity, assessed by applying the Shannon-Wiener Diversity Index (H'), and the total carbon (C; vegetation C plus soil organic carbon) storage per unit area. Plot points are colour-coded by land-use category as Figure 4.1. Lines show the fit of the model to the data points.

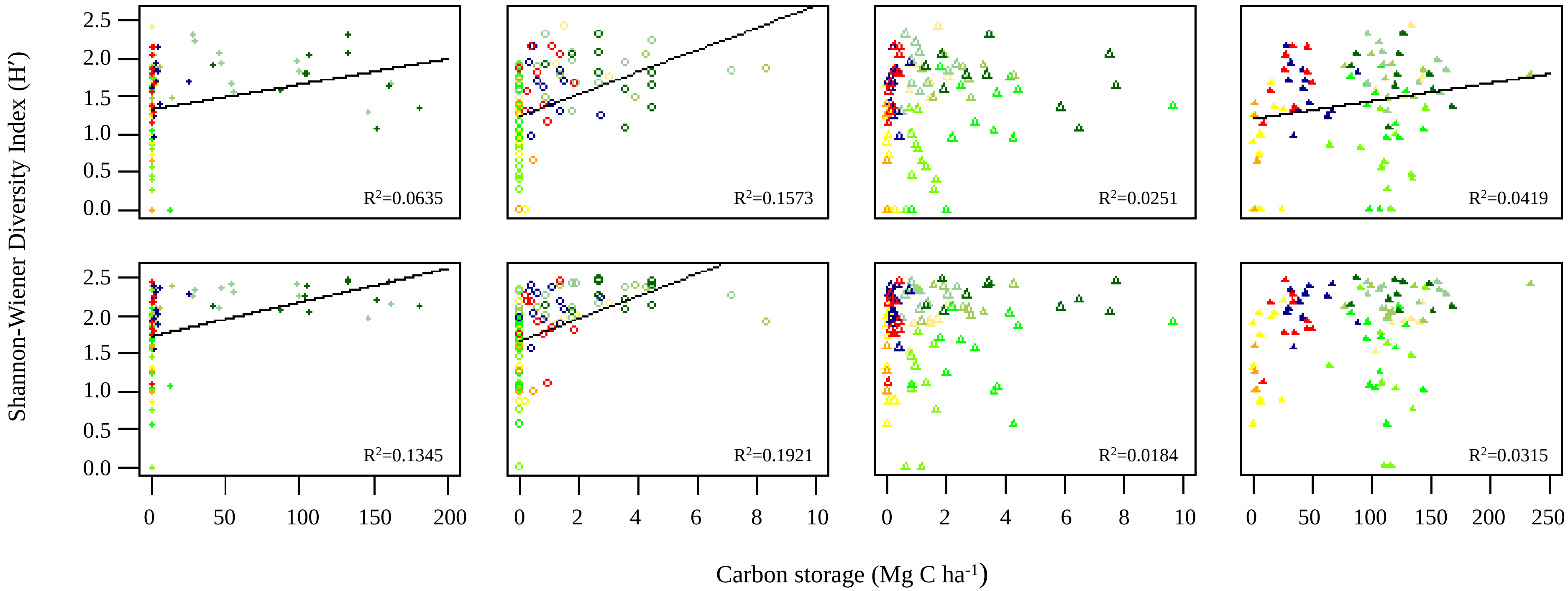

Figure 4.10 The relationship between bird diversity, assessed by applying the Shannon-Wiener Diversity Index (H'), and tree (4 m+; filled circle, left plots), woody vegetation (1-4 m; open circle, centre-left plots), herbaceous vegetation (open triangle, centre-right plots), and soil organic (filled triangle, right plots) carbon storage. Top row shows results for wintering bird diversity and bottom row for breeding bird diversity. Plot points are colour-coded to show the land-use categories as Figure 4.1, which were not included in models but are shown here to illustrate trends within them. Model best fit lines are shown for significant interactions only. Note differing scales on x-axes.

4.3.4 Principal Components Analysis and Cluster Analysis of bird communities

A Principal Components Analysis (PCA) with a specified maximum output of five Principal Components (PCs) on the correlation matrix of *i*) 37 wintering bird species and *ii*) 46 breeding bird species recorded in Durham (see Appendix 7 for a full species list), explained 61.3% and 54.2% of the variation among bird assemblages within point-count samples respectively (Appendix 10). The first two PCs, explained 35.7% and 33.3% of the variation in wintering and breeding bird assemblages respectively, and are plotted in ordination space in Figure 4.11. Many species formed dense clusters towards the centre the PCA plots, indicating that they were either equally distributed amongst land-use categories, or that they were infrequently recorded, and hence, had little influence over the first two PCs. Nevertheless, a number of species stood out as being particularly abundant within certain land-use categories. In winter, PC1 was characterised by occurrence and abundance of black-headed gull *Chroicocephalus ridibundus*, which largely reflected point-counts carried out in the *amenity grassland* and, to a lesser extent, *commercial* land-use categories (note the numerous samples representing these land-uses clustered around black-headed gull in Figure 4.11a). As such, these land-uses both provided important winter habitat for black-headed gull, which was infrequent elsewhere within the urban matrix. PC2 was mainly influenced by occurrence and abundance of common starling *Sturnus vulgaris* and Eurasian jackdaw *Corvus monedula*, and, to a lesser extent, by house sparrow *Passer domesticus* and Eurasian collared dove *Streptopelia decaocto.* This reflected point-counts carried out within the *suburban* and *urban with garden* land-uses. A second group of *suburban* and *urban with garden* point-count samples were clustered around blackbird *Turdus merula*, winter wren *Troglodytes troglodytes*, great tit *Parus major* and blue tit *Cyanistes caeruleus,* and hence, were closer to *woodland* and *parkland* point-count samples in ordination space, with many samples from the latter two land-use categories also clustered around Eurasian blackbird, winter wren and great tit. A further group of samples was clustered around carrion crow *Corvus corone* and long-tailed tit *Aegithalos caudatus*, and included all point-counts within the *grassland* land-use category, along with samples from other relatively open habitats, such as the *amenity grassland*, *scrub* and *commercial* land-uses.

Concerning the PCA carried out on breeding bird data (Figure 4.11b), PC1 was largely influenced by occurrence and abundance of common woodpigeon *Columba palumbas*, winter wren, great tit and blue tit, which were most frequently recorded in *woodland* and *parkland* relative to other land-use categories. Indeed, all point-count samples carried out within these land-use categories were clustered around these species, highlighting the similarity among samples, and the importance of the land-uses as breeding habitat for the species. PC2 was mostly influenced by common starling, house sparrow, Eurasian blackbird and Eurasian collared dove, which were most strongly associated with *suburban* and/or *urban with garden* land-use categories. Eurasian jackdaw was strongly negatively associated with both PC1 and PC2, reflecting the species' relatively low abundance in *woodland*, *parkland* and *suburban* land-use categories relative to other land-use categories, most notably, *amenity grassland*, *commercial*, *grassland* and *urban no garden*. See Appendix 10 for a full list of eigenvectors relating to these PCA.

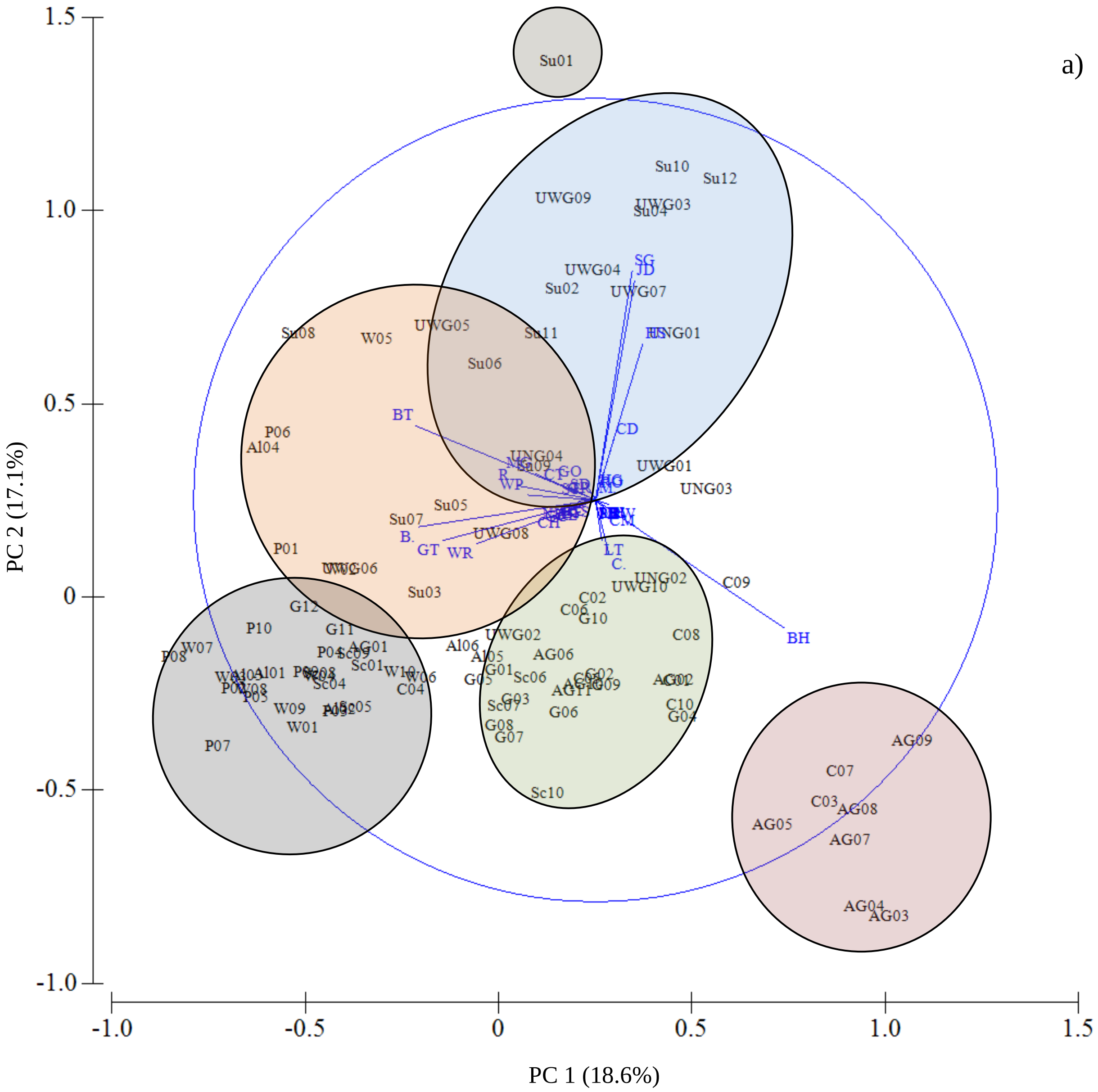

Figure 4.11 Continued overleaf

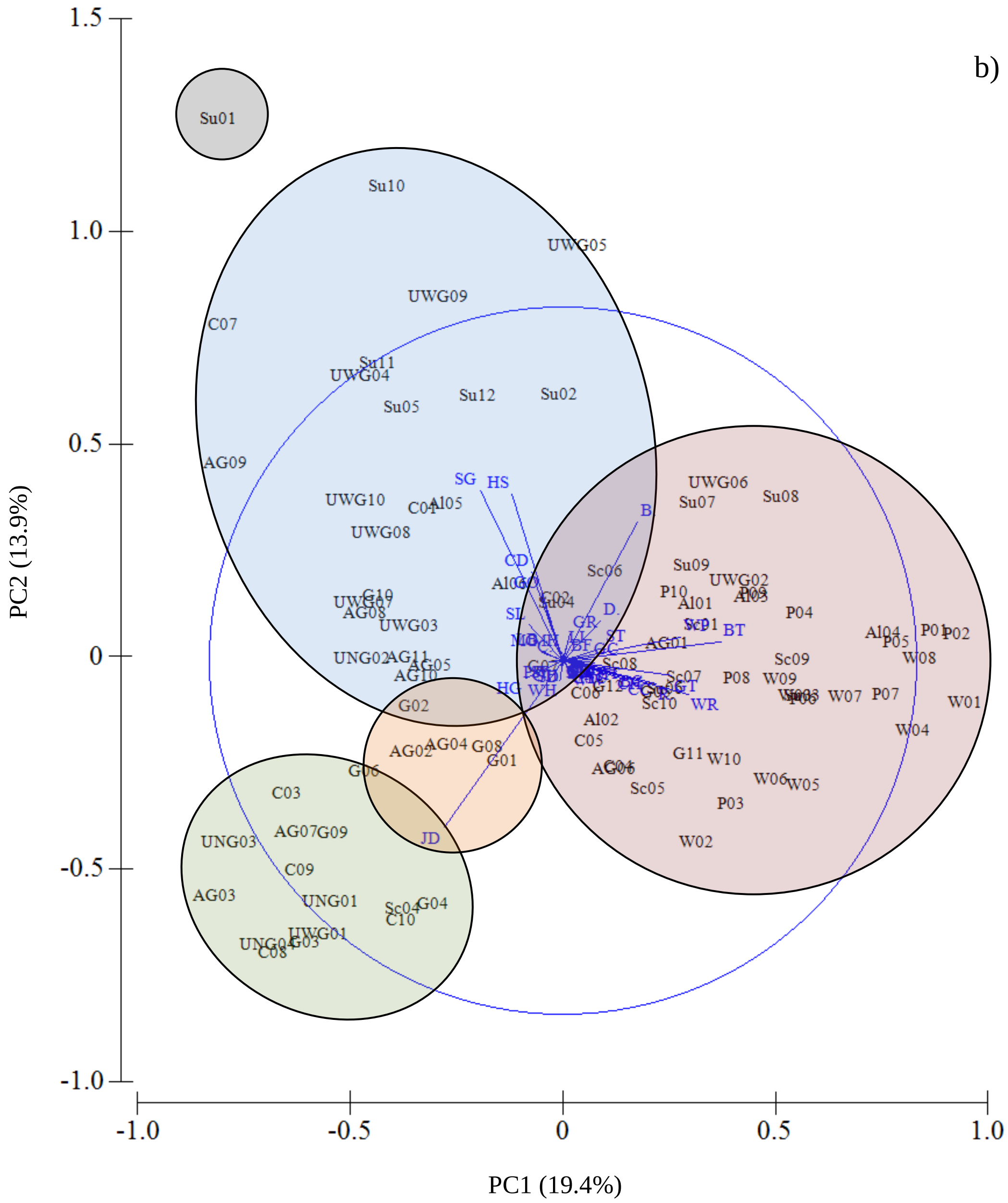

Figure 4.11 Principal Components Analysis (PCA) plot of a) wintering, and b) breeding bird communities within the city of Durham, UK, as defined by Principal Component (PC) 1 *versus* PC 2, which together account for 35.7% and 33.3% of the total variation in species occurrence and abundance in wintering and breeding bird communities respectively. Labelled point-count samples carried out in different land-use categories are shown in ordination space. Labels with prefix Al=allotment; AG=amenity grassland; C=commercial; G=grassland; P=parkland; Su=suburban; UNG=urban no garden; UWG=urban with garden; Sc=scrub; W=woodland. Species names are shown as the standard British Trust for Ornithology (BTO) codes. A complete list of codes for the species recorded in this study are included in Appendix 7. Results of Cluster Analysis (CA; group-averaging) performed on a dissimilarity matrix (Euclidean Distance [ED]) of the sample data are shown as coloured groupings of similar samples (dissimilarity level=1.35).

4.4 DISCUSSION

4.4.1 Carbon storage and bird species richness and diversity

The relationship between carbon (C) storage and bird species richness and diversity within the city of Durham was generally a positive one. Of the urban land-use categories, *woodland* and *parkland* stored the greatest total vegetation C and soil organic carbon (SOC) per unit area, owing to the many large trees, deep topsoils and a lack of impervious surfaces. Significantly, *woodland* and *parkland* were also two of the most valuable land-use categories for wintering and breeding bird species richness and diversity; indeed, Principal Components Analysis (PCA) and Cluster Analysis (CA) showed that the assemblage of birds within these two land-uses were very similar (Figure 4.11). The spatial heterogeneity of woodland in particular, with its typically complex vertical structure and diverse species composition of vegetation, is associated both with high bird species richness (Tilghman, 1987; Savard *et al*., 2000) and organic C storage (Díaz *et al*., 2009; Cavanaugh *et al*., 2014). Whilst trees were not as numerous within *parkland*, this land-use category contained many of the largest trees recorded within the study, and a greater proportion with a diameter at breast height (dbh) of 100 cm or more, and a lesser proportion of less than 25 cm, than any other land-use category (54% of all trees >100 cm dbh were recorded in *parkland*; Appendix 6). Besides being important stores of C within urban areas, large, old trees contribute disproportionately towards the high biodiversity value of urban parkland (Cornelis and Hermy, 2004; Stagoll *et al*., 2012; Le Roux *et al*., 2014; Nielsen *et al*., 2014). Older and larger trees are more likely than smaller trees to develop cavities (Carlson *et al*., 1998; Le Roux *et al*., 2014), from which hole-nesting bird species profit (Sandström *et al*., 2006). Biaduń and Zmihorski (2011) argued, in a study in Poland, that parkland tree age was more important than parkland area and degree of isolation for determining bird species richness.

Allotment and, in particular, *scrub* land-uses also contained high bird species richness and diversity in Durham, as well as containing relatively high total C storage (vegetation C plus SOC) per unit area; although far less C was stored in these land-uses than in either *woodland* or *parkland*, principally a result of there being fewer large trees in the former land-uses. *Allotments* were a valuable habitat for wintering birds, relative to other land-use categories, whereas they were relatively less important for breeding birds in the spring. This may reflect better foraging conditions and supplemental food supplies in winter, but a general lack of nesting sites in spring, when food is more widely available in other land-uses.

The highly human-modified land-use categories *urban no garden* and *commercial* had lowest total C storage values per unit area, and had consistently low C values across all C pools. This was attributable to a combination of the high proportion of impervious surfaces and built-up cover, a lack of large trees, and where they existed, shallow topsoils. These two land-use categories also had among the lowest species richness and diversity of both wintering and breeding birds, and had the two lowest aggregated species richness values. Notwithstanding the lower sampling effort relative to other land-use categories, which may have inherently lead to fewer species being detected within the *urban no garden* land-use category (see Table 4.1 for sample sizes), for those land-use categories with the highest and lowest C storage values per unit area, there was a positive correlation between C storage and bird species richness and diversity. However, the relationship was not clear-cut throughout the entire matrix of urban land-use categories.

Perhaps the most obvious contradiction in the relationship between C storage and bird species richness and diversity was in the *suburban* and *urban with garden* land-use categories. Despite being of relatively low total C storage value, these land-use categories had more or less equal wintering and breeding bird species richness and diversity to the higher C storage value *woodland* and *parkland* categories. Indeed, there was no significance in the differences between them (see Appendices 8 and 9 for Kruskal-Wallis *post-hoc* test results). However, this is consistent with the theory that, within the bounds of the urban matrix, bird diversity is often high at low to intermediate levels of urbanisation (Blair, 1996; Chase and Walsh, 2006). The collection of domestic gardens in residential land-uses offers a high level of structural diversity and micro-habitat heterogeneity, and as such, is important for urban biodiversity (Gaston *et al*., 2005; Davies *et al*., 2009; Goddard *et al*., 2010). In addition, there is a high prevalence of supplementary feeding by humans within residential areas of the UK (Cowie and Hinsley, 1988; Davies *et al*., 2012; Amrhein, 2014). The availability of supplemental food is particularly important to birds in winter, when it may strongly increase the range of species and number of individuals that visit a garden (Chamberlain *et al*., 2005; Daniels and Kirkpatrick, 2006). The potential for a subsequent increase in overwinter survival (e.g. Brittingham and Temple, 1988) could manifest in a more populous and speciose community of breeding birds the following spring (Chamberlain *et al*., 2009). Another food source in such areas is litter and edible garbage (Sandström *et al*., 2006), which is often exploited by corvids and wintering gulls (Laridae; Rock, 2005; Maciusik *et al*., 2010). Further, nest-boxes in domestic gardens provide nesting sites that would otherwise not be available for hole-nesting species (Newton, 1998; Davies *et al*., 2009), and residential architecture often provides nesting opportunities for species such as barn swallow *Hirundo rustica* (Nizynska-Bubel and Kopij, 2007), Eurasian jackdaw *Corvus monedula* (Röell, 1978), common starling *Sturnus vulgaris* and house sparrow *Passer domesticus* (Siriwardena *et al*., 2002; Evans *et al*., 2009). The latter two are species of national conservation concern (Eaton *et al*., 2009) that were infrequently recorded outside of residential land-use categories in the current study (see Appendix 7 for species lists). Indeed, the high importance of the *suburban* and *urban with garden* land-uses to common starling and house sparrow, relative to other urban land-uses, was highlighted by PCA (Figure 4.11). As supplemental feeding and provision of artificial nest sites are independent of vegetation diversity and structure, and because they are peculiar to the residential land-use categories, these factors complicate the spatial relationship between C storage and bird species richness and diversity in urban environments. However, it should be noted that within the group of residential land-use categories, with the exception of winter diversity, the relationship between C storage and bird species richness and diversity was positive (i.e. bird species richness and diversity, and total C storage per unit area were highest in *suburban* and lowest in *urban no garden*).

The benefits to urban birds provided by supplemental feeding and provision of artificial nest sites prevail in residential areas despite the potential for increased predation pressure from introduced species. The density of domestic cat *Felis catus* in urban residential areas far exceeds the maximum density of similarly-sized native carnivores in urban areas of the UK, such as red fox *Vulpes vulpes* and Eurasian badger *Meles meles* (Baker *et al*., 2008). Therefore, predation by cats is potentially a significant cause of mortality in urban bird populations. Indeed, van Heezik *et al*. (2010) have estimated that predation rates on some bird species exceed their estimated urban population sizes, and urban populations of these species persist only because they draw upon source populations located at the urban fringe. Further, over-abundance of predators may incite a *fear factor*, whereby prey behaviour, including foraging and habitat-use, is altered, resulting in reduced fecundity and marked decreases in abundances of some birds (Lima, 1987; Beckerman *et al*., 2007).

The correlations between C storage and biodiversity were relatively weak for the land-use categories of *amenity grassland* and *grassland*. Despite these land-use categories having moderate C storage value, they supported only low levels of bird species richness and diversity. In winter, these land-uses provide limited foraging for what, in northern Europe, is largely a woodland-adapted assemblage of species (Jokimäki *et al*., 2014). Indeed, many of the species recorded within these categories were associated with small patches of woody or scrubby vegetation. Exceptions to this were gulls, some corvids and common starling, which were often seen to forage on the turf of sports fields and other intensively-managed grasslands, often in large numbers. Indeed, PCA highlighted the occurrence and abundance of black-headed gull *Chroicocephalus ridibundus* in *amenity grassland* as a major source of dissimilarity in bird assemblages among point-count samples and land-use categories. Such disproportionate numbers in few species contributed towards the low Shannon-Wiener Diversity Index score of *amenity grassland*. In spring, these two land-use categories, *amenity grassland* in particular, offer limited nesting opportunities for most species. That said, *grassland* was important for breeding Afro-Palaearctic migrant warblers, many species of which have undergone population declines over recent decades (Sanderson *et al*., 2006; Ockendon *et al*., 2012), and as such, are of conservation concern. Five of the six migrant warblers recorded by this study were observed utilising this land-use category, and the UK red-listed common grasshopper-warbler *Locustella naevia* was exclusive to it. In the US, the presence of such migrant insectivorous species is considered a measure of *avifaunal quality* (see Walcott, 1974).

Although remnant natural habitat patches are often small, the matrix of land-use types and the associated small-scale changes to land cover, may promote high levels of beta-diversity in urban areas (Rebele, 1994; Niemelä, 1999). Therefore, towns and cities could potentially accommodate a greater number of bird species than equivalent-sized patches of high C storage value woodland or parkland. Indeed, although *woodland* and *parkland* together recorded 65%, 63% and 61% of all the wintering, breeding and aggregated total bird species recorded in Durham respectively, the remaining land-use categories, in decreasing order of C storage value, continued to add additional species (Figure 4.5). This was particularly true of *scrub*, which, like *grassland*, provided important habitat for breeding migratory warblers. Only when the lowest C storage value land-use categories *commercial* and *urban no garden* were reached, did species richness cease to increase; thus, implying that not only are these land-uses of lowest C storage value, but they also add little or nothing to beta-diversity. Indeed, there were no wintering or breeding species recorded exclusively within the *urban no garden* land-use category (Figure 4.5). In order to maximise C storage within the urban matrix, retention of urban land-use categories with higher C storage value per unit area should be preferred over that of categories with lower C storage value. However, increasing urban C storage through increasing woodland habitat may not be beneficial to overall urban bird species richness if this is achieved at the expense of lesser C storage value scrub and grassland habitats.

On a regional scale, the abundance of individuals within species recorded by the point-count samples across the city of Durham were unremarkable, and, in general, reflected relative regional abundances (*cf*. Westerberg and Bowey, 2000; Bowey and Newsome, 2012). Notable exceptions however, include Eurasian collared dove *Streptopelia decaocto* (2.8k pairs), house sparrow (25k pairs), common starling (20k pairs) and European goldfinch *Carduelis carduelis* (3k pairs), which were arguably recorded in greater numbers within the city than suggested by their estimated abundances for County Durham (shown in parentheses) as per Bowey and Newsome (2012). This likely reflected these species' affinity with urban and man-made environments (e.g. Coombs *et al*., 1981; Siriwardena *et al*., 2002; Evans *et al*., 2009). Another, and perhaps more intriguing, exception was the case with willow warbler *Phylloscopus trochilus* and common chiffchaff *P. collybita*, two closely-related migratory congeners. The willow warbler has far greater estimated county abundance than common chiffchaff (28k pairs *vs* 7.1k pairs; Westerberg and Bowey, 2000), but was recorded far less within Durham city during this study (8 records *vs* 35 records; Appendix 7). The former species is also reported to frequent a greater variety of habitat types (Saether, 1983; Simms, 1985), but the opposite was found within Durham city; willow warbler was confined to *scrub*, but common chiffchaff was recorded, in order of deceasing abundance, within the *parkland*, *scrub* and *woodland* land-uses (Appendix 7). The reasons behind this apparent contradiction are not clear, but it may be that current management of parkland and woodland trees within the city better suits common chiffchaff, which shows a greater dependence on mature trees (Simms, 1985), whereas the willow warbler is principally seen in earlier seral stages (Saether, 1983). Alternatively, as the two species are ecologically very similar and are inter-specifically aggressive in sympatry (Simms, 1985), the fractionally smaller common chiffchaff (Simms, 1985) may be competitively excluded from woodland habitats in the wider landscape, and congregate in what could be perceived as inferior habitats within the city.

When generalised linear models (GLMs) testing for relationships between C storage and *i*) bird species richness, and *ii*) bird diversity, included land-use as a categorical explanatory variable, there was no significance in the slopes of the relationships (see methodology, section 4.2.6.3). That is to say, that there were no correlations between C storage and bird species richness and diversity within any of the land-use categories, and regardless of the C storage value of, for example, a *woodland* quadrat, it supported no more species, or had no greater diversity, than any other *woodland* quadrat. Further, these GLMs did not reveal any significant interactions between C storage per unit area and land-use category; thus, bird species richness and diversity responded similarly to increasing C storage within all land-use categories. However, when GLMs were run omitting land-use as a categorical explanatory variable, there were significant positive relationships between C storage and wintering, breeding and aggregated total bird species richness (Table 4.2) and diversity (Table 4.3). This showed that locations within the urban matrix with higher total C storage value per unit area were also those with greater bird species richness and diversity. These locations tended to be within *woodland* and *parkland*, but it was the land-use *per se*, rather than the variation in C storage within it, that promoted bird species richness and diversity. When bird species richness and diversity were related to the component C pools separately, consistent positive relationships were found with increasing tree and, in particular, woody vegetation C storage. This reinforces the view that increased biomass of trees, understory, scrub and other woody vegetation, provides valuable habitat for birds. Relationships with herbaceous vegetation C and SOC were weakly positive, and often insignificant (Table 4.2 and 4.3); therefore, the biomass and cover of herbaceous vegetation, and soil cover and depth, had little influence over bird species richness and diversity.

4.4.2 Conclusions and implications for urban planning

In general, the relationship between C storage and bird species richness and diversity within the the city of Durham was a positive one, and provided that bird diversity does indeed act as a biodiversity indicator in urban areas, then a positive relationship may also hold between C storage and biodiversity as a whole. Sequestering and storing C, especially within woody vegetation and trees, should benefit biodiversity by maintaining or creating a larger area of habitat suitable for species. *Woodland* was the most beneficial land-use for C storage, whilst also providing habitat for a more speciose and diverse community of birds than any other urban land-use. However, approximately half of all species recorded within the entire urban matrix were not recorded in *woodland* (Figure 4.5), and the current diversity of land-use types within the urban matrix of Durham is required to maintain beta-diversity amongst urban birds; but diversity in land-use types may compromise the C storage capacity of the urbanised area.

Certain studies have argued that densification of built-up areas can benefit biodiversity at the city-scale rather than sprawling, low-density development (e.g. Sandström *et al*., 2006; Sushinsky *et al*., 2013). This works on the premise that high-density housing is clustered with large interstitial areas of greenspace, which maintain functional areas of habitat for biodiversity and urban-sensitive species. Such spatial configuration could also optimise urban C storage capacity. However, in the UK, increasing greenspace patch size will be difficult to achieve (Evans *et al*., 2009), as the design and infrastructure of many towns and cities is already established (Breheny, 1997). Alternatively, conservation efforts could concentrate on those species most adapted to urban environments at the expense of those that may gain greater benefit from conservation efforts in rural environments (Evans *et al*., 2009). Perhaps the most notable species that could potentially gain from such a planning strategy are common starling and house sparrow. In north-east England, densities of the former species have been estimated at 243 birds and 168 birds per km^2 of urban and suburban habitat respectively, compared to just 16 birds per km^2 of arable habitat in the same region (Robinson *et al*., 2002); likewise, urban and suburban densities of house sparrow have been estimated at 237 birds and 349 birds per km^2 respectively, compared to 26 birds per km^2 of arable habitat (Siriwardena *et al*., 2002). Considering results from the present study, this planning strategy could potentially involve retention of low- to moderate-density housing and garden space, as these residential land-uses support a greater abundance and diversity of *suburban adaptors* (*sensu* Blair and Launer, 1997) over high-density housing. New-build could take place on existing areas of scrub, grassland and amenity grassland, as these land-uses are of moderate C storage value only, whilst high C value woodland and parkland are retained to mitigate urban C emissions. However, given the projected increases in urban human populations, this approach would likely mean a prompt return to urban encroachment upon rural areas, which challenges current UK policy aimed at urban densification. In view of such conflicts, an alternative and perhaps controversial strategy could be to relinquish urban C storage and biodiversity conservation efforts altogether, and instead, concentrate on potentially greater opportunities to address these issues within the surrounding countryside.

The intensification of farming practices in the UK following the introduction of the Common Agricultural Policy (CAP) in 1947, and the consequent increases to productivity (Matson *et al.*, 1997), has promoted a gradual decrease in the area of land devoted to agricultural production (Bibby, 2009). Although some of the decrease has accommodated the growth in urban land-uses, it has also released rural land for reforestation and afforestation. Indeed, the forested area of the UK has doubled since 1947 (Forestry Commission, 2014), and a considerable portion of the increase has occurred on agricultural land (Freibauer *et al*., 2004; Bibby, 2009). Therefore, compaction of urban agglomerations into small, explicit areas should benefit regional C stores by making yet more rural land available, where management for C storage can yield greater gains through its potential for reforestation and hedgerow preservation, with potentially positive side-effects on regional biodiversity.

It is apparent that there is not a *win-win* situation (*sensu* Rosenzweig, 2003), whereby covariance between C storage and biodiversity is optimised in urban areas. Exactly where compromises should occur, and what the most effective and efficient conservation strategy is, remains unclear. Initially, biodiversity priorities in urban environments will require urgent assessment (i.e. should efforts concentrate on conserving the species best adapted to urban environments, or should they aim to maximise beta-diversity across the urban matrix?), then the most effective planning policy for conserving both urban biodiversity and C storage can be established, with results from the present study acting as a guide. Finally, the decisions made will also demand consideration for the continued health and well-being of urban human populations, and this will require additional greenspace and amenity land (see Bolund and Hunhammar, 1999; Fuller *et al*., 2007), putting further pressure on the finite area of land available.

Chapter 5:
Final conclusions and future challenges

The Millennium Ecosystem Assessment (MA, 2005a) carried ecosystem service science into the fore by highlighting human-induced degradation and loss of services, and the significance of these losses for humanity. The MA recognised that service delivery is intrinsically linked to biodiversity, and following failure to meet the Convention on Biological Diversity (CBD) 2010 targets, ecosystem services were incorporated into the revised 2020 targets. The adoption of an ecosystem services approach to biodiversity conservation is intended to allow for an economic value to be placed upon biodiversity that can be recognised by governments and decision-makers, and should provide an incentive to protect biodiversity and broaden the diversity of support. One of the major mechanisms driving biodiversity and ecosystem service loss is land-use change by urbanisation. As global urban human populations are set to continue increasing into the foreseeable future, the effect of urbanisation on biodiversity, ecosystem services and ultimately, human well-being is an increasingly important area of scientific research. Land-use change is also a major source of atmospheric greenhouse gas (GHG) emissions and subsequent climate change forcing. Consequently, the Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC) makes a provision for some signatories to report land-use change activities. Carbon (C) storage is considered a regulating ecosystem service, as it alleviates the rate of climate change by reducing atmospheric carbon dioxide (CO_2), the primary GHG emitted through human activities. In this thesis, I have studied the effect that land-use change by urbanisation has on C storage, and the potential for spatial congruence between C storage and biodiversity in representative towns and cities of north-east England, with a view to inform on the feasibility of an ecosystem services approach to conserving C and biodiversity in urban areas. The key results and findings were:

- The contiguous urban extent of Darlington, Durham and Newcastle increased considerably between 1945 and the present, by 67%, 229% and 65% respectively.
- The increases in contiguous urban extent reduced the C storage capacity of each of the study areas by approximately one third.
- Decreases in C storage were caused by loss of agriculture and replacement with urban land-uses of lower C storage value per unit area, most notably, low- to moderate-density residential and commercial land-uses.
- Most of the C lost was from the soils of the study areas, as the surface area occupied by soil, and soil depth, are reduced in urban land-uses compared to agriculture.
- There was a degree of spatial congruence between C storage and bird species richness and diversity within the city of Durham. Land-uses with highest C storage value per unit area also tended to have highest species richness and diversity, and land-uses with lowest C storage value tended to have lowest species richness and diversity. However, low- to moderate-density residential land-uses had high species richness and diversity despite having relatively low C storage value.
- The current mix of urban land-use categories, of varying C storage value, increased beta-diversity across the urban matrix of Durham.
- When not categorised by land-use, there were significant positive spatial relationships between total vegetation C and soil organic carbon (SOC) storage, and *i*) bird species richness and *ii*) bird diversity in Durham.
- The C storage value of trees (4 m+) and, in particular, woody vegetation (1-4 m), had significant positive relationships with bird species richness and diversity. Although

positive, the relationships between the value of the soil and herbaceous vegetation C pools and bird species richness and diversity were weak.

- Principal Components Analysis (PCA) revealed similarities between some land-use categories in their wintering and/or breeding bird communities; notably, *commercial* was similar to *amenity grassland*, *suburban* was similar to *urban with garden*, and *woodland* was similar to *parkland*. There appeared to be some divergence between the communities of built-up land-uses and those of semi-natural greenspace.

My results and findings have highlighted trade-offs when addressing C emissions and biodiversity targets in urban areas. In Chapter Two I demonstrated that to revert to the planning policy of the decades following the end of the Second World War (thus, to promote expansion of low- to moderate-density housing into surrounding rural landscapes) would result in considerable C loss in the area occupied. However, in Chapter Four, I showed that low- to moderate-density housing is more beneficial for urban biodiversity than high-density housing. These results provoke the urban densification *versus* urban sprawl debate (e.g. Breheny, 1997; Lin and Fuller, 2013), as low-density housing (i.e. *suburban*) was found to have greater C storage capacity and biodiversity value than high-density housing (i.e *urban no garden*), which offered little or nothing in both respects; but, as low-density housing requires more area, it promotes urban expansion and encroachment into surrounding rural landscapes, and within the urban matrix, it occupies land that could otherwise accommodate greenspace with higher C storage and biodiversity value, such woodland, parkland or scrub.

Of the urban land-use categories, I found that woodland and parkland had greatest C storage value, and increasing the area devoted to these would be the most desirable option to optimise urban C storage capacity, which would also benefit many species. However, heterogeneity within and among urban greenspaces is necessary to maintain beta-diversity across the entire urban landscape, and this would require retention of moderate C storage value scrub and grassland, thus, compromising on the C storage potential of the urbanised area. In general, woodland and parkland habitat did increase within my three study areas between 1945 and the present, but this did not translate into increases in the percentage of the urbanised area occupied by these habitats. For example, in Durham, there was a 59 ha increase (+89.7%) in woodland between 1945 and 2009 (see Chapter 2, Figure 2.1), but the percentage cover of woodland in 2009 was just 8% of the land occupied by the urbanised area, compared to 14% in 1945. So, although the area of habitat with high C storage and biodiversity value may increase within urban areas over time, as urban areas expand, these semi-natural habitats may become smaller relative to the area of land occupied by the surrounding matrix of built environment. Hence, semi-natural habitat becomes increasingly vulnerable to edge-effects (Breuste *et al*., 2008; Isaac *et al*., 2014) and isolation, both from other urban greenspaces and from the rural landscape at the urban fringe (see Chapter 2, Figure 2.2). That said, prior studies on urban birds have shown that the spatial location and isolation of greenspace is of less importance to species richness and diversity than greenspace area and vegetation age and structure (Jokimäki, 1999; Fernández-Juricic, 2000; Chamberlain *et al*., 2007), and therefore, large, established areas of greenspace should be retained. Birds however, have reduced dispersal limitations relative to many other taxonomic groups, and in this instance they may not provide a wholly reliable proxy for biodiversity. Some animal groups, for example, large-bodied or flightless invertebrates (Sadler *et al*., 2006), and small- to medium-sized mammals (Angold *et al*., 2006), may be more susceptible to isolation, and a system of corridors between greenspaces should be established and maintained to promote diversity among poorly dispersing taxa in expanding urban environments. In this respect, there is particular scope to increase the permeability of commercial development to wildlife. The area devoted to commercial land-use increased significantly within all three of my study areas (Chapter 2, Figure 2.1), and much of this increase took place at the urban fringe (Chapter 2, Figure 2.2).

Patches of greenspace within commercial areas were typically restricted to lawn and low, shrubby vegetation, but by incorporating more woody vegetation and trees within their design, the potential for commercial developments to act as wildlife refuges, corridors and areas of species exchange at the urban/rural interface could be vastly improved. Also, given that their location is often at the urban fringe, new commercial areas, as well as peripheral housing estates, are ideally placed to incorporate remnant semi-natural vegetation into their design.

Our challenge now and for the future is to manage our urban areas in such a way that they not only continue to sequester and store C, but that they also retain, or preferably improve upon, current levels of biodiversity. Further to these demands, our urban areas must also provide the ecosystem services and set of physical conditions that maintain the well-being of their human inhabitants, whilst also preserving our rural heritage and the area of land devoted to food production. This is a tall order, and if, as my thesis predicts, this is not achievable within the finite area of land available, we must be prepared to make compromises. This could include prioritising *urban exploiters* or *suburban adaptors* in urban biodiversity conservation strategies, or retaining urban greenspace valuable to biodiversity but with sub-optimal C storage value, or reducing the space per capita by clustering high-density residential and commercial land-uses within the urban matrix.

Ultimately, it is likely that human health and well-being will hold political sway, and that this will be the over-riding factor in our decisions concerning land use and land-use change; but we must not fail to acknowledge the roles that C storage and biodiversity play in achieving this. Past decisions concerning land-use change may have been made whilst ignorant of their consequences, but we can no longer use this argument in defence of our actions; we now have greater understanding of what we must and must not do. If we do not meet our commitment to alleviate climate change by reducing C emissions release, and if we fail once more in our attempts to halt biodiversity loss, it will be because we have lacked the desire and the incentive to do so.

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Appendices

List of Appendices

Appendix 1 Allometric equations used to estimate tree biomass.

Species recorded	Equation						
	Species	Formula	a	b	c	d	Reference
Pseudotsuga sp.	*Pseudotsuga menziesii*	$AB=aD^b$	0.0808	2.5282	-	-	Ter-Mikaelian and Korzukhin (1997)
Acer campestre	*Acer saccharum*	$AB=aD^b$	0.1008	2.5735	-	-	Ter-Mikaelian and Korzukhin (1997)
Acer pseudoplatanus	*Acer saccharum*	$AB=aD^b$	0.1008	2.5735	-	-	Ter-Mikaelian and Korzukhin (1997)
Acer sp.	*Acer saccharum*	$AB=aD^b$	0.1008	2.5735	-	-	Ter-Mikaelian and Korzukhin (1997)
Aesculus hippocastanum	*Aesculus indica*	$\ln(AB)=a+b(\ln(D))$	2.6572	0.9451	-	-	Adhikari *et al*. (1995)
Alnus cordata	*Alnus glutinosa*	$AB=aD^b$	0.0003090	2.022126	-	-	Zianis *et al*. (2005)
Alnus glutinosa	*Alnus glutinosa*	$AB=aD^b$	0.0003090	2.022126	-	-	Zianis *et al*. (2005)
Betula pendula	*Betula pendula*	$AB=aD^b$	0.00087	2.28639	-	-	Zianis *et al*. (2005)
Betula sp.	*Betula pendula*	$AB=aD^b$	0.00087	2.28639	-	-	Zianis *et al*. (2005)
Carpinus betulus	*Ulmus americana*	$AB=aD^b$	0.0825	2.468	-	-	Ter-Mikaelian and Korzukhin (1997)
Carpinus sp.	*Ulmus americana*	$AB=aD^b$	0.0825	2.468	-	-	Ter-Mikaelian and Korzukhin (1997)
Castanea sativa	*Fagus sylvatica*	$AB=aD^b$	0.1143	2.503	-	-	Zianis *et al*. (2005)
Chamaecyparis sp.	*Chamaecyparis nootkatensis*	$AB=aD^b$	0.2498	2.1118	-	-	Ter-Mikaelian and Korzukhin (1997)
Coniferous	Coniferous	$AB=aD^b$	7.295	1.395	-	-	Davies *et al*. (2011)
Corylus avellana	*Betula pendula*	$AB=aD^b$	0.00087	2.28639	-	-	Zianis *et al*. (2005)
Crataegus monogyna	*Sorbus aucuparia*	$AB=aD^bH^c$	0.0634	2.1552	0.2877	-	Snorrason and Einarsson (2006)
Cupressus leylandii	*Chamaecyparis nootkatensis*	$AB=aD^b$	0.2498	2.1118	-	-	Ter-Mikaelian and Korzukhin (1997)
Deciduous	Deciduous	$AB=aH^b$	0.566	2.315	-	-	Davies et al. (2011)
Eucalyptus sp.	*Eucalyptus* spp.	$\ln(AB)=a+b(\ln(D))$	-1.762	2.2644	-	-	Zianis *et al*. (2005)
Fagus sp.	*Fagus sylvatica*	$AB=aD^b$	0.1143	2.503	-	-	Zianis *et al*. (2005)
Fagus sylvatica	*Fagus sylvatica*	$AB=aD^b$	0.1143	2.503	-	-	Zianis *et al*. (2005)
Fraxinus excelsior	*Fraxinus americana*	$AB=aD^b$	0.1063	2.4798	-	-	Ter-Mikaelian and Korzukhin (1997)

Species recorded	Equation						
	Species	Formula	a	b	c	d	Reference
Fraxinus sp.	*Fraxinus americana*	$AB=aD^{b}$	0.1063	2.4798	-	-	Ter-Mikaelian and Korzukhin (1997)
Ilex sp.	*Ilex dipyrena*	$AB=a+b(\ln(D))$	0.7752	0.906	-	-	Adhikari *et al*. (1995)
Laburnum sp.	Deciduous	$AB=aH^{b}$	0.566	2.315	-	-	Davies *et al*. (2011)
Larix decidua	*Larix laricina*	$AB=aD^{b}$	0.1359	2.298	-	-	Ter-Mikaelian and Korzukhin (1997)
Laurus nobilis	Deciduous	$AB=aH^{b}$	0.566	2.315	-	-	Davies *et al*. (2011)
Malus sp.	*Sorbus aucuparia*	$AB=aD^{b}H^{c}$	0.0634	2.1552	0.288	-	Snorrason and Einarsson (2006)
Pinus ponderosa	*Pinus sylvestris*	$AB=a(D+1)^{[b+c*\log(D)]}H^{d}$	0.0146	2.3868	-0.0618	0.8581	Zianis et al. (2005)
Pinus sp.	*Pinus sylvestris*	$AB=a(D+1)^{[b+c*\log(D)]}H^{d}$	0.0146	2.3868	-0.0618	0.8581	Zianis et al. (2005)
Pinus sylvestris	*Pinus sylvestris*	$AB=a(D+1)^{[b+c*\log(D)]}H^{d}$	0.0146	2.3868	-0.0618	0.8581	Zianis et al. (2005)
Populus balsamifera	*Populus trichocarpa*	$AB=aD^{b}H^{c}$	0.0717	1.8322	0.6397	-	Zianis et al. (2005)
Populus canescens	Salicaceae (incl. poplars)	$AB=aD^{b}$	0.0616	2.5094	-	-	Ter-Mikaelian and Korzukhin (1997)
Populus nigra x	Salicaceae (incl. poplars)	$AB=aD^{b}$	0.0616	2.5094	-	-	Ter-Mikaelian and Korzukhin (1997)
Populus sp.	Salicaceae (incl. poplars)	$AB=aD^{b}$	0.0616	2.5094	-	-	Ter-Mikaelian and Korzukhin (1997)
Populus tremula	*Populus tremula*	$AB=aD^{b}$	0.0519	2.5450	-	-	Zianis *et al*. (2005)
Prunus avium	*Prunus serotina*	$AB=aD^{b}$	0.0716	2.6174	-	-	Ter-Mikaelian and Korzukhin (1997)
Prunus laurocerasus	*Prunus serotina*	$AB=aD^{b}$	0.0716	2.6174	-	-	Ter-Mikaelian and Korzukhin (1997)
Prunus sp.	*Prunus serotina*	$AB=aD^{b}$	0.0716	2.6174	-	-	Ter-Mikaelian and Korzukhin (1997)
Quercus cerris	*Quercus rubra*	$AB=aD^{b}$	0.1130	2.4572	-	-	Ter-Mikaelian and Korzukhin (1997)
Quercus petraea	*Quercus rubra*	$AB=aD^{b}$	0.1130	2.4572	-	-	Ter-Mikaelian and Korzukhin (1997)
Quercus robur	*Quercus rubra*	$AB=aD^{b}$	0.1130	2.4572	-	-	Ter-Mikaelian and Korzukhin (1997)
Quercus rubra	*Quercus rubra*	$AB=aD^{b}$	0.1130	2.4572	-	-	Ter-Mikaelian and Korzukhin (1997)
Quercus sp.	*Quercus rubra*	$AB=aD^{b}$	0.1130	2.4572	-	-	Ter-Mikaelian and Korzukhin (1997)
Rhododendron sp.	Deciduous	$AB=aH^{b}$	0.566	2.315	-	-	Davies *et al*. (2011)
Robinia pseudoacacia	*Fraxinus americana*	$AB=aD^{b}$	0.1063	2.4798	-	-	Ter-Mikaelian and Korzukhin (1997)

Species recorded	Equation						
	Species	Formula	a	b	c	d	Reference
Salix alba	Salicaceae	$AB=aD^b$	0.0616	2.5094	-	-	Ter-Mikaelian *et al*. (1997)
Salix capraea	Salicaceae	$AB=aD^b$	0.0616	2.5094	-	-	Ter-Mikaelian *et al*. (1997)
Salix cinerea	Salicaceae	$AB=aD^b$	0.0616	2.5094	-	-	Ter-Mikaelian *et al*. (1997)
Salix sp.	Salicaceae	$AB=aD^b$	0.0616	2.5094	-	-	Ter-Mikaelian *et al*. (1997)
Sambucus nigra	Deciduous	$AB=aH^b$	0.566	2.315	-	-	Davies *et al*. (2011)
Sorbus aria	*Sorbus aucuparia*	$AB=aD^bH^c$	0.0634	2.1552	0.2877	-	Snorrason and Einarsson (2006)
Sorbus aucuparia	*Sorbus aucuparia*	$AB=aD^bH^c$	0.0634	2.1552	0.2877	-	Snorrason and Einarsson (2006)
Sorbus x intermedia	*Sorbus aucuparia*	$AB=aD^bH^c$	0.0634	2.1552	0.2877	-	Snorrason and Einarsson (2006)
Taxus baccata	*Tsuga canadensis*	$AB=aD^b$	0.0622	2.4500	-	-	Ter-Mikaelian *et al*. (1997)
Tilia sp.	*Tilia cordata*	$ABW=a+b(\ln(D))$	-2.6788	2.4542	-	-	Zianis *et al*. (2005)
Ulmus glabra	*Ulmus americana*	$AB=aD^b$	0.0825	2.4680	-	-	Ter-Mikaelian *et al*. (1997)
Ulmus sp.	*Ulmus americana*	$AB=aD^b$	0.0825	2.4680	-	-	Ter-Mikaelian *et al*. (1997)

AB=Total above-ground biomass (incl. foliage)

ABW=Above-ground woody biomass (excl. Foliage)

D=diameter at breast height as measured in the field

H=Canopy height as measured in the field

Appendix 2 Kruskal-Wallis *post-hoc* test results for difference in carbon stored per unit area among land-use categories in Darlington, Durham and Newcastle.

a) Total vegetation carbon and soil organic carbon storage

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Agriculture: Crop/pasture	Allotment	21.806	96.048	FALSE
Agriculture: Crop/pasture	Amenity Grassland	15.794	73.439	FALSE
Agriculture: Crop/pasture	Commercial	117.598	69.309	TRUE
Agriculture: Crop/pasture	Grassland	0.087	72.606	FALSE
Agriculture: Crop/pasture	Agriculture: hedgerow	51.627	80.549	FALSE
Agriculture: Crop/pasture	Parkland	41.898	74.348	FALSE
Agriculture: Crop/pasture	Scrub	13.694	73.439	FALSE
Agriculture: Crop/pasture	Suburban	68.106	66.983	TRUE
Agriculture: Crop/pasture	Urban no garden	125.944	80.549	TRUE
Agriculture: Crop/pasture	Urban with garden	84.544	73.439	TRUE
Agriculture: Crop/pasture	Woodland	66.008	72.606	FALSE
Allotment	Amenity Grassland	37.600	94.559	FALSE
Allotment	Commercial	139.404	91.388	TRUE
Allotment	Grassland	21.893	93.914	FALSE
Allotment	Agriculture: hedgerow	29.821	100.181	FALSE
Allotment	Parkland	20.092	95.267	FALSE
Allotment	Scrub	35.500	94.559	FALSE
Allotment	Suburban	89.911	89.638	TRUE
Allotment	Urban no garden	147.750	100.181	TRUE
Allotment	Urban with garden	106.350	94.559	TRUE
Allotment	Woodland	44.202	93.914	FALSE
Amenity grassland	Commercial	101.804	67.230	TRUE
Amenity grassland	Grassland	15.707	70.624	FALSE
Amenity grassland	Agriculture: hedgerow	67.421	78.767	FALSE
Amenity grassland	Parkland	57.692	72.414	FALSE
Amenity grassland	Scrub	2.100	71.480	FALSE
Amenity grassland	Suburban	52.311	64.830	FALSE
Amenity grassland	Urban no garden	110.150	78.767	TRUE
Amenity grassland	Urban with garden	68.750	71.480	FALSE
Amenity grassland	Woodland	81.802	70.624	TRUE
Commercial	Grassland	117.511	66.319	TRUE
Commercial	Agriculture: hedgerow	169.225	74.931	TRUE
Commercial	Parkland	159.496	68.222	TRUE
Commercial	Scrub	103.904	67.230	TRUE
Commercial	Suburban	49.493	60.111	FALSE
Commercial	Urban no garden	8.346	74.931	FALSE
Commercial	Urban with garden	33.054	67.230	FALSE
Commercial	Woodland	183.606	66.319	TRUE
Grassland	Agriculture: hedgerow	51.714	77.991	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Grassland	Parkland	41.985	71.569	FALSE
Grassland	Scrub	13.607	70.624	FALSE
Grassland	Suburban	68.018	63.884	TRUE
Grassland	Urban no garden	125.857	77.991	TRUE
Grassland	Urban with garden	84.457	70.624	TRUE
Grassland	Woodland	66.095	69.757	FALSE
Agriculture: hedgerow	Parkland	9.729	79.616	FALSE
Agriculture: hedgerow	Scrub	65.321	78.767	FALSE
Agriculture: hedgerow	Suburban	119.733	72.786	TRUE
Agriculture: hedgerow	Urban no garden	177.571	85.435	TRUE
Agriculture: hedgerow	Urban with garden	136.171	78.767	TRUE
Agriculture: hedgerow	Woodland	14.381	77.991	FALSE
Parkland	Scrub	55.592	72.414	FALSE
Parkland	Suburban	110.003	65.858	TRUE
Parkland	Urban no garden	167.842	79.616	TRUE
Parkland	Urban with garden	126.442	72.414	TRUE
Parkland	Woodland	24.110	71.569	FALSE
Scrub	Suburban	54.411	64.830	FALSE
Scrub	Urban no garden	112.250	78.767	TRUE
Scrub	Urban with garden	70.850	71.480	FALSE
Scrub	Woodland	79.702	70.624	TRUE
Suburban	Urban no garden	57.839	72.786	FALSE
Suburban	Urban with garden	16.439	64.830	FALSE
Suburban	Woodland	134.114	63.884	TRUE
Urban no garden	Urban with garden	41.400	78.767	FALSE
Urban no garden	Woodland	191.952	77.991	TRUE
Urban with garden	Woodland	150.552	70.624	TRUE

b) Tree (4 m+) carbon store

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Agriculture: Crop/pasture	Allotment	7.375	96.048	FALSE
Agriculture: Crop/pasture	Amenity Grassland	15.550	73.439	FALSE
Agriculture: Crop/pasture	Commercial	35.096	69.309	FALSE
Agriculture: Crop/pasture	Grassland	9.857	72.606	FALSE
Agriculture: Crop/pasture	Agriculture: hedgerow	131.429	80.549	TRUE
Agriculture: Crop/pasture	Parkland	149.842	74.348	TRUE
Agriculture: Crop/pasture	Scrub	84.000	73.439	TRUE
Agriculture: Crop/pasture	Suburban	98.419	66.983	TRUE
Agriculture: Crop/pasture	Urban no garden	22.786	80.549	FALSE
Agriculture: Crop/pasture	Urban with garden	61.375	73.439	FALSE
Agriculture: Crop/pasture	Woodland	163.714	72.606	TRUE
Allotment	Amenity Grassland	8.175	94.559	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Commercial	27.721	91.388	FALSE
Allotment	Grassland	2.482	93.914	FALSE
Allotment	Agriculture: hedgerow	124.054	100.181	TRUE
Allotment	Parkland	142.467	95.267	TRUE
Allotment	Scrub	76.625	94.559	FALSE
Allotment	Suburban	91.044	89.638	TRUE
Allotment	Urban no garden	15.411	100.181	FALSE
Allotment	Urban with garden	54.000	94.559	FALSE
Allotment	Woodland	156.339	93.914	TRUE
Amenity grassland	Commercial	19.546	67.230	FALSE
Amenity grassland	Grassland	5.693	70.624	FALSE
Amenity grassland	Agriculture: hedgerow	115.879	78.767	TRUE
Amenity grassland	Parkland	134.292	72.414	TRUE
Amenity grassland	Scrub	68.450	71.480	FALSE
Amenity grassland	Suburban	82.869	64.830	TRUE
Amenity grassland	Urban no garden	7.236	78.767	FALSE
Amenity grassland	Urban with garden	45.825	71.480	FALSE
Amenity grassland	Woodland	148.164	70.624	TRUE
Commercial	Grassland	25.239	66.319	FALSE
Commercial	Agriculture: hedgerow	96.332	74.931	TRUE
Commercial	Parkland	114.746	68.222	TRUE
Commercial	Scrub	48.904	67.230	FALSE
Commercial	Suburban	63.323	60.111	TRUE
Commercial	Urban no garden	12.310	74.931	FALSE
Commercial	Urban with garden	26.279	67.230	FALSE
Commercial	Woodland	128.618	66.319	TRUE
Grassland	Agriculture: hedgerow	121.571	77.991	TRUE
Grassland	Parkland	139.985	71.569	TRUE
Grassland	Scrub	74.143	70.624	TRUE
Grassland	Suburban	88.562	63.884	TRUE
Grassland	Urban no garden	12.929	77.991	FALSE
Grassland	Urban with garden	51.518	70.624	FALSE
Grassland	Woodland	153.857	69.757	TRUE
Agriculture: hedgerow	Parkland	18.414	79.616	FALSE
Agriculture: hedgerow	Scrub	47.429	78.767	FALSE
Agriculture: hedgerow	Suburban	33.009	72.786	FALSE
Agriculture: hedgerow	Urban no garden	108.643	85.435	TRUE
Agriculture: hedgerow	Urban with garden	70.054	78.767	FALSE
Agriculture: hedgerow	Woodland	32.286	77.991	FALSE
Parkland	Scrub	65.842	72.414	FALSE
Parkland	Suburban	51.423	65.858	FALSE
Parkland	Urban no garden	127.056	79.616	TRUE
Parkland	Urban with garden	88.467	72.414	TRUE
Parkland	Woodland	13.872	71.569	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Scrub	Suburban	14.419	64.830	FALSE
Scrub	Urban no garden	61.214	78.767	FALSE
Scrub	Urban with garden	22.625	71.480	FALSE
Scrub	Woodland	79.714	70.624	TRUE
Suburban	Urban no garden	75.634	72.786	TRUE
Suburban	Urban with garden	37.044	64.830	FALSE
Suburban	Woodland	65.295	63.884	TRUE
Urban no garden	Urban with garden	38.589	78.767	FALSE
Urban no garden	Woodland	140.929	77.991	TRUE
Urban with garden	Woodland	102.339	70.624	TRUE

c) Woody vegetation (1-4 m) carbon store

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Agriculture: Crop/pasture	Allotment	86.625	95.677	FALSE
Agriculture: Crop/pasture	Amenity Grassland	0.000	72.726	FALSE
Agriculture: Crop/pasture	Commercial	31.923	68.516	FALSE
Agriculture: Crop/pasture	Grassland	12.929	71.877	FALSE
Agriculture: Crop/pasture	Agriculture: hedgerow	103.071	79.958	TRUE
Agriculture: Crop/pasture	Parkland	112.763	73.652	TRUE
Agriculture: Crop/pasture	Scrub	116.100	72.726	TRUE
Agriculture: Crop/pasture	Suburban	92.516	66.142	TRUE
Agriculture: Crop/pasture	Urban no garden	31.536	79.958	FALSE
Agriculture: Crop/pasture	Urban with garden	83.725	72.726	TRUE
Agriculture: Crop/pasture	Woodland	144.833	71.877	TRUE
Allotment	Amenity Grassland	86.625	94.966	FALSE
Allotment	Commercial	54.702	91.782	FALSE
Allotment	Grassland	73.696	94.317	FALSE
Allotment	Agriculture: hedgerow	16.446	100.612	FALSE
Allotment	Parkland	26.138	95.677	FALSE
Allotment	Scrub	29.475	94.966	FALSE
Allotment	Suburban	5.891	90.023	FALSE
Allotment	Urban no garden	55.089	100.612	FALSE
Allotment	Urban with garden	2.900	94.966	FALSE
Allotment	Woodland	58.208	94.317	FALSE
Amenity grassland	Commercial	31.923	67.519	FALSE
Amenity grassland	Grassland	12.929	70.928	FALSE
Amenity grassland	Agriculture: hedgerow	103.071	79.106	TRUE
Amenity grassland	Parkland	112.763	72.726	TRUE
Amenity grassland	Scrub	116.100	71.787	TRUE
Amenity grassland	Suburban	92.516	65.108	TRUE
Amenity grassland	Urban no garden	31.536	79.106	FALSE
Amenity grassland	Urban with garden	83.725	71.787	TRUE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Amenity grassland	Woodland	144.833	70.928	TRUE
Commercial	Grassland	18.995	66.604	FALSE
Commercial	Agriculture: hedgerow	71.148	75.254	FALSE
Commercial	Parkland	80.840	68.516	TRUE
Commercial	Scrub	84.177	67.519	TRUE
Commercial	Suburban	60.593	60.370	TRUE
Commercial	Urban no garden	0.387	75.254	FALSE
Commercial	Urban with garden	51.802	67.519	FALSE
Commercial	Woodland	112.910	66.604	TRUE
Grassland	Agriculture: hedgerow	90.143	78.326	TRUE
Grassland	Parkland	99.835	71.877	TRUE
Grassland	Scrub	103.171	70.928	TRUE
Grassland	Suburban	79.588	64.159	TRUE
Grassland	Urban no garden	18.607	78.326	FALSE
Grassland	Urban with garden	70.796	70.928	FALSE
Grassland	Woodland	131.905	70.057	TRUE
Agriculture: hedgerow	Parkland	9.692	79.958	FALSE
Agriculture: hedgerow	Scrub	13.029	79.106	FALSE
Agriculture: hedgerow	Suburban	10.555	73.099	FALSE
Agriculture: hedgerow	Urban no garden	71.536	85.802	FALSE
Agriculture: hedgerow	Urban with garden	19.346	79.106	FALSE
Agriculture: hedgerow	Woodland	41.762	78.326	FALSE
Parkland	Scrub	3.337	72.726	FALSE
Parkland	Suburban	20.247	66.142	FALSE
Parkland	Urban no garden	81.227	79.958	TRUE
Parkland	Urban with garden	29.038	72.726	FALSE
Parkland	Woodland	32.070	71.877	FALSE
Scrub	Suburban	23.584	65.108	FALSE
Scrub	Urban no garden	84.564	79.106	TRUE
Scrub	Urban with garden	32.375	71.787	FALSE
Scrub	Woodland	28.733	70.928	FALSE
Suburban	Urban no garden	60.980	73.099	FALSE
Suburban	Urban with garden	8.791	65.108	FALSE
Suburban	Woodland	52.317	64.159	FALSE
Urban no garden	Urban with garden	52.189	79.106	FALSE
Urban no garden	Woodland	113.298	78.326	TRUE
Urban with garden	Woodland	61.108	70.928	FALSE

d) Herbaceous vegetation carbon store

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Agriculture: Crop/pasture	Allotment	49.958	96.048	FALSE
Agriculture: Crop/pasture	Amenity Grassland	74.033	73.439	TRUE
Agriculture: Crop/pasture	Commercial	173.449	69.309	TRUE
Agriculture: Crop/pasture	Grassland	12.762	72.606	FALSE
Agriculture: Crop/pasture	Agriculture: hedgerow	112.083	80.549	TRUE
Agriculture: Crop/pasture	Parkland	79.754	74.348	TRUE
Agriculture: Crop/pasture	Scrub	33.808	73.439	FALSE
Agriculture: Crop/pasture	Suburban	130.946	66.983	TRUE
Agriculture: Crop/pasture	Urban no garden	190.476	80.549	TRUE
Agriculture: Crop/pasture	Urban with garden	140.583	73.439	TRUE
Agriculture: Crop/pasture	Woodland	31.095	72.606	FALSE
Allotment	Amenity Grassland	24.075	94.559	FALSE
Allotment	Commercial	123.490	91.388	TRUE
Allotment	Grassland	37.196	93.914	FALSE
Allotment	Agriculture: hedgerow	62.125	100.181	FALSE
Allotment	Parkland	29.796	95.267	FALSE
Allotment	Scrub	16.150	94.559	FALSE
Allotment	Suburban	80.988	89.638	FALSE
Allotment	Urban no garden	140.518	100.181	TRUE
Allotment	Urban with garden	90.625	94.559	FALSE
Allotment	Woodland	18.863	93.914	FALSE
Amenity grassland	Commercial	99.415	67.230	TRUE
Amenity grassland	Grassland	61.271	70.624	FALSE
Amenity grassland	Agriculture: hedgerow	38.050	78.767	FALSE
Amenity grassland	Parkland	5.721	72.414	FALSE
Amenity grassland	Scrub	40.225	71.480	FALSE
Amenity grassland	Suburban	56.913	64.830	FALSE
Amenity grassland	Urban no garden	116.443	78.767	TRUE
Amenity grassland	Urban with garden	66.550	71.480	FALSE
Amenity grassland	Woodland	42.938	70.624	FALSE
Commercial	Grassland	160.687	66.319	TRUE
Commercial	Agriculture: hedgerow	61.365	74.931	FALSE
Commercial	Parkland	93.694	68.222	TRUE
Commercial	Scrub	139.640	67.230	TRUE
Commercial	Suburban	42.502	60.111	FALSE
Commercial	Urban no garden	17.027	74.931	FALSE
Commercial	Urban with garden	32.865	67.230	FALSE
Commercial	Woodland	142.353	66.319	TRUE
Grassland	Agriculture: hedgerow	99.321	77.991	TRUE
Grassland	Parkland	66.992	71.569	FALSE
Grassland	Scrub	21.046	70.624	FALSE
Grassland	Suburban	118.184	63.884	TRUE
Grassland	Urban no garden	177.714	77.991	TRUE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Grassland	Urban with garden	127.821	70.624	TRUE
Grassland	Woodland	18.333	69.757	FALSE
Agriculture: hedgerow	Parkland	32.329	79.616	FALSE
Agriculture: hedgerow	Scrub	78.275	78.767	FALSE
Agriculture: hedgerow	Suburban	18.863	72.786	FALSE
Agriculture: hedgerow	Urban no garden	78.393	85.435	FALSE
Agriculture: hedgerow	Urban with garden	28.500	78.767	FALSE
Agriculture: hedgerow	Woodland	80.988	77.991	TRUE
Parkland	Scrub	45.946	72.414	FALSE
Parkland	Suburban	51.192	65.858	FALSE
Parkland	Urban no garden	110.722	79.616	TRUE
Parkland	Urban with garden	60.829	72.414	FALSE
Parkland	Woodland	48.659	71.569	FALSE
Scrub	Suburban	97.138	64.830	TRUE
Scrub	Urban no garden	156.668	78.767	TRUE
Scrub	Urban with garden	106.775	71.480	TRUE
Scrub	Woodland	2.713	70.624	FALSE
Suburban	Urban no garden	59.530	72.786	FALSE
Suburban	Urban with garden	9.637	64.830	FALSE
Suburban	Woodland	99.851	63.884	TRUE
Urban no garden	Urban with garden	49.893	78.767	FALSE
Urban no garden	Woodland	159.381	77.991	TRUE
Urban with garden	Woodland	109.488	70.624	TRUE

e) Soil carbon store

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Agriculture: Crop/pasture	Allotment	28.159	97.654	FALSE
Agriculture: Crop/pasture	Amenity Grassland	13.356	71.228	FALSE
Agriculture: Crop/pasture	Commercial	131.286	67.222	TRUE
Agriculture: Crop/pasture	Grassland	2.730	70.420	FALSE
Agriculture: Crop/pasture	Agriculture: hedgerow	6.319	93.156	FALSE
Agriculture: Crop/pasture	Parkland	7.760	72.110	FALSE
Agriculture: Crop/pasture	Scrub	20.106	71.228	FALSE
Agriculture: Crop/pasture	Suburban	82.459	64.966	TRUE
Agriculture: Crop/pasture	Urban no garden	139.627	78.124	TRUE
Agriculture: Crop/pasture	Urban with garden	97.506	71.228	TRUE
Agriculture: Crop/pasture	Woodland	13.873	70.420	FALSE
Allotment	Amenity Grassland	41.514	96.278	FALSE
Allotment	Commercial	159.445	93.353	TRUE
Allotment	Grassland	25.429	95.681	FALSE
Allotment	Agriculture: hedgerow	21.839	113.464	FALSE
Allotment	Parkland	20.398	96.932	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Scrub	48.264	96.278	FALSE
Allotment	Suburban	110.618	91.742	TRUE
Allotment	Urban no garden	167.786	101.485	TRUE
Allotment	Urban with garden	125.664	96.278	TRUE
Allotment	Woodland	14.286	95.681	FALSE
Amenity grassland	Commercial	117.931	65.206	TRUE
Amenity grassland	Grassland	16.086	68.497	FALSE
Amenity grassland	Agriculture: hedgerow	19.675	91.712	FALSE
Amenity grassland	Parkland	21.116	70.234	FALSE
Amenity grassland	Scrub	6.750	69.328	FALSE
Amenity grassland	Suburban	69.103	62.878	TRUE
Amenity grassland	Urban no garden	126.271	76.395	TRUE
Amenity grassland	Urban with garden	84.150	69.328	TRUE
Amenity grassland	Woodland	27.229	68.497	FALSE
Commercial	Grassland	134.016	64.322	TRUE
Commercial	Agriculture: hedgerow	137.606	88.637	TRUE
Commercial	Parkland	139.047	66.168	TRUE
Commercial	Scrub	111.181	65.206	TRUE
Commercial	Suburban	48.828	58.301	FALSE
Commercial	Urban no garden	8.341	72.675	FALSE
Commercial	Urban with garden	33.781	65.206	FALSE
Commercial	Woodland	145.159	64.322	TRUE
Grassland	Agriculture: hedgerow	3.589	91.086	FALSE
Grassland	Parkland	5.030	69.415	FALSE
Grassland	Scrub	22.836	68.497	FALSE
Grassland	Suburban	85.189	61.961	TRUE
Grassland	Urban no garden	142.357	75.643	TRUE
Grassland	Urban with garden	100.236	68.497	TRUE
Grassland	Woodland	11.143	67.657	FALSE
Agriculture: hedgerow	Parkland	1.441	92.399	FALSE
Agriculture: hedgerow	Scrub	26.425	91.712	FALSE
Agriculture: hedgerow	Suburban	88.778	86.939	TRUE
Agriculture: hedgerow	Urban no garden	145.946	97.165	TRUE
Agriculture: hedgerow	Urban with garden	103.825	91.712	TRUE
Agriculture: hedgerow	Woodland	7.554	91.086	FALSE
Parkland	Scrub	27.866	70.234	FALSE
Parkland	Suburban	90.219	63.876	TRUE
Parkland	Urban no garden	147.387	77.219	TRUE
Parkland	Urban with garden	105.266	70.234	TRUE
Parkland	Woodland	6.113	69.415	FALSE
Scrub	Suburban	62.353	62.878	FALSE
Scrub	Urban no garden	119.521	76.395	TRUE
Scrub	Urban with garden	77.400	69.328	TRUE
Scrub	Woodland	33.979	68.497	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Suburban	Urban no garden	57.168	70.594	FALSE
Suburban	Urban with garden	15.047	62.878	FALSE
Suburban	Woodland	96.332	61.961	TRUE
Urban no garden	Urban with garden	42.121	76.395	FALSE
Urban no garden	Woodland	153.500	75.643	TRUE
Urban with garden	Woodland	111.379	68.497	TRUE

Appendix 3 The estimated vegetation carbon and soil organic carbon storage within land-use categories in a) Darlington and b) Durham in 1945 and 2009, and c) Newcastle in 1945 and 2012 calculated using the means of 50 x 50 m quadrat samples.

a) Darlington

Land-use category	Carbon storage (Mg)									
	1945					2009				
	Trees	Woody	Herbaceous	Soils	Total	Trees	Woody	Herbaceous	Soils	Total
Agriculture	3,408	154	5,781	122,210	131,553	7	0	11	237	255
Allotment	2	166	140	14,779	15,088	1	48	41	4,290	4,380
Amenity grassland	67	0	127	14,746	14,940	105	0	201	23,315	23,622
Commercial	230	121	24	2,684	3,060	357	188	37	4,152	4,733
Grassland	17	3	97	3,250	3,367	15	3	90	3,007	3,116
Parkland	6,340	207	85	11,660	18,293	6,097	199	82	11,213	17,591
Residential:										
Urban no garden	28	30	0	187	246	21	23	0	141	186
Urban with garden	224	73	20	3,157	3,475	390	128	35	5,494	6,046
Suburban	2,282	524	152	24,812	27,770	5,213	1,197	347	56,675	63,433
Scrub	71	75	54	2,347	2,547	479	505	360	15,782	17,126
Woodland	1,980	40	40	1,744	3,804	4,186	85	84	3,686	8,041
Total	14,651	1,396	6,520	201,576	224,143	16,871	2,377	1,288	127,991	148,528

b) Durham

Land-use category	Carbon storage (Mg)									
	1945					2009				
	Trees	Woody	Herbaceous	Soils	Total	Trees	Woody	Herbaceous	Soils	Total
Agriculture	3,658	166	6,204	131,166	141,194	0	0	0	0	0
Allotment	0	35	30	3,137	3,202	0	12	10	1,032	1,053
Amenity grassland	11	0	21	2,408	2,440	61	0	116	13,444	13,620
Commercial	32	17	3	372	425	161	85	17	1,878	2,141
Grassland	20	4	114	3,823	3,961	51	11	299	9,980	10,340
Parkland	1,802	59	24	3,314	5,198	4,371	143	59	8,038	12,611
Residential:										
Urban no garden	1	1	0	4	5	1	1	0	4	5
Urban with garden	150	49	13	2,109	2,321	367	120	33	5,173	5,694
Suburban	714	164	48	7,763	8,689	2,905	667	193	31,582	35,348
Scrub	93	98	70	3,047	3,307	253	266	190	8,314	9,022
Woodland	10,198	207	205	8,979	19,589	19,351	393	388	17,038	37,170
Total	16,678	799	6,732	166,122	190,331	27,521	1,698	1,304	96,482	127,005

c) Newcastle

Land-use category	Carbon storage (Mg)									
	1945					2012				
	Trees	Woody	Herbaceous	Soils	Total	Trees	Woody	Herbaceous	Soils	Total
Agriculture	5,476	248	9,287	196,334	211,345	0	0	0	0	0
Allotment	3	202	170	17,983	18,359	1	49	41	4,330	4,421
Amenity grassland	53	0	100	11,627	11,780	150	0	287	33,202	33,639
Commercial	230	121	24	2,679	3,054	401	211	41	4,668	5,321
Grassland	274	57	1,595	53,253	55,178	233	48	1,360	45,408	47,050
Parkland	4,237	138	57	7,792	12,224	7,395	242	99	13,599	21,335
Residential:										
Urban no garden	51	56	1	343	451	14	16	0	96	127
Urban with garden	1,271	417	114	17,923	19,725	2,512	823	226	35,418	38,980
Suburban	2,470	567	164	26,847	30,048	5,425	1,246	361	58,976	66,008
Scrub	144	152	108	4,734	5,138	853	900	641	28,099	30,493
Woodland	3,191	65	64	2,809	6,129	5,693	116	114	5,012	10,935
Total	17,398	2,022	11,684	342,325	373,430	22,677	3,650	3,171	228,810	258,307

Appendix 4 Results of a) two-way ANOVA and b) Tukey HSD tests testing for differences in the soil organic carbon (SOC) densities of soil cores taken from different depth intervals at different urban land-use categories. Samples were collected from Durham, UK. Bold p-values denote significant differences.

a)

Variable	*df*	F	P
Soil depth	4	8.704	**<0.001**
Land-use category	10	1.162	0.321

b)

Soil depth interval (cm)		Difference	P
0-5.5	5.5-11	0.0029	0.943
11-16.5	5.5-11	-0.0020	0.985
16.5-22	5.5-11	-0.0046	0.775
22-27.5	5.5-11	-0.0234	**<0.001**
0-5.5	11-16.5	0.0049	0.707
16.5-22	11-16.5	-0.0026	0.966
22-27.5	11-16.5	-0.0214	**<0.001**
0-5.5	16.5-22	0.0074	0.327
22-27.5	16.5-22	-0.0189	**0.001**
0-5.5	22-27.5	0.0263	**<0.001**

Appendix 5 Kruskal-Wallis *post-hoc* test results for difference in carbon stored per unit area among urban land-use categories in the different carbon pools in Durham.

a) Total vegetation and soil organic carbon storage

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Allotment	Amenity Grassland	9.152	44.667	FALSE
Allotment	Commercial	53.233	45.448	TRUE
Allotment	Grassland	10.333	44.005	FALSE
Allotment	Parkland	16.867	45.448	FALSE
Allotment	Scrub	1.833	47.531	FALSE
Allotment	Suburban	33.500	44.005	FALSE
Allotment	Urban no garden	56.833	56.811	TRUE
Allotment	Urban with garden	40.933	45.448	FALSE
Allotment	Woodland	21.567	45.448	FALSE
Amenity Grassland	Commercial	44.082	38.455	TRUE
Amenity Grassland	Grassland	1.182	36.738	FALSE
Amenity Grassland	Parkland	26.018	38.455	FALSE
Amenity Grassland	Scrub	7.318	40.895	FALSE
Amenity Grassland	Suburban	24.348	36.738	FALSE
Amenity Grassland	Urban no garden	47.682	51.387	FALSE
Amenity Grassland	Urban with garden	31.782	38.455	FALSE
Amenity Grassland	Woodland	30.718	38.455	FALSE
Commercial	Grassland	42.900	37.684	TRUE
Commercial	Parkland	70.100	39.360	TRUE
Commercial	Scrub	51.400	41.747	TRUE
Commercial	Suburban	19.733	37.684	FALSE
Commercial	Urban no garden	3.600	52.068	FALSE
Commercial	Urban with garden	12.300	39.360	FALSE
Commercial	Woodland	74.800	39.360	TRUE
Grassland	Parkland	27.200	37.684	FALSE
Grassland	Scrub	8.500	40.171	FALSE
Grassland	Suburban	23.167	35.930	FALSE
Grassland	Urban no garden	46.500	50.813	FALSE
Grassland	Urban with garden	30.600	37.684	FALSE
Grassland	Woodland	31.900	37.684	FALSE
Parkland	Scrub	18.700	41.747	FALSE
Parkland	Suburban	50.367	37.684	TRUE
Parkland	Urban no garden	73.700	52.068	TRUE
Parkland	Urban with garden	57.800	39.360	TRUE
Parkland	Woodland	4.700	39.360	FALSE
Scrub	Suburban	31.667	40.171	FALSE
Scrub	Urban no garden	55.000	53.895	TRUE
Scrub	Urban with garden	39.100	41.747	FALSE
Scrub	Woodland	23.400	41.747	FALSE
Suburban	Urban no garden	23.333	50.813	FALSE

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Suburban	Urban with garden	7.433	37.684	FALSE
Suburban	Woodland	55.067	37.684	TRUE
Urban no garden	Urban with garden	15.900	52.068	FALSE
Urban no garden	Woodland	78.400	52.068	TRUE
Urban with garden	Woodland	62.500	39.360	TRUE

b) Tree (4 m+) carbon storage

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Allotment	Amenity Grassland	9.152	44.667	FALSE
Allotment	Commercial	53.233	45.448	TRUE
Allotment	Grassland	10.333	44.005	FALSE
Allotment	Parkland	16.867	45.448	FALSE
Allotment	Scrub	1.833	47.531	FALSE
Allotment	Suburban	33.500	44.005	FALSE
Allotment	Urban no garden	56.833	56.811	TRUE
Allotment	Urban with garden	40.933	45.448	FALSE
Allotment	Woodland	21.567	45.448	FALSE
Amenity Grassland	Commercial	44.082	38.455	TRUE
Amenity Grassland	Grassland	1.182	36.738	FALSE
Amenity Grassland	Parkland	26.018	38.455	FALSE
Amenity Grassland	Scrub	7.318	40.895	FALSE
Amenity Grassland	Suburban	24.348	36.738	FALSE
Amenity Grassland	Urban no garden	47.682	51.387	FALSE
Amenity Grassland	Urban with garden	31.782	38.455	FALSE
Amenity Grassland	Woodland	30.718	38.455	FALSE
Commercial	Grassland	42.900	37.684	TRUE
Commercial	Parkland	70.100	39.360	TRUE
Commercial	Scrub	51.400	41.747	TRUE
Commercial	Suburban	19.733	37.684	FALSE
Commercial	Urban no garden	3.600	52.068	FALSE
Commercial	Urban with garden	12.300	39.360	FALSE
Commercial	Woodland	74.800	39.360	TRUE
Grassland	Parkland	27.200	37.684	FALSE
Grassland	Scrub	8.500	40.171	FALSE
Grassland	Suburban	23.167	35.930	FALSE
Grassland	Urban no garden	46.500	50.813	FALSE
Grassland	Urban with garden	30.600	37.684	FALSE
Grassland	Woodland	31.900	37.684	FALSE
Parkland	Scrub	18.700	41.747	FALSE
Parkland	Suburban	50.367	37.684	TRUE
Parkland	Urban no garden	73.700	52.068	TRUE
Parkland	Urban with garden	57.800	39.360	TRUE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Parkland	Woodland	4.700	39.360	FALSE
Scrub	Suburban	31.667	40.171	FALSE
Scrub	Urban no garden	55.000	53.895	TRUE
Scrub	Urban with garden	39.100	41.747	FALSE
Scrub	Woodland	23.400	41.747	FALSE
Suburban	Urban no garden	23.333	50.813	FALSE
Suburban	Urban with garden	7.433	37.684	FALSE
Suburban	Woodland	55.067	37.684	TRUE
Urban no garden	Urban with garden	15.900	52.068	FALSE
Urban no garden	Woodland	78.400	52.068	TRUE
Urban with garden	Woodland	62.500	39.360	TRUE

c) Woody vegetation (1-4 m) carbon storage

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity Grassland	24.917	44.667	FALSE
Allotment	Commercial	17.317	45.448	FALSE
Allotment	Grassland	24.917	44.005	FALSE
Allotment	Parkland	24.983	45.448	FALSE
Allotment	Scrub	14.333	47.531	FALSE
Allotment	Suburban	9.042	44.005	FALSE
Allotment	Urban no garden	17.792	56.811	FALSE
Allotment	Urban with garden	6.133	45.448	FALSE
Allotment	Woodland	33.733	45.448	FALSE
Amenity Grassland	Commercial	7.600	38.455	FALSE
Amenity Grassland	Grassland	0.000	36.738	FALSE
Amenity Grassland	Parkland	49.900	38.455	TRUE
Amenity Grassland	Scrub	39.250	40.895	FALSE
Amenity Grassland	Suburban	33.958	36.738	FALSE
Amenity Grassland	Urban no garden	7.125	51.387	FALSE
Amenity Grassland	Urban with garden	31.050	38.455	FALSE
Amenity Grassland	Woodland	58.650	38.455	TRUE
Commercial	Grassland	7.600	37.684	FALSE
Commercial	Parkland	42.300	39.360	TRUE
Commercial	Scrub	31.650	41.747	FALSE
Commercial	Suburban	26.358	37.684	FALSE
Commercial	Urban no garden	0.475	52.068	FALSE
Commercial	Urban with garden	23.450	39.360	FALSE
Commercial	Woodland	51.050	39.360	TRUE
Grassland	Parkland	49.900	37.684	TRUE
Grassland	Scrub	39.250	40.171	FALSE
Grassland	Suburban	33.958	35.930	FALSE
Grassland	Urban no garden	7.125	50.813	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Grassland	Urban with garden	31.050	37.684	FALSE
Grassland	Woodland	58.650	37.684	TRUE
Parkland	Scrub	10.650	41.747	FALSE
Parkland	Suburban	15.942	37.684	FALSE
Parkland	Urban no garden	42.775	52.068	FALSE
Parkland	Urban with garden	18.850	39.360	FALSE
Parkland	Woodland	8.750	39.360	FALSE
Scrub	Suburban	5.292	40.171	FALSE
Scrub	Urban no garden	32.125	53.895	FALSE
Scrub	Urban with garden	8.200	41.747	FALSE
Scrub	Woodland	19.400	41.747	FALSE
Suburban	Urban no garden	26.833	50.813	FALSE
Suburban	Urban with garden	2.908	37.684	FALSE
Suburban	Woodland	24.692	37.684	FALSE
Urban no garden	Urban with garden	23.925	52.068	FALSE
Urban no garden	Woodland	51.525	52.068	FALSE
Urban with garden	Woodland	27.600	39.360	FALSE

d) Herbaceous vegetation carbon storage

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity Grassland	6.742	44.667	FALSE
Allotment	Commercial	44.833	45.448	FALSE
Allotment	Grassland	20.083	44.005	FALSE
Allotment	Parkland	5.533	45.448	FALSE
Allotment	Scrub	15.792	47.531	FALSE
Allotment	Suburban	31.417	44.005	FALSE
Allotment	Urban no garden	52.333	56.811	FALSE
Allotment	Urban with garden	34.033	45.448	FALSE
Allotment	Woodland	22.267	45.448	FALSE
Amenity Grassland	Commercial	38.091	38.455	FALSE
Amenity Grassland	Grassland	26.826	36.738	FALSE
Amenity Grassland	Parkland	1.209	38.455	FALSE
Amenity Grassland	Scrub	22.534	40.895	FALSE
Amenity Grassland	Suburban	24.674	36.738	FALSE
Amenity Grassland	Urban no garden	45.591	51.387	FALSE
Amenity Grassland	Urban with garden	27.291	38.455	FALSE
Amenity Grassland	Woodland	29.009	38.455	FALSE
Commercial	Grassland	64.917	37.684	TRUE
Commercial	Parkland	39.300	39.360	FALSE
Commercial	Scrub	60.625	41.747	TRUE
Commercial	Suburban	13.417	37.684	FALSE
Commercial	Urban no garden	7.500	52.068	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Commercial	Urban with garden	10.800	39.360	FALSE
Commercial	Woodland	67.100	39.360	TRUE
Grassland	Parkland	25.617	37.684	FALSE
Grassland	Scrub	4.292	40.171	FALSE
Grassland	Suburban	51.500	35.930	TRUE
Grassland	Urban no garden	72.417	50.813	TRUE
Grassland	Urban with garden	54.117	37.684	TRUE
Grassland	Woodland	2.183	37.684	FALSE
Parkland	Scrub	21.325	41.747	FALSE
Parkland	Suburban	25.883	37.684	FALSE
Parkland	Urban no garden	46.800	52.068	FALSE
Parkland	Urban with garden	28.500	39.360	FALSE
Parkland	Woodland	27.800	39.360	FALSE
Scrub	Suburban	47.208	40.171	TRUE
Scrub	Urban no garden	68.125	53.895	TRUE
Scrub	Urban with garden	49.825	41.747	TRUE
Scrub	Woodland	6.475	41.747	FALSE
Suburban	Urban no garden	20.917	50.813	FALSE
Suburban	Urban with garden	2.617	37.684	FALSE
Suburban	Woodland	53.683	37.684	TRUE
Urban no garden	Urban with garden	18.300	52.068	FALSE
Urban no garden	Woodland	74.600	52.068	TRUE
Urban with garden	Woodland	56.300	39.360	TRUE

e) Soil organic carbon storage

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity Grassland	10.076	44.667	FALSE
Allotment	Commercial	63.067	45.448	TRUE
Allotment	Grassland	14.750	44.005	FALSE
Allotment	Parkland	5.267	45.448	FALSE
Allotment	Scrub	6.042	47.531	FALSE
Allotment	Suburban	44.083	44.005	TRUE
Allotment	Urban no garden	66.667	56.811	TRUE
Allotment	Urban with garden	49.967	45.448	TRUE
Allotment	Woodland	2.567	45.448	FALSE
Amenity Grassland	Commercial	52.991	38.455	TRUE
Amenity Grassland	Grassland	4.674	36.738	FALSE
Amenity Grassland	Parkland	4.809	38.455	FALSE
Amenity Grassland	Scrub	4.034	40.895	FALSE
Amenity Grassland	Suburban	34.008	36.738	FALSE
Amenity Grassland	Urban no garden	56.591	51.387	TRUE
Amenity Grassland	Urban with garden	39.891	38.455	TRUE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Amenity Grassland	Woodland	7.509	38.455	FALSE
Commercial	Grassland	48.317	37.684	TRUE
Commercial	Parkland	57.800	39.360	TRUE
Commercial	Scrub	57.025	41.747	TRUE
Commercial	Suburban	18.983	37.684	FALSE
Commercial	Urban no garden	3.600	52.068	FALSE
Commercial	Urban with garden	13.100	39.360	FALSE
Commercial	Woodland	60.500	39.360	TRUE
Grassland	Parkland	9.483	37.684	FALSE
Grassland	Scrub	8.708	40.171	FALSE
Grassland	Suburban	29.333	35.930	FALSE
Grassland	Urban no garden	51.917	50.813	TRUE
Grassland	Urban with garden	35.217	37.684	FALSE
Grassland	Woodland	12.183	37.684	FALSE
Parkland	Scrub	0.775	41.747	FALSE
Parkland	Suburban	38.817	37.684	TRUE
Parkland	Urban no garden	61.400	52.068	TRUE
Parkland	Urban with garden	44.700	39.360	TRUE
Parkland	Woodland	2.700	39.360	FALSE
Scrub	Suburban	38.042	40.171	FALSE
Scrub	Urban no garden	60.625	53.895	TRUE
Scrub	Urban with garden	43.925	41.747	TRUE
Scrub	Woodland	3.475	41.747	FALSE
Suburban	Urban no garden	22.583	50.813	FALSE
Suburban	Urban with garden	5.883	37.684	FALSE
Suburban	Woodland	41.517	37.684	TRUE
Urban no garden	Urban with garden	16.700	52.068	FALSE
Urban no garden	Woodland	64.100	52.068	TRUE
Urban with garden	Woodland	47.400	39.360	TRUE

Appendix 6 The number and size of trees recorded in the different land-use categories in Durham. Proportions are colour-coded in shades of green through yellow to red, with true green denoting highest proportions, yellow denoting moderate proportions, and true red denoting lowest proportions.

Land-use category	Mean no. of trees per sample	Proportion of total number of trees within size class (dbh)					
		Up to 25 cm	>25 to 50 cm	>50 to 75 cm	>75 to 100 cm	>100 to 125 cm	>125 cm
Allotment	0.83	1.00	0.00	0.00	0.00	0.00	0.00
Amenity Grassland	0.27	0.67	0.33	0.00	0.00	0.00	0.00
Commercial	5.20	1.00	0.00	0.00	0.00	0.00	0.00
Grassland	1.40	0.93	0.00	0.00	0.07	0.00	0.00
Parkland	18.10	0.38	0.33	0.18	0.08	0.03	0.01
Suburban	8.17	0.65	0.31	0.04	0.00	0.00	0.00
Urban no garden	0.50	1.00	0.00	0.00	0.00	0.00	0.00
Urban with garden	3.10	0.68	0.32	0.00	0.00	0.00	0.00
Scrub	10.10	0.91	0.08	0.01	0.00	0.00	0.00
Woodland	60.30	0.52	0.32	0.13	0.03	0.01	0.00

Appendix 7 The wintering (Wi.) and breeding (Br.) bird species recorded in point-count surveys within Durham their standard British Trust for Ornithology (BTO) codes. Land-use categories are presented, from left to right, in order of declining total vegetation carbon and soil organic carbon value per unit area. Sample numbers (*n*) were repeated in winter and spring.

Species (BTO Code)	Land-use category/Count																			
	Woodland (*n*=10)		Parkland (*n*=10)		Allotment (*n*=6)		Scrub (*n*=8)		Amenity grassland (*n*=11)		Grassland (*n*=12)		Suburban (*n*=12)		Urban with garden (*n*=10)		Commercial (*n*=10)		Urban no garden (*n*=4)	
	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.
Eurasian Sparrowhawk *Accipiter nisus* (SH)							2													
Common Pheasant *Phasianus colchicus* (PH)		2		3						1	2	2								
Common Moorhen *Gallinula chloropus* (MH)							1	1						3						
Common Coot *Fulica atra* (CO)								2												
Black-headed Gull *Chroicocephalus ridibundus* (BH)							13		117				1		5		16	1		
European Herring Gull *Larus argentatus* (HG)	1		2						1	38			4					2		
Lesser Black-backed Gull *L. fuscus* (LB)										8								4		
Common Gull *L. canus* (CM)									2											
Stock Dove *Columba oenas* (SD)	1	1								1										
Common Woodpigeon *C. palumbus* (WP)	7	28	25	45	7	10	4	12	4	5	20	12	16	39	4	16	2	25	2	3
Eurasian Collared Dove *Streptopelia decaocto* (CD)						2							12	11	8	11	2			5
Tawny Owl *Strix aluco* (TO)		2																		
Common Swift *Apus apus* (SI)																9				1
Great Spotted Woodpecker *Dendrocopos major* (GS)	1	3										1								
Barn swallow *Hirundo rustica* (SL)						4				5		3		4		1		10		
Pied/White Wagtail *Motacilla alba* (PW)															1		3	5		
Winter Wren *Troglodytes troglodytes* (WR)	17	29	16	15	9	10	13	12	1	2	7	6	1	6	2	5		4		
Hedge Accentor *Prunella modularis* (D.)	3		3	12	6	7	4	15	2	1	2	6	5	14	5	11	2	3		1

Species (BTO Code)	Land-use category/Count																			
	Woodland (n=10)		Parkland (n=10)		Allotment (n=6)		Scrub (n=8)		Amenity grassland (n=11)		Grassland (n=12)		Suburban (n=12)		Urban with garden (n=10)		Commercial (n=10)		Urban no garden (n=4)	
	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.
European Robin *Erithacus rubecula* (R.)	8	21	15	15	8	3	16	7	4	5	7	3	12	6	7	2	5	7	3	2
Song Thrush *Turdus philomelos* (ST)		5	2	8	1	1		4			1	1		4	1	2				
Redwing *T. iliacus* (RE)			16								1									
Mistle Thrush *T. viscivorus* (M.)		2		1		1									1					
Eurasian Blackbird *T. merula* (B.)	18	27	35	36	30	18	5	21	12	13	15	14	13	47	6	34	13	6	1	5
Garden Warbler *Sylvia borin* (GW)								1												
Blackcap *S. atricapilla* (BC)		9		5		3		4		1		1				1				
Common Whitethroat *S. communis* (WH)								8		1		7								
Common Grasshopper-warbler *Locustella naevia* (GH)												3								
Willow Warbler *Phylloscopus trochilus* (WW)								7				1								
Common Chiffchaff *P. colybita* (CC)		5		12				8		3		3		2				2		
Goldcrest *Regulus regulus* (GC)	3	2	2	4	2					1			1	2						
Spotted Flycatcher *Muscicapa striata* (SF)		1																		
Great Tit *Parus major* (GT)	26	22	26	19	14	9	12	5	1	2	16	11	10	10	7	10	3	4		
Coal Tit *Periparus ater* (CT)	6	4	3	4	2	8								1	5					
Blue Tit *Cyanistes caeruleus* (BT)	48	32	43	28	8	12	22	9	6	9	10	9	33	20	22	17	1	5	4	1
Long-tailed Tit *Aegithalos caudatus* (LT)	8	1	3		1			2	10	1										
Wood Nuthatch *Sitta europaea* (NH)	8	5	1								1			1						
Eurasian Treecreeper *Certhia familiaris* (TC)		5	2					1												
Black-billed Magpie *Pica pica* (MG)	9	2	10	3	3	4	10	7	6	11	7	7	10	5	16	8	5	3	1	
Eurasian Jay *Garrulus glandarius* (J.)	1	1			3		1													
Eurasian Jackdaw *Corvus monedula* (JD)	21	6	13	6	5			10	2	6	2	24	37	9	31	29	3	34	36	33
Rook *C. frugilegus* (RO)													1							

Species (BTO Code)	Land-use category/Count																			
	Woodland (*n*=10)		Parkland (*n*=10)		Allotment (*n*=6)		Scrub (*n*=8)		Amenity grassland (*n*=11)		Grassland (*n*=12)		Suburban (*n*=12)		Urban with garden (*n*=10)		Commercial (*n*=10)		urban no garden (*n*=4)	
	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.	Wi.	Br.
Carrion Crow *C. corone* (C.)	4	5	6	12			5		6	8	10	2	2	7		4	4	4	5	6
Common Starling *Sturnus vulgaris* (SG)				1						20	1	1	137	31	24	22		8		
House Sparrow *Passer domesticus* (HS)					6	3		1					25	28	22	23	7	6	2	
Eurasian Chaffinch *Fringilla coelebs* (CH)		9	3	8	2	1	9	7		3	3	7		8	1	1		1		
Eurasian Linnet *Carduelis cannabina* (LI)								10						5						
Lesser Redpoll *C. cabaret* (LR)											2									
European Goldfinch *C. carduelis* (GO)	1			4	10	3		2		2		3	3	12	3	7	2	10		2
European Greenfinch *C. chloris (GR)*					3						4	1	1	5	1	6	2	3		
Eurasian Bullfinch *Pyrrhula pyrrhula* (BF)			1	2	2	2		1												
Yellowhammer *Emberiza citrinella* (Y.)								1												
Total	**191**	**229**	**227**	**243**	**122**	**101**	**117**	**158**	**174**	**147**	**111**	**128**	**324**	**280**	**172**	**219**	**70**	**147**	**54**	**59**

Appendix 8 Kruskal-Wallis *post-hoc* test results for difference in bird species richness among land-use categories in Durham.

a) Wintering bird species richness

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Allotment	Amenity grassland	39.644	44.667	FALSE
Allotment	Commercial	42.217	45.448	FALSE
Allotment	Grassland	29.833	44.005	FALSE
Allotment	Parkland	9.583	45.448	FALSE
Allotment	Scrub	2.417	47.531	FALSE
Allotment	Suburban	1.792	44.005	FALSE
Allotment	Urban no garden	39.167	56.811	FALSE
Allotment	Urban with garden	1.117	45.448	FALSE
Allotment	Woodland	3.833	45.448	FALSE
Amenity grassland	Commercial	2.573	38.455	FALSE
Amenity grassland	Grassland	9.811	36.738	FALSE
Amenity grassland	Parkland	49.227	38.455	TRUE
Amenity grassland	Scrub	37.227	40.895	FALSE
Amenity grassland	Suburban	41.436	36.738	TRUE
Amenity grassland	Urban no garden	0.477	51.387	FALSE
Amenity grassland	Urban with garden	38.527	38.455	TRUE
Amenity grassland	Woodland	43.477	38.455	TRUE
Commercial	Grassland	12.383	37.684	FALSE
Commercial	Parkland	51.800	39.360	TRUE
Commercial	Scrub	39.800	41.747	FALSE
Commercial	Suburban	44.008	37.684	TRUE
Commercial	Urban no garden	3.050	52.068	FALSE
Commercial	Urban with garden	41.100	39.360	TRUE
Commercial	Woodland	46.050	39.360	TRUE
Grassland	Parkland	39.417	37.684	TRUE
Grassland	Scrub	27.417	40.171	FALSE
Grassland	Suburban	31.625	35.930	FALSE
Grassland	Urban no garden	9.333	50.813	FALSE
Grassland	Urban with garden	28.717	37.684	FALSE
Grassland	Woodland	33.667	37.684	FALSE
Parkland	Scrub	12.000	41.747	FALSE
Parkland	Suburban	7.792	37.684	FALSE
Parkland	Urban no garden	48.750	52.068	FALSE
Parkland	Urban with garden	10.700	39.360	FALSE
Parkland	Woodland	5.750	39.360	FALSE
Scrub	Suburban	4.208	40.171	FALSE
Scrub	Urban no garden	36.750	53.895	FALSE
Scrub	Urban with garden	1.300	41.747	FALSE
Scrub	Woodland	6.250	41.747	FALSE
Suburban	Urban no garden	40.958	50.813	FALSE

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Suburban	Urban with garden	2.908	37.684	FALSE
Suburban	Woodland	2.042	37.684	FALSE
Urban no garden	Urban with garden	38.050	52.068	FALSE
Urban no garden	Woodland	43.000	52.068	FALSE
Urban with garden	Woodland	4.950	39.360	FALSE

b) Breeding bird species richness

Comparison		Observation	Critical	Significant
Land-use category 1	Land-use category 2	difference	difference	difference
Allotment	Amenity grassland	10.758	44.667	FALSE
Allotment	Commercial	8.117	45.448	FALSE
Allotment	Grassland	14.375	44.005	FALSE
Allotment	Parkland	35.583	45.448	FALSE
Allotment	Scrub	28.583	47.531	FALSE
Allotment	Suburban	25.542	44.005	FALSE
Allotment	Urban no garden	19.667	56.811	FALSE
Allotment	Urban with garden	16.433	45.448	FALSE
Allotment	Woodland	35.633	45.448	FALSE
Amenity grassland	Commercial	2.641	38.455	FALSE
Amenity grassland	Grassland	3.617	36.738	FALSE
Amenity grassland	Parkland	46.341	38.455	TRUE
Amenity grassland	Scrub	39.341	40.895	FALSE
Amenity grassland	Suburban	36.299	36.738	FALSE
Amenity grassland	Urban no garden	8.909	51.387	FALSE
Amenity grassland	Urban with garden	27.191	38.455	FALSE
Amenity grassland	Woodland	46.391	38.455	TRUE
Commercial	Grassland	6.258	37.684	FALSE
Commercial	Parkland	43.700	39.360	TRUE
Commercial	Scrub	36.700	41.747	FALSE
Commercial	Suburban	33.658	37.684	FALSE
Commercial	Urban no garden	11.550	52.068	FALSE
Commercial	Urban with garden	24.550	39.360	FALSE
Commercial	Woodland	43.750	39.360	TRUE
Grassland	Parkland	49.958	37.684	TRUE
Grassland	Scrub	42.958	40.171	TRUE
Grassland	Suburban	39.917	35.930	TRUE
Grassland	Urban no garden	5.292	50.813	FALSE
Grassland	Urban with garden	30.808	37.684	FALSE
Grassland	Woodland	50.008	37.684	TRUE
Parkland	Scrub	7.000	41.747	FALSE
Parkland	Suburban	10.042	37.684	FALSE
Parkland	Urban no garden	55.250	52.068	TRUE
Parkland	Urban with garden	19.150	39.360	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Parkland	Woodland	0.050	39.360	FALSE
Scrub	Suburban	3.042	40.171	FALSE
Scrub	Urban no garden	48.250	53.895	FALSE
Scrub	Urban with garden	12.150	41.747	FALSE
Scrub	Woodland	7.050	41.747	FALSE
Suburban	Urban no garden	45.208	50.813	FALSE
Suburban	Urban with garden	9.108	37.684	FALSE
Suburban	Woodland	10.092	37.684	FALSE
Urban no garden	Urban with garden	36.100	52.068	FALSE
Urban no garden	Woodland	55.300	52.068	TRUE
Urban with garden	Woodland	19.200	39.360	FALSE

c) Total bird species richness

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity grassland	20.568	44.667	FALSE
Allotment	Commercial	17.750	45.448	FALSE
Allotment	Grassland	19.625	44.005	FALSE
Allotment	Parkland	22.150	45.448	FALSE
Allotment	Scrub	18.750	47.531	FALSE
Allotment	Suburban	18.833	44.005	FALSE
Allotment	Urban no garden	31.500	56.811	FALSE
Allotment	Urban with garden	12.300	45.448	FALSE
Allotment	Woodland	20.750	45.448	FALSE
Amenity grassland	Commercial	2.818	38.455	FALSE
Amenity grassland	Grassland	0.943	36.738	FALSE
Amenity grassland	Parkland	42.718	38.455	TRUE
Amenity grassland	Scrub	39.318	40.895	FALSE
Amenity grassland	Suburban	39.402	36.738	TRUE
Amenity grassland	Urban no garden	10.932	51.387	FALSE
Amenity grassland	Urban with garden	32.868	38.455	FALSE
Amenity grassland	Woodland	41.318	38.455	TRUE
Commercial	Grassland	1.875	37.684	FALSE
Commercial	Parkland	39.900	39.360	TRUE
Commercial	Scrub	36.500	41.747	FALSE
Commercial	Suburban	36.583	37.684	FALSE
Commercial	Urban no garden	13.750	52.068	FALSE
Commercial	Urban with garden	30.050	39.360	FALSE
Commercial	Woodland	38.500	39.360	FALSE
Grassland	Parkland	41.775	37.684	TRUE
Grassland	Scrub	38.375	40.171	FALSE
Grassland	Suburban	38.458	35.930	TRUE
Grassland	Urban no garden	11.875	50.813	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Grassland	Urban with garden	31.925	37.684	FALSE
Grassland	Woodland	40.375	37.684	TRUE
Parkland	Scrub	3.400	41.747	FALSE
Parkland	Suburban	3.317	37.684	FALSE
Parkland	Urban no garden	53.650	52.068	TRUE
Parkland	Urban with garden	9.850	39.360	FALSE
Parkland	Woodland	1.400	39.360	FALSE
Scrub	Suburban	0.083	40.171	FALSE
Scrub	Urban no garden	50.250	53.895	FALSE
Scrub	Urban with garden	6.450	41.747	FALSE
Scrub	Woodland	2.000	41.747	FALSE
Suburban	Urban no garden	50.333	50.813	FALSE
Suburban	Urban with garden	6.533	37.684	FALSE
Suburban	Woodland	1.917	37.684	FALSE
Urban no garden	Urban with garden	43.800	52.068	FALSE
Urban no garden	Woodland	52.250	52.068	TRUE
Urban with garden	Woodland	8.450	39.360	FALSE

Appendix 9 Kruskal-Wallis *post-hoc* test results for difference in bird diversity (as assessed by applying the Shannon-Wiener Diversity Index [H']) among land-use categories in Durham.

a) Wintering bird species diversity

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity grassland	48.576	44.667	TRUE
Allotment	Commercial	42.667	45.448	FALSE
Allotment	Grassland	29.708	44.005	FALSE
Allotment	Parkland	4.433	45.448	FALSE
Allotment	Scrub	0.708	47.531	FALSE
Allotment	Suburban	12.042	44.005	FALSE
Allotment	Urban no garden	42.917	56.811	FALSE
Allotment	Urban with garden	4.767	45.448	FALSE
Allotment	Woodland	1.167	45.448	FALSE
Amenity grassland	Commercial	5.909	38.455	FALSE
Amenity grassland	Grassland	18.867	36.738	FALSE
Amenity grassland	Parkland	53.009	38.455	TRUE
Amenity grassland	Scrub	49.284	40.895	TRUE
Amenity grassland	Suburban	36.534	36.738	FALSE
Amenity grassland	Urban no garden	5.659	51.387	FALSE
Amenity grassland	Urban with garden	43.809	38.455	TRUE
Amenity grassland	Woodland	47.409	38.455	TRUE
Commercial	Grassland	12.958	37.684	FALSE
Commercial	Parkland	47.100	39.360	TRUE
Commercial	Scrub	43.375	41.747	TRUE
Commercial	Suburban	30.625	37.684	FALSE
Commercial	Urban no garden	0.250	52.068	FALSE
Commercial	Urban with garden	37.900	39.360	FALSE
Commercial	Woodland	41.500	39.360	TRUE
Grassland	Parkland	34.142	37.684	FALSE
Grassland	Scrub	30.417	40.171	FALSE
Grassland	Suburban	17.667	35.930	FALSE
Grassland	Urban no garden	13.208	50.813	FALSE
Grassland	Urban with garden	24.942	37.684	FALSE
Grassland	Woodland	28.542	37.684	FALSE
Parkland	Scrub	3.725	41.747	FALSE
Parkland	Suburban	16.475	37.684	FALSE
Parkland	Urban no garden	47.350	52.068	FALSE
Parkland	Urban with garden	9.200	39.360	FALSE
Parkland	Woodland	5.600	39.360	FALSE
Scrub	Suburban	12.750	40.171	FALSE
Scrub	Urban no garden	43.625	53.895	FALSE
Scrub	Urban with garden	5.475	41.747	FALSE
Scrub	Woodland	1.875	41.747	FALSE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Suburban	Urban no garden	30.875	50.813	FALSE
Suburban	Urban with garden	7.275	37.684	FALSE
Suburban	Woodland	10.875	37.684	FALSE
Urban no garden	Urban with garden	38.150	52.068	FALSE
Urban no garden	Woodland	41.750	52.068	FALSE
Urban with garden	Woodland	3.600	39.360	FALSE

b) Breeding bird species diversity

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Allotment	Amenity grassland	14.326	44.667	FALSE
Allotment	Commercial	8.917	45.448	FALSE
Allotment	Grassland	14.375	44.005	FALSE
Allotment	Parkland	31.933	45.448	FALSE
Allotment	Scrub	23.521	47.531	FALSE
Allotment	Suburban	18.958	44.005	FALSE
Allotment	Urban no garden	25.917	56.811	FALSE
Allotment	Urban with garden	6.883	45.448	FALSE
Allotment	Woodland	33.133	45.448	FALSE
Amenity grassland	Commercial	5.409	38.455	FALSE
Amenity grassland	Grassland	0.049	36.738	FALSE
Amenity grassland	Parkland	46.259	38.455	TRUE
Amenity grassland	Scrub	37.847	40.895	FALSE
Amenity grassland	Suburban	33.284	36.738	FALSE
Amenity grassland	Urban no garden	11.591	51.387	FALSE
Amenity grassland	Urban with garden	21.209	38.455	FALSE
Amenity grassland	Woodland	47.459	38.455	TRUE
Commercial	Grassland	5.458	37.684	FALSE
Commercial	Parkland	40.850	39.360	TRUE
Commercial	Scrub	32.438	41.747	FALSE
Commercial	Suburban	27.875	37.684	FALSE
Commercial	Urban no garden	17.000	52.068	FALSE
Commercial	Urban with garden	15.800	39.360	FALSE
Commercial	Woodland	42.050	39.360	TRUE
Grassland	Parkland	46.308	37.684	TRUE
Grassland	Scrub	37.896	40.171	FALSE
Grassland	Suburban	33.333	35.930	FALSE
Grassland	Urban no garden	11.542	50.813	FALSE
Grassland	Urban with garden	21.258	37.684	FALSE
Grassland	Woodland	47.508	37.684	TRUE
Parkland	Scrub	8.413	41.747	FALSE
Parkland	Suburban	12.975	37.684	FALSE
Parkland	Urban no garden	57.850	52.068	TRUE

Comparison		Observation difference	Critical difference	Significant difference
Land-use category 1	Land-use category 2			
Parkland	Urban with garden	25.050	39.360	FALSE
Parkland	Woodland	1.200	39.360	FALSE
Scrub	Suburban	4.563	40.171	FALSE
Scrub	Urban no garden	49.438	53.895	FALSE
Scrub	Urban with garden	16.638	41.747	FALSE
Scrub	Woodland	9.613	41.747	FALSE
Suburban	Urban no garden	44.875	50.813	FALSE
Suburban	Urban with garden	12.075	37.684	FALSE
Suburban	Woodland	14.175	37.684	FALSE
Urban no garden	Urban with garden	32.800	52.068	FALSE
Urban no garden	Woodland	59.050	52.068	TRUE
Urban with garden	Woodland	26.250	39.360	FALSE

Appendix 10 Results of Principal Components Analysis (PCA): Eigenvectors (coefficients in the linear combinations of variables making up Principal Components [PCs]).

a) Wintering birds

Variable	PC1	PC2	PC3	PC4	PC5
Eurasian Sparrowhawk	0.000	-0.007	0.001	0.018	0.003
Common Pheasant	0.000	-0.011	0.000	0.021	0.010
Common Moorhen	0.002	-0.008	-0.009	-0.029	-0.002
Black-headed Gull	0.470	-0.319	-0.263	-0.687	-0.197
European Herring Gull	0.003	0.024	0.023	-0.031	-0.035
Common Gull	0.029	-0.026	-0.018	-0.054	-0.007
Stock Dove	-0.005	0.011	0.023	-0.022	-0.012
Common Woodpigeon	-0.170	0.012	0.257	0.017	-0.454
Eurasian Collared Dove	0.045	0.150	-0.205	-0.023	-0.013
Great Spotted Woodpecker	-0.008	-0.005	0.001	-0.001	0.005
Pied/White Wagtail	0.034	-0.011	-0.006	-0.003	-0.013
Winter Wren	-0.296	-0.109	-0.005	-0.184	-0.018
Hedge Accentor	-0.043	-0.002	-0.122	0.047	-0.026
European Robin	-0.197	0.036	-0.017	-0.085	0.129
Song Thrush	-0.032	0.001	0.025	-0.013	-0.029
Redwing	-0.036	-0.014	0.017	-0.009	0.010
Mistle Thrush	0.000	0.003	0.012	-0.004	-0.003
Eurasian Blackbird	-0.440	-0.067	-0.232	0.030	-0.527
Goldcrest	-0.062	-0.017	0.007	-0.029	-0.029
Great Tit	-0.380	-0.101	-0.070	-0.084	0.136
Coal Tit	-0.070	0.035	0.001	-0.084	-0.087
Blue Tit	-0.447	0.184	-0.029	-0.521	0.405
Long-tailed Tit	0.016	-0.102	-0.062	-0.155	-0.103
Wood Nuthatch	-0.067	-0.011	0.029	-0.064	0.027
Eurasian Treecreeper	-0.017	-0.002	0.009	-0.015	0.007
Black-billed Magpie	-0.151	0.066	-0.208	-0.166	-0.293
Eurasian Jay	-0.024	0.004	0.020	-0.006	-0.044
Eurasian Jackdaw	0.097	0.546	0.589	-0.353	-0.190
Rook	0.007	0.018	-0.012	0.007	-0.008
Carrion Crow	0.034	-0.136	0.087	-0.049	0.304
Common Starling	0.091	0.570	-0.558	0.036	0.070
House Sparrow	0.117	0.388	-0.148	0.046	-0.081
Eurasian Chaffinch	-0.081	-0.032	-0.060	0.003	0.077
Lesser Redpoll	0.004	-0.008	0.002	0.020	0.010
European Goldfinch	-0.026	0.044	-0.071	0.020	-0.133
European Greenfinch	-0.005	0.003	-0.024	0.059	-0.044
Eurasian Bullfinch	-0.024	-0.009	-0.014	0.003	-0.026
Eigenvalue (% variation explained)	0.223 (18.6)	0.205 (17.1)	0.119 (9.9)	0.103 (8.6)	0.085 (7.1)

b) Breeding birds

Variable	PC1	PC2	PC3	PC4	PC5
Common Pheasant	0.011	-0.003	0.004	-0.035	-0.001
Common Moorhen	-0.002	0.023	-0.007	0.015	-0.039
Common Coot	0.005	-0.004	0.018	0.017	0.010
Black-headed Gull	0.001	-0.004	-0.008	0.000	-0.008
European Herring Gull	-0.107	-0.051	0.137	-0.135	-0.268
Lesser Black-backed Gull	-0.061	0.026	0.113	-0.135	-0.138
Stock Dove	-0.001	-0.015	0.009	-0.026	-0.041
Common Woodpigeon	0.334	0.067	-0.550	-0.072	-0.621
Eurasian Collared Dove	-0.088	0.250	-0.126	0.044	0.077
Tawny Owl	0.017	-0.004	-0.001	-0.016	0.006
Common Swift	-0.040	-0.004	-0.020	0.043	0.105
Great Spotted Woodpecker	0.018	-0.021	-0.003	-0.040	0.025
Swallow	-0.095	0.101	0.081	-0.181	-0.016
Pied/White Wagtail	-0.029	-0.002	0.009	-0.021	-0.063
Winter Wren	0.354	-0.095	-0.005	-0.027	0.202
Hedge Accentor	0.106	0.112	-0.158	0.413	0.257
European Robin	0.263	-0.066	0.089	-0.321	-0.034
Song Thrush	0.113	0.036	-0.053	-0.043	-0.012
Mistle Thrush	0.028	-0.004	0.005	-0.026	-0.014
Eurasian Blackbird	0.211	0.394	-0.277	0.186	0.242
Garden Warbler	0.002	0.000	0.003	0.020	-0.010
Blackcap	0.153	-0.028	0.060	-0.010	0.080
Common Whitethroat	-0.009	-0.057	0.066	0.136	0.044
Common Grasshopper-warbler	-0.006	-0.013	0.042	0.028	0.004
Willow Warbler	0.017	-0.025	0.017	0.124	0.023
Common Chiffchaff	0.176	-0.053	-0.009	0.064	0.023
Goldcrest	0.080	0.003	-0.004	-0.023	-0.008
Spotted Flycatcher	0.007	-0.001	0.004	-0.001	-0.004
Great Tit	0.308	-0.042	-0.033	-0.144	0.203
Coal Tit	0.090	-0.006	-0.023	-0.084	0.010
Blue Tit	0.447	0.053	0.046	-0.356	0.275
Long-tailed Tit	0.016	-0.004	0.031	0.020	0.022
Wood Nuthatch	0.050	-0.011	-0.004	-0.067	-0.029
Eurasian Treecreeper	0.055	-0.020	0.002	-0.059	-0.026
Black-billed Magpie	-0.059	0.023	-0.019	-0.146	0.136
Eurasian Jay	0.005	-0.005	0.002	-0.015	0.010
Eurasian Jackdaw	-0.337	-0.473	-0.652	-0.219	0.336
Carrion Crow	-0.017	0.008	-0.125	-0.282	-0.044
Common Starling	-0.234	0.482	0.011	-0.473	0.130
House Sparrow	-0.145	0.472	-0.153	0.040	0.078
Eurasian Chaffinch	0.148	-0.034	-0.052	0.147	-0.061
Eurasian Linnet	0.008	0.035	0.047	0.026	0.051
European Goldfinch	-0.061	0.188	-0.196	0.004	-0.181

Variable	PC1	PC2	PC3	PC4	PC5
European Greenfinch	0.020	0.077	-0.087	0.058	-0.060
Eurasian Bullfinch	0.015	0.010	-0.014	0.056	-0.054
Yellowhammer	0.003	-0.007	0.000	0.003	0.012
Eigenvalue (% variation explained)	0.233 (19.4)	0.156 (13.9)	0.111 (9.2)	0.072 (6.0)	0.068 (5.7)