Spatial and temporal variation in the functional diversity of non-breeding wader communities across British estuaries

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Abstract

Many wader species depend on estuarine ecosystems during the non-breeding season. However, many estuaries around the world are under intense pressure from human impacts, greatly influencing the composition of wintering wader communities. Changes in communities have been documented using species richness and evenness. However, these measures do not account for the fact that coexisting species differ widely in the level of distinctness of the ecological roles they fulfil. Considering whole communities in terms of the range of traits, the ecological roles represented by each species and the mechanisms that regulate community assembly, is a more powerful method of understanding variation in community composition. In this thesis, national-scale datasets are used to explore spatial and temporal variation in the functional diversity (FD) of wintering wader communities across UK estuaries. Using null model analysis, I show that wintering wader communities, overall, are more functionally similar than expected from a random community with equivalent number of species, suggesting that environmental conditions have the strongest influence on structuring these communities. The relative influence of structuring processes appears to be changing through time, as communities are becoming more functionally diverse than expected by chance. Using different environmental datasets, I explore the spatial and temporal variation in FD and identify potential drivers. Furthermore, I investigate which species are more likely to contribute to changes in FD. Using data from WeBS Low Tide Counts, I go on to show a tendency for functionally similar species to aggregate within the intertidal area. The thesis findings emphasize the likely importance of environmental factors for wader community assembly. Understanding the processes underlying community assembly can help in understanding community responses to environmental change and improve conservation and management plans.

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General Introduction

Integrating functional traits for the understanding of biodiversity change

The continued demands of a rapidly growing human population are predicted to increase the degradation of ecosystems worldwide, with many biomes and biogeochemical cycles being deeply impacted by human actions (Vitousek *et al*., 1997). Although, historically, human activities have modified the distribution of habitat types across the globe (MEA, 2012) the rate of land use change has dramatically increased over the last century and many habitats have been severely degraded during this period (Goldewijk, 2001). Over the same period, the rates of exploitation of natural resources and introduction of non-native and invasive species have also increased dramatically (MEA 2012, and references therein). The impacts of the Anthropocene era on the global environment have mostly resulted in a general decline in biodiversity and shifts in species composition of natural communities. Over recent decades, these global changes have highlighted the need to preserve the diversity of ecological communities and to understand the potential consequences of biodiversity loss, which ultimately can affect the well-being of human populations through changes in ecosystems services (MEA, 2012). Therefore, evaluating and assessing biodiversity has become instrumental as a means of monitoring the environment (McCann, 2000). Several diversity indices have been developed which aim to measure different aspects of biological diversity and assess the health of ecological communities and ecosystems (Magurran, 2004).

Changes in biodiversity have been mostly documented using both species richness (the number of different species) and species evenness (the relative abundance of species within the community) (Loreau *et al*., 2002; Lepš 2004; Schmid & Hector, 2004). However, the multidimensionality of diversity means that using a single index compresses and reduces the complexity of ecological systems. Indices focused solely on species numbers and abundances ignore the degree of interspecific similarity or dissimilarity across species, and therefore do not account for the fact that some species may have stronger impacts than others upon their common ecosystem (Grime, 1998; Petchey & Gaston, 2002; Petchey, 2004; Valone & Schutzenhofer, 2004). Furthermore, there has been a growing recognition that ecosystem level processes may not be affected by species richness *per se* but, instead, the effects of biodiversity on ecosystem processes are mostly driven by species traits (Walker, 1992; Díaz & Cabido, 2001; Tilman, 2001; Petchey & Gaston, 2002; Hooper *et al*., 2005). This has resulted in a shift of the traditional and static view of communities towards a more functional and dynamic approach which focuses on the role of each species within the community, by using the value of species traits (Petchey & Gaston, 2006).

Functional traits, functional diversity and their ecological importance

Functional traits refer to ecological attributes of species that influence their performance (McGill *et al*., 2006). Functional traits relate species to both ecosystem processes (functional effect traits), such as productivity or pollination, as well as to their interaction with biotic and abiotic factors (functional response traits), such as resource availability or climatic variations. As such, functional traits reflect adaptations to different physical and biotic environments and can be morphological (*e.g*. body size, beak size), physiological (*e.g*. salinity tolerance), reproductive (*e.g*., seed or egg size), ecological (*e.g*. habitat breadth) or behavioural (*e.g*. feeding method) (Bremner *et al*., 2003; Dumay *et al*., 2004; Lepš *et al*., 2006). Functional response traits are commonly used to understand the variation in species distributions in response to environmental change (Hooper *et al*., 2002), whereas functional effect traits are mostly used in to investigate and infer the linkage between biodiversity and ecosystem functioning (Hooper *et al*., 2002). Interestingly the link between functional response and effect traits remains unclear, as these may or may not be correlated with each other (Lavorel & Garnier, 2002) and this is a matter of current debate within theoretical ecology.

Functional diversity (FD) measures the extent of functional trait variation within natural communities. For example, two communities with the same number of species may be more or less functionally diverse depending on how similar or different are the functional traits among species within both communities. Given that functional diversity incorporates information on a variety of life-history traits and ecological roles, it has been shown to be a more suitable indicator of ecosystem function than taxonomic indices (Díaz & Cabido, 2001; Petchey & Gaston, 2006). Additionally, substantial theoretical and empirical evidence supports the idea that functional diversity better explains variation in ecosystem processes (Hooper *et al*., 2005), and ecosystem services (Díaz *et al*., 2007), and can therefore provide a basis for understanding and predicting consequences of biodiversity changes in ecosystems.

Understanding the spatial and temporal variation in community FD and its drivers is important not only because it is associated with changes in ecosystem functioning but also because the presence of different sets of functional traits in a given community may suggest the operation of different community assembly processes (see section below) (McGill *et al*., 2006; Mouillot *et al*., 2007; Petchey *et al*., 2007; Thompson *et al*., 2010). However, to date, very few empirical studies have investigated how functional diversity varies along environmental and/or temporal gradients (but see de Bello *et al*., 2006; Mayfield *et al*., 2006; Flynn *et al*., 2009; Gerisch *et al*., 2011), and also how functional diversity may respond to global environmental change (but see Mayfield *et al*., 2010; Buisson *et al*., 2012). For instance, a decrease in FD could be expected in human-modified systems, which tend to be environmentally homogeneous and host more generalist species with similar functional traits whilst excluding species with relatively unique traits (McKinney & Lockwood, 1999). However, the few studies that have examined variation in FD along environmental/anthropogenic gradients have revealed contrasting patterns and further analysis is required in order to achieve consensus. Moreover, it is still unclear whether the prevailing effect of human action promotes the coexistence of more functionally similar or more functionally different species. Understanding the processes underlying community assembly can influence debate on these issues and may thus help to refine conservation strategies aimed at maintaining biological diversity, as well as understanding community responses to environmental change.

Functional diversity: a tool for disentangling community structure

For decades, ecologists have debated the importance of different processes in determining the assembly and maintenance of ecological communities, with particular consideration of the effects of environmental factors, biological interactions and random or neutral processes (Clements, 1936; Hubbell, 2001; Leibold *et al*., 2004; McGill, 2010; Pavoine & Bonsall, 2011; Münkemüller *et al.*, 2012). Neutral theory is predicated on the idea that communities represent random assemblages from a regional species pool, with species coexisting independently of their traits and all individuals of all species being equivalent in terms of their competitive ability, dispersal ability and fitness (Hubbell, 2001, 2005, 2006). In contrast, the classical view of community assembly (*i.e*. niche-based models) considers that a portion of species in the regional pool is excluded from membership of a particular local community through various biotic and environmental filters. The relative strength of these mechanisms/filters determines which traits or trait values occur in the local community. Environmental filtering will constrain specific traits from the species pool, resulting in coexisting species sharing more similar traits (underdispersion: species are likely to be more similar than expected by chance). Conversely, competitive exclusion, a primary biotic mechanism, will limit the trait similarity between coexisting species, resulting in coexisting species being more dissimilar in their traits and thus generating overdispersion of traits.

In order to facilitate investigation into the role of species' traits in community assembly and structure a number of recent studies have integrated measures of functional diversity (*e.g.* Petchey & Gaston, 2002; Mason *et al*., 2005; Cornwell *et al*., 2006; Mouillot *et al*., 2007; Petchey *et al*., 2007; Algar *et al*., 2011; de Bello, 2012). These studies have predominately focused on measuring differences between observed functional diversity and the functional diversity expected under a null model, as a means of providing evidence supporting or opposing the operation of non-neutral processes (Ricklefs & Travis, 1980; Mouillot *et al*., 2007; Petchey *et al*., 2007; Thompson *et al*., 2010; de Bello, 2012). These studies suggest that environmental factors will lead to a lower functional diversity than expected by chance (Cornwell *et al*., 2006), while competitive exclusion will lead to a greater FD than expected by chance (*e.g.* Holdaway & Sparrow, 2006; Petchey *et al*., 2007; Thompson *et al*., 2010).

It has been suggested that the role of the structuring mechanisms may be scale-dependent (Zobel, 1997; Kraft *et al*., 2007; Funk *et al*., 2008), with environmental effects likely to be stronger at larger scales (Díaz, Cabido & Casanoves, 1998; Cornwell, Schwilk & Ackerly, 2006), whereas competitive exclusion effects are likely to have greater influence at smaller scales (Cavender-Bares *et al*., 2004; Slingsby & Verboom, 2006). These structuring mechanisms are not mutually exclusive and can co-occur simultaneously across scales (de Bello *et al*., 2006; Mouillot *et al*., 2007). For example, low water availability, a stressful environmental condition, may constrain the traits arriving from the species pool allowing only for a narrow range of similar traits to be present in the community (*e.g*. drought resistance traits), but simultaneously it may also cause an intensification of competitive interactions between similar species as a result of limiting resources. There is currently very little empirical evidence for how the relative strength of mechanisms structuring communities may vary along environmental gradients, and this is an issue that urgently requires further research, as the current fast pace of environmental change is likely to alter the strength of the mechanism regulating community composition.

Waders across the globe

Wader (Charadrii) species can have very large distribution ranges and can occupy numerous biomes throughout the world (Hayman *et al*., 1986). Most wader species are migratory and there are many species that breed at arctic and subarctic latitudes and winter from temperate regions to Patagonia and South Africa. This group of birds is generally associated with wetlands (both coastal and inland) but a few are also found in other habitats (*e.g*. arid & semi-arid, Stone curlews *Burhinus oedicnemus*; open plains, Upland sandpiper *Bartramia longicauda*; mountain ranges, Dotterel *Charadrius morinellus*). During the non-breeding season most waders inhabit tidal habitats, feeding in the inter-tidal zone at low tide and roosting above the high water mark at high tide. They display a remarkable range of morphological, behavioural and ecological traits that reflect the multiplicities of responses to the resources consumed, and also adaptations to their environmental conditions. Common wader prey includes macro-benthos, particularly polychaetes, crustaceans and molluscs, which are abundant in estuarine systems. However, these prey taxa are not equally important to all waders. The quantity and type of food resource used by each wader species and the methods to acquire them (foraging strategies) are closely linked to each species' morphology. For example, to a large extent prey size and burrowing depth are correlated with the wader species' bill size, hardness and shape

(O'Connor, 1981; Ferns 1992). Plovers have the shortest bills of all waders and tend to locate prey by sight and feed by pecking on the surface of the sediment, whereas godwits, with long and sensitive bills, locate prey by touch while probing deep within the burrows of their prey like lugworms and ragworms (Figure 1). In contrast, the majority of sandpipers forage by sight, visually scanning a search area (in some cases while walking) and then, when signs of prey are located, either pecking at prey on the surface of the sediment or probing deeper in order to locate them.

The wide distribution of waders across biomes, and their wide range of foraging methods and adaptations, provides an excellent study system in which to investigate patterns of functional diversity across wader communities and how it might vary along distinct environmental gradients.

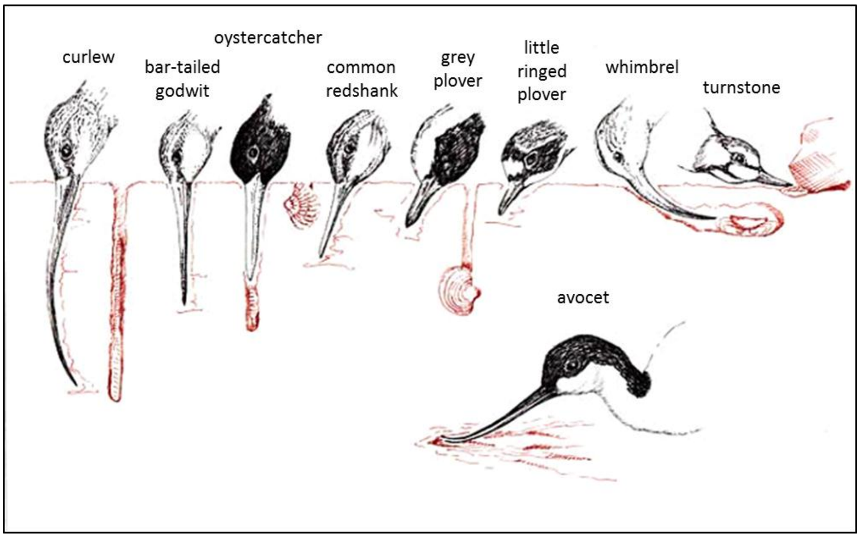

Figure 1. Bill size and shape of various waders in relation to the depth of prey species. From left to right: curlew (*Numenius arquata*), bar-tailed godwit (*Limosa lapponica*), oystercatcher (*Haematopus ostralegus*), common redshank (*Tringa totanus*), grey plover (*Pluvialis squatarola*), little ringed plover (*Charadrius dubius*), whimbrel (*Numenius phaeopus*), turnstone (*Arenaria interpres*) and avocet (*Recurvirostra avosetta*). Reproduced from studentmag.acsedu.com/Articles/Seabirds-and-Waterbirds.aspx

Wintering wader communities in the UK

The United Kingdom with its extensive areas of highly productive estuarine environments, its relatively mild winter owing to the influence of the Gulf Stream (van de Kam *et al.*, 2004), and its location on one of the major flyways for Arctic nesting species, is internationally important for several wintering wader populations. The UK holds over 20% of the populations of 10 species across the flyway (Musgrove *et al.,* 2011). However, as with estuarine areas elsewhere, a high proportion of the UK's human population is concentrated near the coast (particularly around estuaries), resulting in continuous anthropogenic pressures on this ecosystem. Almost 90% of UK estuaries have already been affected by land claim and marinas, recreational and housing schemes and tidal power barrages are common around estuaries in Britain (Davidson *et al*., 1991). The potential vulnerability of both habitats and waterbird species to these pressures has provided the impetus for national-scale monitoring of waterbird populations, through the Wetland Bird Survey (WeBS). The UK is also a signatory country to the Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention), the Convention on the Conservation of Migratory Species of Wild Animals (CMS), the African-Eurasian Migratory Waterbird Agreement (AEWA), and the Convention on Biological Diversity (CBD). In addition, the UK, as part of the European Union, is required to enforce the Birds Directive 2009/147/EC and Habitats Directive 92/43/EEC (Bern Convention). These conventions and directives require the UK to set-up and maintain a monitoring scheme for waders and other waterbird populations and to promote their conservation.

In the early 1970s, a monitoring scheme was implemented in the UK, in order to assess population status and trends of waterbird species, firstly as the Birds of Estuaries Enquiry (BoEE) and latterly as the Wetland Bird Survey (WeBS). The current WeBS is a joint scheme of the British Trust for Ornithology (BTO), Royal Society for the Protection of Birds (RSPB) and Joint Nature Conservation Committee (JNCC), in association with Wildfowl & Wetlands Trust (WWT). WeBS Core Counts are synchronised monthly counts carried out across the majority of wetland types in the UK on predetermined dates, thus minimizing the likelihood of double-counting some individuals or missing others. A recent addition to this scheme has been developed, the Low Tide Counts, which are undertaken on selected estuaries for identifying key areas used by waders during this period of the tidal cycle. Both datasets provide a valuable resource for the large-scale study of waterbird populations and communities.

The monitoring of waders across Britain provides the data required for designating the importance of individual sites for these populations (*e.g*. Stroud et al., 2001) and also to quantify national-scale population trends (population size, distribution and temporal trends) (Thaxter *et al*., 2010). Following decades in which populations of several waterbirds had increased, some are now declining, such as ringed plover and dunlin (Holt *et al*., 2011). Conversely, other species such as the avocet and the black-tailed godwit have been increasing since the start of these monitoring programs. In addition, the distribution of many species has also changed since the 1970s, with evidence that the mid-winter centroid of the range of several species is now further eastwards and/or northwards than in previous decades (Rehfisch *et al*., 2004; Maclean *et al*., 2008). These levels of variation in population trends and distribution have been analysed in an attempt to identify and understand the factors underlying changes in abundance and distribution of species at the population level. Previous studies have suggested that changes in wader abundance may be related to a combination of factors that include habitat loss resulting from land claim, dredging and urbanization (Goss-Custard *et al*., 1995, 2006; Dolman & Sutherland, 1995), human disturbance (Gill *et al*., 2001; Burton *et al*., 2002; West *et al*., 2002), shell-fisheries (Atkinson *et al*., 2010) and changes in the amount of organic nutrients discharged into coastal waters, resulting in changes in invertebrate prey communities (Alves *et al*., 2012). However, much less research has been focused on understanding wader community level dynamics and the processes influencing community assembly (but see Hill *et al*., 1993; Rehfisch *et al*., 1997; Atkinson *et al*., 2010).

To date, only two large-scale studies on wader communities across UK have investigated variation in community composition (Hill *et al*., 1993; Rehfisch *et al*., 1997). The early study by Hill and co-workers (1993) revealed that wader composition is influenced by physical estuarine characteristics, in particular by the type of intertidal habitat and the tidal range, alongside salinity, ammonium-N concentration in water, percentage dissolved oxygen and biochemical oxygen demand. Rehfisch and colleagues (1997) identified seven environmental variables that influence community composition, including the morphological, sedimentological and geographical characteristics of the estuary (estuary length, channel and shore width, exposure to swell, sediment type, longitude and latitude). Both studies produced a classification of communities according to species composition. Hill and co-workers identified four wader community types according to latitude, tidal range and total estuary area whereas Rehfisch and colleagues (1997) identified seven communities, where latitude, longitude and estuary length discriminated the groups. Differences between these studies might be attributed to: (i) the difference between the taxonomic breadths of species studied, since Rehfisch *et al*. included also wildfowl species such as pintail and wigeon; and/or (ii) the difference between the number of sites included, since Hill *et al*. included 109 estuaries and Rehfisch *et al*. only 27, hence, it is likely that the variation in environmental factors may be different. Despite these differences, both studies converge on the effect of geographical position and size of estuary in influencing wader community composition. However, neither study considered resource use, which is likely to be an important if not predominant factor driving community dynamics. The processes that sustain wader communities and allow species' co-existence remain poorly understood. Furthermore, we do not know (i) how these processes vary along environmental gradients and whether they are changing through time, and (ii) how population changes influence the composition and structure of whole communities. Understanding the processes underlying community assembly is key for understanding community responses to environmental change, because changes in the relative strength of the processes structuring communities can result in changes in community composition and consequently, in changes to ecosystem functioning.

Thesis structure

In this thesis, the two national-scale surveys of wader distribution in the UK (WeBs Core and Low Tide counts) are used to explore (i) spatial and temporal variation in functional diversity of wintering wader species, (ii) the variation in community structure along environmental gradients and (iii) how changes in wintering population size contribute to changing patterns of functional diversity and community structure.

The wide range of morphological, behavioural and ecological characteristics of waders, and their high winter dependency in estuarine habitats, results in a model study system in which functional diversity can be used to understand the processes determining (wader) communities, as well as the functional ecological significance of community structure and complexity. In **chapter one**, winter WeBS Core Counts collected between 1980/81 and 2006/07 are used to explore the geographical and temporal variation in functional diversity and community structure across 100 British estuaries. Overall, wintering wader communities show greater similarity in functional trait states than expected from a random community with equivalent numbers of species. Furthermore, this similarity amongst species appears to be changing through time. The potential drivers and mechanisms underlying these patterns are discussed.

Wader functional diversity estimations in chapter one were calculated using presence-absence data, thus limiting the changes in functional diversity to only be sensitive to changes in species local extinction or colonization, while being insensitive to changes in population size. Surprisingly, it is currently unknown how population size and site occupancy might impact community structure. In **chapter two**, I therefore examine the association between temporal trends in population size and wintering occupancy for wader communities on 83 estuaries around Britain. This analysis revealed that the direction and magnitude of changes in wintering wader population size and occupancy are species-specific. Then, using the estimates extracted from chapter one of the deviation between observed and expected functional diversity, I explore the impact of changes in species distribution on spatial and temporal patterns in functional diversity and community structure.

Despite the wealth of scientific research evaluating factors underlying changes in population abundance, there is relatively little understanding of the consequences of changes in population size for changes in occupancy and local abundance. In **chapter three**, I tackle this issue by investigating the patterns of change in local abundance and site occupancy of wintering wader species throughout Britain over the last two decades (from 1980/81 to 2006/07). While large changes in site occupancy were apparent for a few species, changes in total wintering population size were typically manifest as changes in local abundances rather than in occupation of sites. This analysis provides insights into the processes influencing changes in local abundance and range expansion during periods of population fluctuations and possible ecological correlates of changes in population size are explored.

The geographical variation in functional diversity of wintering wader communities across Britain may be due to variation in environmental conditions operating at the same spatial scale, and the direction and magnitude of change in functional diversity may be associated with changes in environmental conditions. Therefore, in **chapter four**, I use the previously estimated deviations of observed from expected functional diversity to explore geographical variation in community structure in relation to the estuarine morphology, climatic conditions and anthropogenic activities. I also investigate if the magnitude and direction of annual changes in deviations of observed from expected FD relates to changes in climatic conditions or other habitat-derived factors.

Patterns of species co-existence are normally assessed using trait-based (as in this thesis) or species-based (spatial dispersion) approaches to determine whether species traits converge or diverge, or whether species aggregate or segregate spatially in relation to null expectations. Although both approaches share the common aim of identifying the mechanisms by which species co-exist, it is not known whether a relationship between spatial and trait dispersion exists. In **chapter five**, using Low Tide Counts, I therefore explore spatial distribution within and between species. For the latter, I examine whether co-occurrence patterns differed from null expectations across the eight sites included in this analysis. I then examine the relationship between species-pair co-occurrence patterns and species-pair functional differences, and test whether co-occurring species tend to be more or less functionally dissimilar. The possible mechanisms driving the observed patterns are discussed.

Finally, the **General Conclusions** provides a synthesis of the main results from the thesis, their implications for conservation planning and future directions of this work.

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Chapter one

Functional diversity across space and time: trends in wader communities on British estuaries

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Abstract

Aim British estuarine ecosystems support large populations of protected migratory waders. Understanding how wader communities vary spatially and how they may be changing temporally can greatly improve understanding of these dynamic ecosystems. Here we explore the variation in functional diversity (using a range of morphological and ecological traits) in order to identify the processes shaping wader communities on British estuaries and how these processes may be changing.

Methods We use national survey data (Wetland Bird Survey) from 1980/81 to 2006/07 winter to calculate functional diversity (FD) – an index that measures trait dispersion - in wader communities on 100 estuaries. We test for evidence of non-random patterns of diversity and explore the relative importance of two key processes, environmental filtering and competition, in shaping these communities.

Results The observed FD was significantly and positively associated with species richness and to a lesser extent estuary area, followed by longitude. An increase in observed FD was observed since 1980, supported by a small but significant slope. In the majority of cases, changes in FD were mirrored by changes in species richness. Observed FD was on average lower than expected by chance, as indicated by a negative value of observed minus expected FD. However, this difference became less negative over time, with observed minus expected FD values increasing slightly, but significantly, over the study period.

Main conclusions Wader FD varies across British estuaries and the relative influence of the processes by which communities are structured appears to be changing through time. We discuss the potential drivers underlying these patterns and the importance of identifying such drivers for the protection of wader communities.

Keywords Community composition, community structure, competition, environmental filtering, functional diversity, waders.

Introduction

Classically, macro-ecological studies have focused on understanding patterns of biodiversity distribution such as patterns in the frequency distributions of species characteristics (*e.g.* Blackburn & Gaston, 1994), relationships between species characteristics (*e.g.* Stevens, 1989), species richness (*e.g.* Rosenzweig, 1995) and the possible mechanisms driving such patterns (*e.g.* MacArthur & Levins, 1967; Hubbell, 2001). More recently, ecological studies have focused more attention on the implications of global biodiversity decline and ecosystem functioning, focusing on developing measures of functional diversity (reviewed in Petchey & Gaston, 2006; Mouchet *et al.*, 2010).

Functional diversity (hereafter referred to as FD) measures the extent of functional trait dispersion of natural communities (Diaz & Cabido, 2001; Tilman, 2001). FD is a biodiversity metric that carries information on the variety of life styles and ecological roles contributed by species. It provides a basis for an understanding not only of the mechanistic links between biodiversity and ecosystems (Diaz & Cabido, 2001; Tilman, 2001; Hooper *et al*., 2002), but also of which mechanisms act to promote species coexistence and hence community structure (Mouquet *et al*., 2002; Petchey & Gaston, 2002, 2006). Several distinct community assembly dynamics have previously been postulated to explain species coexistence. Neutral theory is predicated on the idea that communities represent random assemblages from a regional pool, with species coexisting independently of their traits and all individuals of all species being functionally equivalent; *i.e.* species are identical in their competitive ability, dispersion and fitness (Hubbell, 2001, 2005, 2006). In contrast, classical assembly rules theory (*i.e.* niche-based models) predicts that communities are assembled non-randomly, based on the similarities or differences in their traits through the dual influences of environmental filtering effects and/or species interactions. The environmental filtering model assumes that abiotic factors act as a filter constraining specific traits within the species pool, hence allowing a relatively narrow range of trait values to be present in natural communities. As a result, the FD of a community will be lower than expected by random assembly and coexisting species will be more functionally similar than expected. Alternatively, models based on species interactions, in particular competition, assume that there will be displacement between species with similar traits and that natural communities will form primarily from species with complementary traits. As a result, the FD of the community will be greater than expected by chance and hence coexisting species will be more functionally dissimilar than expected (*e.g.* Holdaway & Sparrow, 2006; Petchey *et al*., 2007; Thompson *et al*., 2010).

Understanding spatial and temporal variation in community FD is important because different levels of trait dispersion among communities suggest the operation of different assembly rules (*e.g.* McGill *et al*., 2006; Mouillot *et al*., 2007; Petchey *et al*. 2007; Thompson *et al*., 2010) and potential consequences for ecosystem functioning (Kinzig *et al*., 2002). Spatial and temporal anthropogenic gradients are known to modify patterns of community assembly. For example there is evidence that human modified environments promote communities dominated by generalist species (Devictor *et al.*, 2007, 2008). While these communities are often more taxonomically and ecologically restricted (McKinney & Lockwood, 1999), it is uncertain whether the prevailing effect of human impacts is to intensify filtering of community functional diversity relative to regional species pools, or to promote competitive exclusion among functionally similar species. Understanding the processes underlying community assembly can inform conservation strategies to maintain biological diversity and monitor community responses to environmental change.

Non-breeding waders (Charadrii) in Great Britain provide an opportunity to address these issues in community ecology and FD research, not only because they display a remarkable range of morphological, behavioural and ecological traits but also because, outside the breeding season, the majority of wader species entirely depend on wetland habitats, particularly estuaries. The UK attracts a large number of wader species due to its position on one of the major flyways for Arctic nesting species (the East Atlantic flyway), its relatively mild climate during winter, and its extensive areas of highly productive estuarine environments. However, as with estuarine environments elsewhere, British intertidal habitats are under high anthropogenic pressure, with almost 90% of the estuaries affected by land claim (Davidson *et al*., 1991). The consequent vulnerability of both habitats and waterbird species has provided the impetus for national-scale monitoring of waterbird populations, allowing the assessment of population size, distribution and temporal trends and the importance of individual sites for these populations. Currently, much attention is focused on trying to identify and understand the drivers of changes in abundance and distribution of species at the population level, including the effects of habitat loss (*e.g*. Goss-Custard *et al*., 2006; Burton *et al.,* 2010), climate change (*e.g.* Austin & Rehfisch, 2005; Maclean *et al*., 2006, 2008) and other human disturbances (*e.g.* Gill *et al*., 2001; Burton *et al.,* 2002; West *et al*., 2002). To date, however, relatively few attempts have been carried out to understand wader community level dynamics and processes across British estuaries (but see Hill *et al*., 1993; Atkinson *et al*., 2010).

The abundance and distribution of non-breeding waders across British wetlands have been monitored since the late 1960s, presently by the Wetland Bird Survey (WeBS), a joint scheme of the British Trust for Ornithology (BTO), Royal Society for the Protection of Birds (RSPB) and Joint Nature Conservation Committee (JNCC), in association with the Wildfowl & Wetlands Trust (WWT) (Calbrade *et al*., 2010; Thaxter *et al.,* 2010). We investigate this large database, at the level of whole estuaries (equivalent to a landscape scale), in order to (1) examine spatial and temporal variation in FD of wader communities across Great Britain over the last 27 years, and (2) understand the extent to which wader communities are assembled randomly or non-randomly and hence whether there are discernable patterns of community assembly. The observed patterns are discussed in the context of the possible ecological drivers and/or anthropogenic impacts which may underlie such trends.

Methods

Data collection

We used bird count data from 100 estuaries distributed across Great Britain from the WeBS Core Count scheme for the period 1980/81 to 2006/07 in our analysis. Estuary area was derived from a GIS shapefile of estuary boundaries of high tide WeBS Core Count sectors.

Under the WeBS scheme and its predecessors, synchronized monthly counts are carried out at the UK's important wetlands on predetermined dates (minimizing the likelihood of double counting some individuals or missing others) to provide the information needed to monitor the populations of UK non-breeding waterbirds. Detailed information on the survey methodology, count accuracy and completeness are provided in Calbrade *et al*. (2010).

Different wader species occur in Great Britain at different times of the year. Some species are passage and/or winter visitors (*e.g.* grey plover *Pluvialis squatarola*), whereas others are migrant and/or resident breeders with numbers supplemented by visitors in winter (*e.g.* avocet *Recurvirostra avosetta*). WeBS counts are made all year round, though wader populations are at their greatest from October to March. We used only data recorded during winter (November- February) when the number of birds using a site more accurately reflects stable non-breeding population numbers. We restricted the analysis to twenty wintering species, based on their high winter dependency on estuaries rather than other habitats (Table 1). All species are waders with the exception of shelduck *Tadorna tadorna*, which (as elsewhere, *e.g.* Clark & Prys-Jones, 1994) is included here since it is highly dependent on estuaries for winter feeding and has a similar feeding ecology to waders, in particular being reliant on intertidal invertebrate prey.

WeBS counters record all waterbirds seen on a site. However, some species recorded may not typically be considered part of the wintering community, for example, a species only recorded during one month in very low numbers. Consequently, only species occurring on a site in at least 60% of all winter months counted were included within the community at that particular site. Analyses of the data with and without this constraint on species inclusion were conducted and both produced qualitatively very similar results. Hence, we only present the former results.

Table 1. The 20 species of waterbirds included in the analyses. All species are waders with the exception of shelduck *Tadorna tadorna.*

Common name	**Scientific name**
Ringed plover	*Charadrius hiaticula*
Golden plover	*Pluvialis apricaria*
Grey plover	*Pluvialis squatarola*
Lapwing	*Vanellus vanellus*
Oystercatcher	*Haematopus ostralegus*
Avocet	*Recurvirostra avosetta*
Turnstone	*Arenaria interpres*
Sanderling	*Calidris alba*
Dunlin	*Calidris alpina*
Knot	*Calidris canutus*
Purple sandpiper	*Calidris maritima*
Ruff	*Philomachus pugnax*
Bar-tailed Godwit	*Limosa lapponica*
Black-tailed Godwit	*Limosa limosa*
Curlew	*Numenius arquata*
Whimbrel	*Numenius phaeopus*
Spotted redshank	*Tringa erythropus*
Greenshank	*Tringa nebularia*
Redshank	*Tringa totanus*
Shelduck	*Tadorna tadorna*

Measuring observed and expected FD

Waders display a remarkably high level of behavioural and morphological variation, particularly with regards to their feeding apparatus and feeding ecology (Burton, 1974). This results in variation in the types of prey that are exploited. To calculate the community FD at each estuary every year, seven trait types were chosen to capture this key aspect of variation among waders relating to their capacity to exploit food resources (Table 2, see Appendix 1 for descriptions of the foraging methods). Similar combinations of traits have already been used in other studies of avian FD (*e.g.* Petchey *et al*., 2007). The size of the prey can influence the distribution of individuals within estuaries (Alves *et al*., 2013) and could also influence the position of species within the functional space. However, there is no data available regarding the prey size consumed by the majority of the species included in this analysis. However, prey sizes are limited by bill structure and size as well as prey profitability (van de Kam et al., 2004). Furthermore, prey detectability can also influence the types and sizes of prey that are consumed and waders have evolved different mechanisms related to the eyes and pressure – sensory mechanisms within the bill that allows them to increase the detectability of their prey (Gill, 2012). Therefore, the combination of traits presented in Table 2 represents an adaptation of waders to prey type and size, capturing the influence of prey size on the presence/absence of species in estuaries. Trait values were obtained from the BTO data base (http://www.bto.org/about-birds/birdfacts) and from The Birds of the Western Palaearctic on interactive DVD-ROM (2006), using information for populations that occur in UK whenever possible. Mean trait values for species were used for continuous traits, while diet components, foraging methods and traits involved in prey location were divided into independent binary traits, as these are not mutually exclusive (Petchey *et al.*, 2007).

Table 2. Traits used to measure functional diversity with regard to resource use. Trait values were obtained from the British Trust for Ornithology database and from The Birds of the Western Palaearctic on interactive DVD-ROM (2006), using information for populations that occur in UK whenever possible.

Trait	Type	Values	Units/ Categories
Body mass	Continuous	Mean	Gram
Bill length	Continuous	Mean	Centimetre
Tarsus length	Continuous	Mean	Centimetre
Bill shape	Categorical	3 categories	Up-curved, straight, down-curved
Main component of diet	Binary	9 categories	Insects, crustaceans, worms, molluscs, medusa, amphibians, fish, plant material, others
Location of prey	Binary	2 categories	Touch, sight
Main foraging strategy	Binary	10 categories	Pecking, probing, jabbing, stitching, ploughing, scything, foot trembling, turning over objects, hammering, swimming

To calculate the values of FD for each community on each site in each year, we followed Petchey & Gaston's (2002, 2006) methodology, using species presence/absence data. First, the entire species by trait matrix for all 20 species was converted into a distance matrix and this was then clustered to produce the functional dendrogram that describes the functional relationships between species. Gower distance was used throughout because it can deal with data-sets comprising continuous, ordinal and categorical traits (Gower, 1971; Pavoine *et al.*, 2009). UPGMA clustering was used because when compared with other clustering algorithms - single and complete - it produced a dendrogram with the highest cophenetic correlation (c = 0.7) (Appendix 2).

The regional FD (*i.e.* the FD for a community with all 20 species) was measured as the total branch length of the dendrogram and was used to standardize all measures of FD to vary between 0 and 1, where 0 occurs for single species communities and 1 for communities including all 20 species. The local FD (*i.e.* observed FD) was measured as the sum of the branch lengths connecting all the species present in a given community. To calculate expected FD, random communities were assembled, controlling for number of species, under two alternative null models. First, the random communities were assembled assuming that each species from the regional pool has the same chance of occurring. Second, the random communities were constructed based on the relative occurrence of species summed across the data set. In both cases, 1000 independent randomizations were made per estuary site. We confirm that parameter estimates had stabilised after 1000 randomizations. FD was calculated for each of the 1000 random communities and the mean was used as the expected FD for each random community in each site. Analyses of the data using both null models produced qualitatively very similar results. We only present the second approach, as we believe it is more realistic to take into account the frequency of occurrence of species. However, we note that, to date, there is no consensus on how best to generate the random communities for the null models and this is still widely debated (*e.g.* Mason *et al.*, 2007; Thompson *et al.*, 2010; de Bello, 2011). All analyses were conducted in R (R Development Core Team 2010).

Analysing variation in observed FD

To understand the variation in FD across British estuaries, we used bivariate and multiple regression analysis where observed FD was modelled as a function of species richness, estuary area, latitude and longitude. We tested the fit of all combinations of these four predictors and determined which model had the lowest AIC value, and which set of models together had >0.95 probability of including the best model (Burnham & Anderson, 2001). We also compared the explanatory power of the predictors.

In order to explore changes in species richness and wader FD over time, we used mixed effects models where richness and FD were modelled as a function of year and estuary, with estuary as a random effect. The random structure in the statistical model accounted for some of the variation introduced by each estuary. Estuaries with poor temporal coverage (temporal coverage < 80%) were excluded from the analyses. We assessed the extent to which spatial autocorrelation might be influencing our statistical models by plotting model residuals using the Moran's *I* correlogram function in Spatial Analysis for Macroecology (SAM) software v4.0 (Rangel *et al.*, 2010). Spatial autocorrelation was not significant (P>0.05) for any lag-distance class within our data.

Analysing variation in observed and expected FD

We compared patterns of observed FD of local communities with patterns of expected FD of random communities to investigate community assembly patterns. We used a standardised measure of comparison between observed and expected, the standardised effect size index (SES; Gotelli & McCabe, 2002), calculated as (observed FD – expected FD)/standard deviation of expected FD. Local communities are considered to be assembled at random if SES is not significantly different from zero. However, if SES is significantly greater than 0, then trait divergence/ complementarity is likely to occur due to interspecific competition, whereas if SES is significantly less than 0, trait convergence / similarity due to environmental filtering is likely to be the stronger influence on community structure (Petchey & Gaston, 2007; Hardy, 2008; Thompson *et al*., 2010; de Bello, 2011).

We followed the methodology described in Thompson *et al*. (2010) to estimate if SES: (i) was significantly different from zero; (ii) varied between estuaries; (iii) changed through time, and (iv) changed differently through time between estuaries. Two statistical models were used, where SES was modelled as a function of year and estuary, with estuary as a random effect allowing each estuary to have a different rate of change through time (model 1) and with each estuary having the same rate of change through time (model 2). In both models, year was treated as a continuous variable and accounted for temporal autocorrelation and non-independence caused by repeated measures at the same estuary. Prior to the analyses, year was transformed by subtracting the mean and rescaling to the interval [-1, 1]. Thus, the intercept estimates coincided with the middle point of the time period of this study (year 1993) and the slope estimates were changes in SES expected over half of the time period. The overall intercept of each model is the mean of the intercept values for each estuary.

To address the points described above (i) the overall intercept of model 1 was used and the significance was tested generating a sample from the posterior distribution of the parameter using Markov chain Monte Carlo simulation; (ii) we compared the explanatory power between model 2 and the same model without random effect using a likelihood ratio test; (iii) the significance of the year effect in model 2 was tested with Markov chain Monte Carlo simulation, and (iv) a likelihood ratio test was used to compare the explanatory power between model 1 and model 2 (Thompson *et al.*, 2010).

A sensitivity analysis was conducted in order to assess the influence of uncommon species on the observed patterns of functional diversity and their differences with expected functional diversity. To do this we removed one at a time, the three species with lowest frequencies of occurrence, both from our observed communities and from the regional species pool, and re-ran our analyses. The three species were whimbrel (*Numenius phaeopus*), spotted redshank (*Tringa erythropus*) and ruff (*Philomachus pugnax*). For all three species removals, the changes to the results were negligible and did not alter the overall findings and conclusions from analyses of the complete communities. We therefore only present the results from the latter set of analyses.

Results

Observed functional diversity patterns

For the last year of the study data (2006/7), bivariate tests showed that observed FD across estuaries is strongly positively associated with species richness and to a lesser extent estuary area, followed by longitude (Figure 1). In contrast, there is no significant latitudinal gradient in absolute levels of wader community FD around Great Britain (Figure 1c). Multiple regression models of all combinations of predictors showed that the model with species richness alone had the lowest AIC (-326.1) and a probability (Akaike weight) of 0.84 of being the best model. This model and the model containing both species richness and longitude had a combined probability of 0.986 that they included the best model. However, simultaneously fitting species richness inverted the slope of relationship for longitude to negative. The regression results for each of the other data years tested separately showed essentially the same pattern, hence we present only the results for 2006/7. Spatial autocorrelation was found to be absent from residuals of the best-fit models (Moran's I associated p-values > 0.05).

Overall, an increase in species richness and FD was observed since 1980 (Figure 2) and supported by a small but significant positive slope in both models ($p<0.0001$). Figure 3 shows the spatial distribution of FD at the beginning and the end of the time period and the absolute change in FD.

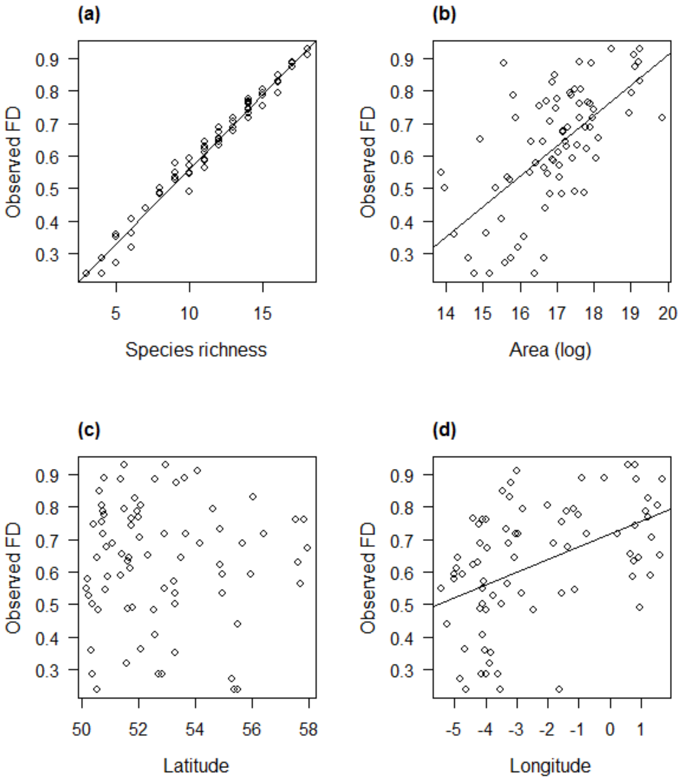

Figure 1. Relationships between observed wader functional diversity across 100 British estuaries and (a) the number of species present, (b) estuary area (log transformed), (c) latitude and (d) longitude. For presentation purposes, only the final year (winter 2006/07) is shown. The solid line is the linear model predicted relationship for (a) R^2=0.9, $p < 0.0001$, (b) R^2=0.5, $p < 0.0001$, (c), R^2=0.01, p=0.1 and (d) R^2=0.2, $p<0.0001$. FD is standardised to the interval [0, 1].

Differences from expected functional diversity

The observed FD in British wader communities was on average lower than expected by chance, as indicated by a negative overall intercept in the mixed models relating SES to year and site (Table 3). The explanatory power of the negative relationship between species richness and SES is very weak (R^2 = 0.04), but statistically significant (p=0.04) (Figure 4.).

Table 3. Parameter estimates from the mixed effects model of variation in SES, the standardised effect size, calculated as (observed FD - expected FD)/standard deviation in expected FD. Also given χ^2 values and associated significance values for each. Significance is given at the 95% confidence interval.

Parameter	Estimate (SE)	χ^2	p
Differences in estuary slopes (random effects)	NA	89.406	<0.00001
Differences in estuary intercepts (random effects)	NA	1085.929	<0.00001
Overall slope (Year effect)	0.01 (0.001)	NA	0.03
Overall intercept	-0.14 (0.06)	NA	0.0003

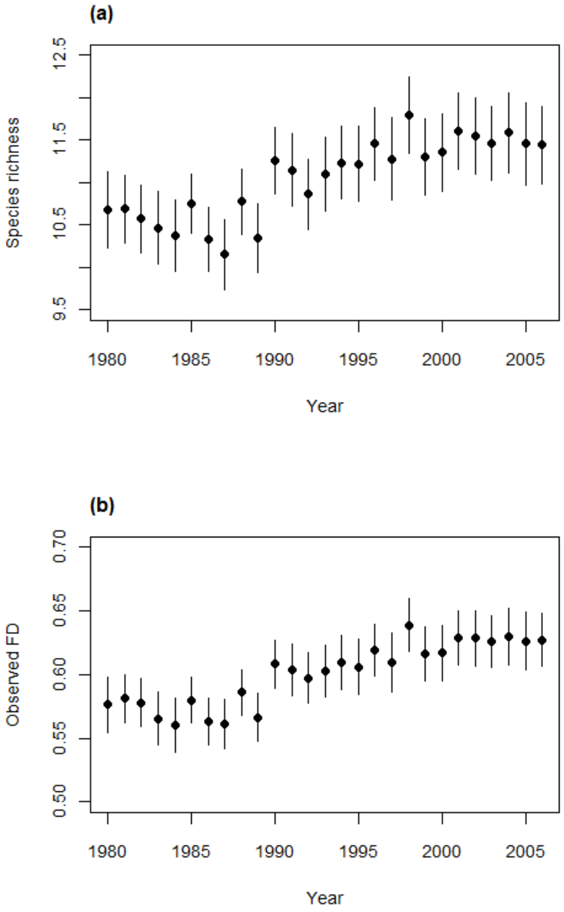

Figure 2. Temporal trend of (a) species richness (slope = 0.05, $p < 0.0001$) and (b) observed functional diversity (slope = 0.003, $p < 0.0001$) in wader communities across British estuaries. For ease of interpretation, mean values of observed FD were calculated for each year and standard errors are represented.

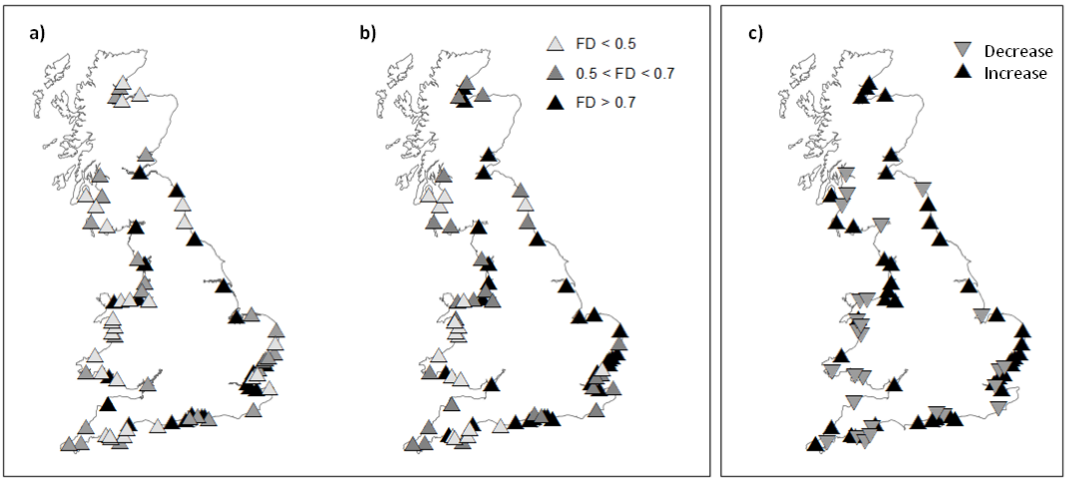

Figure 3. Geographical overview of functional diversity across the estuaries in (a) 1980/81, (b) 2006/07 and (c) the absolute change in functional diversity over this time period.

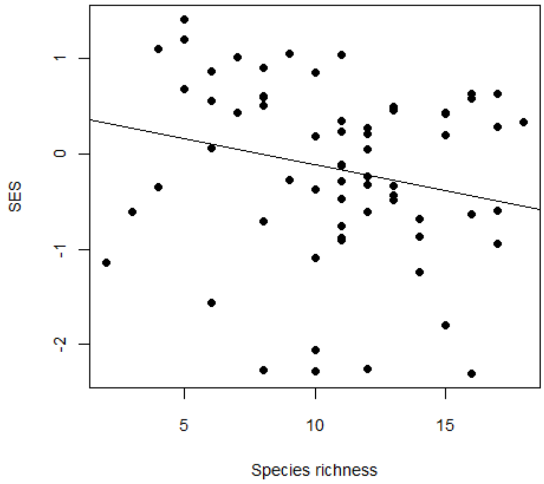

Figure 4. Relationship between the standardised effect size (SES, (observed – expected FD)/ standard deviation of expected FD) and species richness. Data for winter 1993/94 was used as the model intercept estimates were calculated from this year. The solid line is the linear model predicted relationship (R^2=0.04, $p < 0.04$)

Observed and expected FD differed less over time, with the SES values increasing slightly (Figure 5), but significantly over the study period (overall slope in Table 3). At the beginning of the time period the overall observed FD was lower than expected FD across the majority of the estuaries, whilst by the end of the time period, the overall difference shifted towards having a greater FD than expected by chance (Figure 6).

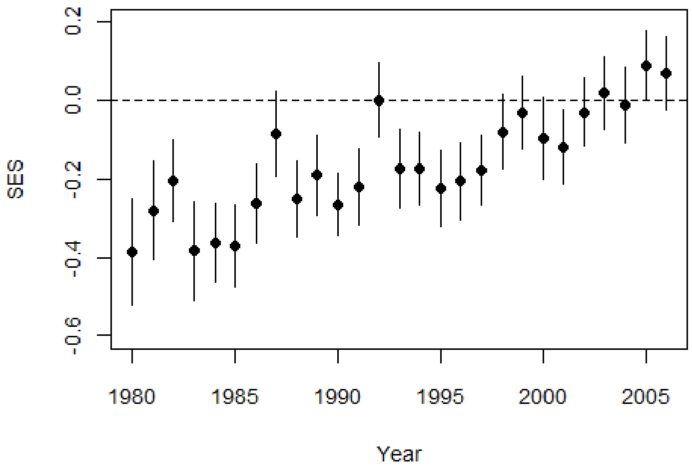

Figure 5. Temporal patterns of deviation of the standardised effect size (SES) from zero in wader communities across British estuaries. For ease of interpretation, mean values of FD difference were calculated for each year and standard errors are represented.

SES varied between estuaries and at different rates, supported by a significant variation between estuaries and a year-estuary interaction (differences in estuary random intercepts and random slopes in Table 3). The estimated value for the variance in the random intercepts ($d^2 = 0.36$), which determines the amount of variation around the overall model intercept, was considerably greater than the variance in the estuary random slope ($d^2 = 0.0004$), which determines the variation in slope at each estuary.

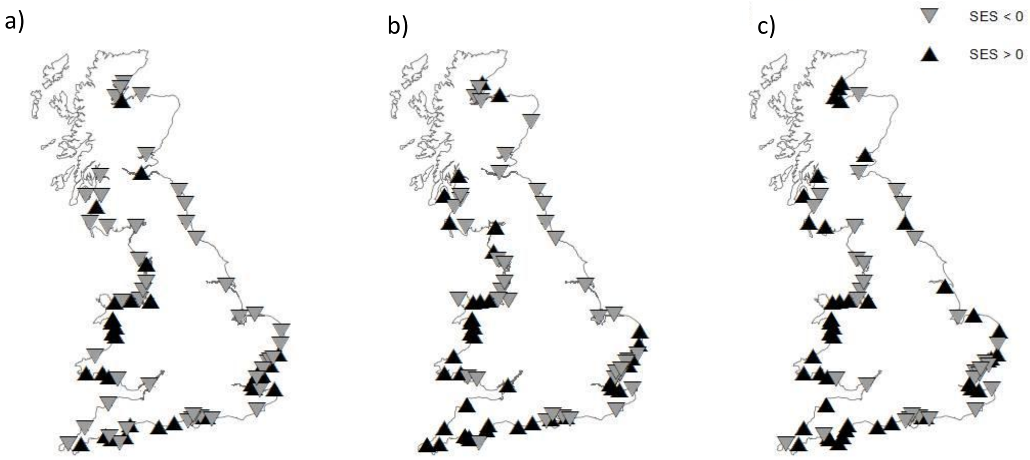

Figure 6. Geographical overview of the standardised effect size (SES) across the estuaries in winters (a) 1980/81, (b) 1993/94 and (c) 2006/07. Grey downward pointing triangles (SES < 0) indicate stronger environmental filtering effects. Black upward pointing triangles (SES > 0) indicate the stronger effect of niche partitioning on community structure.

Discussion

Wintering wader community composition and structure are spatially variable across British estuaries and changes in both observed FD and in the difference between observed and expected FD (SES) have taken place over the course of the study period.

Spatial and temporal changes in wader functional diversity

Functional diversity varies between wader communities, from communities with low absolute values of FD to more functionally diverse communities. As the FD index used in this paper does not account for evenness and measures the dispersion of species in a functional trait space, we can consider it as a measure of functional richness (Petchey & Gaston, 2006) which relates to the amount of functional space occupied by a community (Villéger *et al*., 2008). The variation in the amount of functional space occupied by wader communities is likely to be driven by different environmental factors, such as area and type of intertidal habitat and estuary tidal range that vary between estuaries (Ferns, 1992). In fact, these factors along with other physical attributes of the estuaries are known to influence the composition of wader communities across British estuaries (Hill *et al*., 1992). Although it was beyond the scope of this paper to identify specific environmental drivers of the observed FD patterns, we found a significant influence of longitude on FD (Figure 1). This indicates a gradient of decreasing FD moving west to east across UK estuaries when species richness is accounted for. We also found a significant positive influence of estuary area. However, this is almost certainly attributable to species-area relationships that are likely to result in part from area-habitat heterogeneity relationships. This is supported by the fact that area does not add to model likelihood for any models in which species richness is fitted. The variation in FD seems therefore to be primarily driven by the number of species present in the community; the more species in the community the greater the functional trait space occupied.

Functional diversity is increasing through time across the majority of estuaries (Figure 2 and 3). However, this should be interpreted cautiously. While WeBS coverage from early 1980s is good across the majority of the sites, there are some limitations to count data at the beginning of the time period since the recording effort was not consistent in all the sites covered. Despite this limitation, real increases in the number of species recorded across estuaries in Britain have been observed since the early 1980s (Austin & Rehfisch, 2005; Calbrade *et al.*, 2010), which could result in changes in community composition by the arrival of new species and/or replacement by species with more distinctive traits. As a consequence, variation in the amount of functional space filled by the community may occur, causing changes in FD. As with the spatial patterns of FD (above), since the species selected in this study are quite functionally distinct (Figure 1a), increases in species richness over time will result in a greater functional trait space occupied by communities, hence greater FD. The exploitation of prey of different shape, size and burrowing depth within the sediment, is considered to have played a key role in the evolution of wader morphology and behaviour (Burton, 1974; van de Kam *et al.*, 2004). The relationship between species richness and FD in the present study suggests that there is relatively little evidence of functional redundancy among wader species present in UK estuaries.

Spatial and temporal changes in observed and expected wader functional diversity

Our results reinforce the role of environmental conditions in shaping wader communities at landscape scales because, overall, wader FD is lower than expected by chance (overall intercept, Table 3). These results provide evidence that wintering wader communities show greater similarity in functional traits than expected from a random assembly with equivalent number of species, suggesting that environmental conditions are, to a certain extent, acting as a filter on which species are present at any given site.

In a previous study on FD of 192 species of British breeding bird, there was also a negative departure from levels of FD expected from random community assembly (Petchey *et al*., 2007). As with their study, our results show that, despite the stronger effect of environmental filtering overall, competition could also be structuring wader communities, as indicated by the variation in estuary random intercepts and the positive departures from expected FD observed in some estuaries (Table 3 and Figure 6). Thus, both processes are likely to interact simultaneously but their relative influence might be community specific. Differences in observed minus expected FD between estuaries, are not well explained by the number of species present in the estuary, since the explanatory power of this relationship is very small, even if statistically significant (Figure 4). The evidence for niche partitioning versus environmental filtering varies among UK estuaries, and these differences are likely to be explained by factors operating at a number of scales that influence the presence of wader species in estuaries, including those affecting whole estuaries and those at the more local scale of species interactions.

Differences in the strength of the mechanism(s) assembling bird communities between Petchey *et al.*'s (2007) and this study might be attributable to one or a combination of three factors. (1) The spatial scale of the studies; lower than expected FD occurs at regional scales in Petchey *et al*. (2007), whereas our study is at a finer spatial scale and the levels of niche partitioning and environmental filtering seem to vary between communities. The effect of species interactions are likely to be stronger at finer, more local scales whereas constraining environmental conditions are more likely to explain diversity patterns at larger scales. (2) The different taxonomic breadth of species studied; although we use a similar set of functional traits, Petchey *et al*. (2007) considered a wide range of breeding bird species occurring in the UK, occupying both terrestrial and coastal habitats. Our study focuses on non-breeding wader communities, the structure of which will have been shaped by very different influences. (3) There are differences in the methods used to calculate expected FD and thus in the statistical models used to test whether observed FD differs significantly from expected FD. In particular, Petchey *et al*. (2007) controlled for number of species in calculating expected FD but did not control for the species' frequency of occurrence. As discussed by Thompson *et al*. (2010), when frequency of occurrence is not accounted for, the random communities tend to have relatively high FD as all the species have the same probability of occurring (not accounting for rarity) and, hence, environmental filtering effects are more pronounced. Comparing both types of null model in the present study confirmed this tendency.

Interestingly, we also found evidence for changes in the temporal dynamics of the wader communities on British estuaries. The difference between observed and expected FD became less negative through the study period (Figure 5), with a small but significant year effect (Table 3), suggesting that levels of niche partitioning may have become stronger through time and/or that environmental filtering has become weaker. Some of the wader communities are seen to have shifted from a negative to a positive difference between observed and expected FD over time. Changes in habitat (total area, relative abundance of habitat types and complexity) and in the amount of resource available due to changes in sea level, land claim for agriculture, industry and harbour development or other anthropogenic pressures (*e.g.* shell-fishing), might account for the suggested increase in the strength of competition. According to the limiting similarity theory (Macarthur & Levins, 1967), there will be stronger competition effects between species that are more similar in exploiting the available resource. Thus, following any reduction of resources due to changes or loss of habitat, or expansion in population density and distribution range of particular species, competition for similar resources is predicted to intensify, thereby increasing the chance of one species displacing another that shares its food resources. Under this scenario increased competition may result in a community with species that are more complementary to one another, increasing community FD relative to that expected by chance. However, as mentioned above, the observed patterns might also be attributable to a weaker influence of environmental filtering. Winters in the UK are generally becoming milder and less severe, with an increase in mean temperatures and a decrease in the number of days with ice cover. Previous analysis of WeBS data has shown how the distributions of several wader species wintering on British estuaries have changed in association with these changing climatic conditions (Austin & Rehfisch, 2005; Maclean *et al.*, 2008). These milder conditions might therefore allow a wider spectrum of traits to persist, for a given number of species present, hence reducing the strength of environmental filtering effects.

Many wader species in the UK are protected as features of Special Protection Areas (under the EC Birds Directive 2009/147/EC (formerly 79/409/EEC): Stroud *et al.*, 2001), Ramsar sites (Wetlands of International Importance protected under the Ramsar Convention) and Sites of Special Scientific Interest, while the estuaries themselves are protected under the EC Habitats Directive (92/43/EEC). Clearly, if we wish to protect both bird species and estuaries we need to understand the processes by which communities are sustained in the UK, in particular the processes by which communities are assembled, and how they may be changing. The present study using FD as a diversity measure increases our understanding of trait complementarity amongst wintering wader species and points to likely processes driving species coexistence in British estuaries. As Mouchet and colleagues pointed out recently (2010), we need to understand the relative influence of each process on communities, as both environmental filtering and competition may simultaneously be influencing the community structure. However, disentangling which one has the stronger influence at landscape scale is very challenging, not only because both can act simultaneously but also because they might be community-specific. With the rapid pace of global environmental change, there is a need to understand the extent to which the influence of spatial and temporal anthropogenic effects on functional diversity, through changes in habitat, resource availability and climatic conditions, could be akin to environmental filtering (*e.g*. homogeneous habitat might narrow the spectrum of species and thus the functional traits present) or could be promoting competition. For bird populations in winter, a stable food supply is extremely important in meeting metabolic requirements, especially under low temperatures. Food availability for waders might also be changing due to shifts from bivalve dominated to more worm dominated communities as a result of shellfisheries activities across British estuaries (Atkinson *et al.,* 2010, and references therein). The decrease in bivalve abundance towards a more limited resource may increase competition between species. There is still much to learn about spatial and temporal patterns of community functional diversity. As we have demonstrated, changes in functional trait distributions are occurring in UK wader assemblages, suggesting simultaneous changes in the functioning of estuary ecosystems.

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Chapter two

Impacts of demographic changes in the population of wintering waders on community structure

Abstract

Aim British estuarine ecosystems support large populations of protected migratory wader species, many of which have previously been reported to be declining severely. However, it is still unclear how changes in population size relate to changes in wintering site occupancy and how these population changes may influence changes in the composition and structure of whole wader communities. Here, we use 30 years of monitoring data on winter population size to explore the association between changes in wintering population size and site occupancy. We then explore the variation in functional diversity of communities through the influence of species presence/absence, to identify how species may be influencing community structure. Finally, we explore the variation in species functional traits, in order to further understand similarities amongst species and their influence in the overall community functional diversity and community structure.

Methods We use national survey (Wetland Bird Survey, WeBS) data from winters 1980/81 to 2006/07 of 20 species in 83 estuaries to explore annual trends in wintering population size and site occupancy, using the abundance and presence/absence of each species as response variables and, in both cases, having year as explanatory term. We then model functional diversity estimates for the same 83 communities as a function of species presence/absence to understand the influence of each species on community structure. In order to investigate similarities and differences amongst species, we performed a principal coordinate analysis (PCoA).

Results The direction and magnitude of changes in wintering wader population size and site occupancy across British estuaries are species-specific. A significant association between population size and the number of estuaries occupied occurs for the majority of species. The presence of avocet, spotted redshank, greenshank and shelduck within the community, contributes significantly to greater functional diversity. As expected, species that show a positive effect on functional diversity are also species that lie at the extremes of functional space.

Main conclusions Wintering wader population size and site occupancy are changing across British estuaries and influencing changes in community composition. Changes in functional diversity reveal that coexisting species are becoming more functionally different and that species interactions are becoming stronger and/or abiotic factors becoming weaker in structuring communities. Species that have a positive influence on functional diversity are species that are more functionally distinctive within functional space and that have also expanded their wintering ranges. We discuss the potential mechanisms underlying these community structuring patterns, and their relevance for the protection of wader communities.

Keywords functional diversity, functional traits, population size, site occupancy, wader.

Introduction

Estuaries are amongst the most productive ecosystems in the world (Geider *et al*., 2001). These ecosystems are of great importance for a great variety of species, including plants, invertebrates, fish, waterbirds and mammals (Buck, 1993). However, estuaries have experienced continuous anthropogenic pressures due to their numerous socio-economic functions (Davidson *et al.*, 1991) and, for example, activities such as land reclamation, pollution and over-exploitation of fisheries have greatly influenced the dynamics of several benthic and bird species (*e.g*. Gill *et al*., 2001; Ravenscroft & Beardall, 2003; Goss-Custard *et al*., 2006; Atkinson *et al.*, 2010; Burton *et al.,* 2010; Alves *et al.*, 2012; Sutherland *et al.*, 2012). The ecological importance of these ecosystems has been widely recognised and many estuarine ecosystems are protected under national and international legislation (Convention on Wetlands of International Importance, 'Ramsar', 1971; the EC Birds Directive – Stroud *et al*., 2001). Despite international conservation efforts, many conflicts are apparent between the economic values of estuaries and the effective protection of both habitats and species. Site protection status is typically based on threshold numbers or proportion of populations occurring within the site (*i.e.* a site is considered to be of conservation importance if it regularly holds over 20,000 waterfowl or at least 1% of the national or the biogeographic population of a given species) (Stroud *et al*., 2001). The number of individuals required to meet the 1% threshold, however, has to be reviewed when national population numbers change. Furthermore, it is often not clear why number of individuals and communities composition change within individual sites, especially for migratory species, since these changes might be influenced by processes occurring elsewhere in their distribution range. Understanding how these communities assemble is therefore a key step in understanding community dynamics on estuaries and their use by any species.

Estuarine ecosystems are particularly important for migratory bird species, as they provide wintering and stop over conditions for birds to rest and refuel during non-breeding and migration periods (Fuller, 1982; Ferns, 1992; Delany *et al*., 2009). Within the Paleartic-African migratory corridors, in particular the East Atlantic flyway, 42% of the populations of species of waterbirds, including herons, egrets, swans, ducks, geese and waders, are currently declining (Delany *et al.*, 2009). The United Kingdom is located within this flyway and provides important non-breeding grounds for many wader species (Charadrii), with over a million individuals wintering within its coastal habitats (Holt *et al*., 2011). The UK assumes particular relevance on the East Atlantic flyway, due to its large number and total area of wetlands and associated estuarine systems. In addition, the UK winter temperatures are higher than those of other regions at the same latitude, owing to the influence of the Gulf Stream (van de Kam *et al*., 2004), making it a favoured wintering location for many arctic and subarctic breeding species. The numbers of birds supported on wetlands in the UK have been assessed since 1969 through a nation-wide monitoring scheme, the Wetland Bird Survey (WeBS), providing the data needed for designating important sites (*e.g.* Stroud *et al.*, 2001) and for quantifying national-scale population trends (Thaxter *et al.*, 2010) (see Table 1, for details on population trends). Making use of this data set, previous studies have examined the possible causes of changes in abundance of wintering bird populations on European estuaries in relation to environmental factors operating at a variety of scales (*e.g.* Gill *et al.*, 2001; West *et al.*, 2002; Austin & Rehfisch, 2005; Goss-Custard *et al.*, 2006; Maclean *et al.*, 2008; Burton *et al.,* 2010). However, it is still unclear how these population changes influence the composition and structure of whole communities, and how these changes may impact ecosystem functioning.

Changes in species richness and composition of wintering wader communities across British estuaries over the last 30 years have been accompanied by changes in functional diversity (*i.e.* changes in the functional traits present in the community) and community structure (chapter 1). The relative influence of the mechanisms structuring wader communities on British estuaries over that time period is not constant, with an overall tendency towards an increase in dissimilarity amongst coexisting species (chapter 1). According to niche-model theory, community assembly is influenced by similarities or differences in species traits, through the opposing influences of environmental filtering effects and species interactions (MacArthur & Levins, 1967). Thus, an increase in functional diversity while species richness remains constant suggests that niche partitioning/competition levels might also be increasing (*i.e.* higher character displacement between species due to limiting similarity) and/or that environmental constraints might have been decreasing (*i.e*. the environment allows a wider range of traits to be present in communities). However, wader functional diversity in chapter 1 was calculated using presence-absence data, limiting the changes in functional diversity to be sensitive only to changes in species local extinction or colonization while being insensitive to changes in population size. Surprisingly, it is currently unknown how the influence of changes in population size and site occupancy might impact community structure.

In this study, we use WeBS count data to examine the association between temporal trends in population size and wintering occupancy for wader communities on 83 estuaries around Britain. Then, using the estimates extracted from chapter 1 of deviation of observed from expected functional diversity (thus controlling for the number of species present in each community) we test if the species that are influencing changes in functional diversity and community structure are those with more extreme/different trait states. Species with a greater influence on changes in functional diversity and community structure are expected to be those that are more functionally different, being positioned near the edges of the ecomorphological (functional) space. Hence, if their population sizes and distributions are changing through time, these species will have greater impact on community structure than other species that are more functionally redundant/ similar. Here, we use species abundance data to for the first time to explore how changes in population size and wintering site occupancy influence the community functional diversity and community structure.

Methods

Species selection

We restricted our analyses to the same 20 wintering species (Table 1) used in chapter 1, which were selected based on their high winter dependency on estuaries and inter-tidal invertebrate prey populations. All selected species are waders with the exception of shelduck (*Tadorna tadorna*), which was included in this and previous community analyses as it has similar feeding ecology to waders and is also highly dependent on estuaries (*e.g.* Clark & Prys-Jones, 1994) (hereafter, “waders” refers to all the species in this study). Spotted redshank and whimbrel were also included although they are relatively scarce wintering species in the UK, with populations found only at a few sites as the majority of individuals of both species winter in Africa and only a small proportion remains on British estuaries during winter.

Data collection

Monitoring waterbird species has taken place throughout the UK since 1969/1970 by co-ordinated monthly counts on predetermined dates, thus minimizing the likelihood of missing or double counting individuals (Holt *et al*., 2011). Count accuracy and completeness assessments are carried out for all the species at all sites. Count accuracy is provided by the counter, assessing the count as complete (‘OK’) or incomplete (‘Low’). Then, completeness assessments are made for all the WeBS counts on the basis of each count information. Completeness calculations for large and complex sites are based on a moving window of counts, thus, the addition of new data each year may result in counts assessed as incomplete in previous years now being considered complete, or vice versa, as the species may have changed the sections they use within the estuary. Thus, this method allows the correction of previous counts and completeness assessment. Additional information regarding survey type, methodology, count accuracy and completeness are detailed in Holt *et al*. (2011).

Table 1. The 20 wintering species of waterbirds included in the analyses and their long-term (25 year) population trends in Great Britain (extracted from Thaxter *et al*., 2010). Whimbrel and spotted redshank trends are not available as the majority winter in Africa.

Code	Common name	Scientific name	Long-term population change (%)
RP	Ringed plover	*Charadrius hiaticula*	-9
GP	Golden plover	*Pluvialis apricaria*	500
GV	Grey plover	*Pluvialis squatarola*	71
L_	Lapwing	*Vanellus vanellus*	183
OC	Oystercatcher	*Haematopus ostralegus*	2
AV	Avocet	*Recurvirostra avosetta*	>1000
TT	Turnstone	*Arenaria interpres*	9
SS	Sanderling	*Calidris alba*	69
DN	Dunlin	*Calidris alpina*	-26
KN	Knot	*Calidris canutus*	20
PS	Purple sandpiper	*Calidris maritima*	-43
RU	Ruff	*Philomachus pugnax*	88
BA	Bar-tailed godwit	*Limosa lapponica*	-25
BW	Black-tailed godwit	*Limosa limosa*	518
CU	Curlew	*Numenius arquata*	41
WM	Whimbrel	*Numenius phaeopus*	NA
DR	Spotted redshank	*Tringa erythropus*	NA
GK	Greenshank	*Tringa nebularia*	106
RK	Redshank	*Tringa totanus*	19
SU	Shelduck	*Tadorna tadorna*	-1

We compiled winter data for 83 British estuaries between the winters of 1980/81 and 2006/07, which have been systematically surveyed and the temporal coverage is considered to be complete during this time period. Only species occurring on a site in at least 60% of the winter months in a given year (November to February) are assumed to be part of the winter community and included in the subsequent analysis. Winter mean abundance for each species at each site was calculated using counts between November and February, when the number of birds using sites at these latitudes more accurately reflects stable non-breeding population numbers.

Seven trait types were chosen to capture behavioural and morphological variation among waders relating to their capacity to exploit food resources (as in chapter 1). Trait values were obtained from the BTO data base (http://www.bto.org/about-birds/birdfacts) and from The Birds of the Western Palaearctic on interactive DVD-ROM (2006), using information for populations that occur in UK whenever possible.

Changes in wintering wader population size and occupancy

Wintering population size (*i.e*. total number of individuals per species per year) was calculated as the sum of the winter mean abundances across all the sites where the species was present. We used generalised linear models with Poisson error distribution and log link function to model wintering population size as a function of year, with standard errors adjusted for overdispersion. Non-linear annual trends were explored in all models and included when significant.

Winter mean abundance was transformed to presence/absence data, to calculate the number of sites where a species was present in a given year, *i.e*. site occupancy. Variation in annual site occupancy was modelled as a function of year with generalised linear models with binomial error distribution and logit link function, with standard error adjusted for overdispersion. Non-linear annual trends were included in all models and recorded when significant. We used Spearman correlations to explore the association between the ($\log_{10}$-transformed) population size and the number of estuaries occupied by a species in a given year. All analyses were conducted in statistical package R (2.12.2, R Development Core Team, 2011) using the *glm* function for the described models.

Changes in wintering wader community

Functional diversity (hereafter referred as FD) estimates how dispersed the species of a given community are in trait space. Seven trait types in relation to resource use were used to calculate the FD across wader communities, which included morphological, behavioural and ecological traits (Table 2 in chapter 1). Deviations of observed FD from expected FD have been previously used to understand the mechanisms by which communities are assembled (*e.g*. Petchey *et al*., 2007; Thompson *et al*., 2010; Mendez *et al*., 2012). Expected FD is calculated from the same regional pool (20 species), by assembling 1000 random communities with the same number of species as the real community and calculating their FD. Expected FD is calculated as the mean value of the FD of these random communities. Observed communities are considered to be assembled at random if the difference between observed and expected is not significantly different from zero. However, if the difference is significantly less than zero, then environmental filtering is likely to be the stronger influence on community structure, whereas if it is significantly greater than zero, interspecific competition is likely to be the predominant influence on community structure. We used the standardised effect size estimates of FD (hereafter referred as SES-FD) extracted from chapter 1 to explore the influence of individual species population changes on community changes. SES-FD was calculated as (observed FD – expected FD)/standard deviation of expected FD, for each wader community on each site in each year (Gotelli & McCabe, 2002).

Since functional diversity was measured using presence/absence data, changes in SES-FD will be sensitive to changes in species composition and species richness through colonization and extinction events. Thus, SES-FD was modelled as a function of the presence/absence of each species with estuary and year as random effects. In the model, species were considered as independent variables and year was treated as a continuous variable in the random structure to account for temporal autocorrelation (*i.e.* non-independence caused by repeated measures at the same estuary). The statistical model was carried out using the *lmer* function of the *lme4* package (Bates *et al*., 2011) in R (2.12.2, R Development Core Team, 2011). The best model (minimum adequate model) was selected through backwards removal from the maximal model (when all species were included), using Akaike Information Criteria (AIC) and maximum likelihood ratio tests (ML). The relative importance of each removed term and the goodness-of-fit of the model were determined.

Finally, we performed a principal coordinate analysis (PCoA), using a Gower distance matrix calculated from the same trait matrix as in chapter 1 and comprising the 20 species. The PCoA positions each species within multidimensional functional trait space, determined by the combination of functional trait states of each species. The PCoA was performed using the function *pcoa* from the *ape* package (Paradis *et al*., 2004) in R (2.12.2, R Development Core Team, 2011). We overlaid the traits as arrows in the PCoA plot to explore whether changes in populations and communities might be linked to changes in specific functional traits.

Results

Changes in wintering wader population size and occupancy

Between 1980/81 and 2006/07, the populations of wader species wintering in the UK have experienced contrasting changes in size. Population size trends were statistically significant for 18 species, but not significant for bar-tailed godwit and knot (Table 2a, Figure 1). Dunlin and shelduck suffered an overall decrease in numbers over the time period, whereas curlew, grey plover, lapwing, oystercatcher, purple sandpiper, redshank, ringed plover and turnstone have experienced more recent declines (Figure 1). Avocet, black-tailed godwit, spotted redshank, sanderling and whimbrel showed a linear increase in numbers, with avocet and black-tailed godwit increasing at the fastest rate during this time period (yearly rates of ~0.07 - 0.1%, Table 2a). Greenshank, golden plover and ruff also enjoyed an overall increase in population abundance throughout the analysed time period (Table 2a, Figure 1).

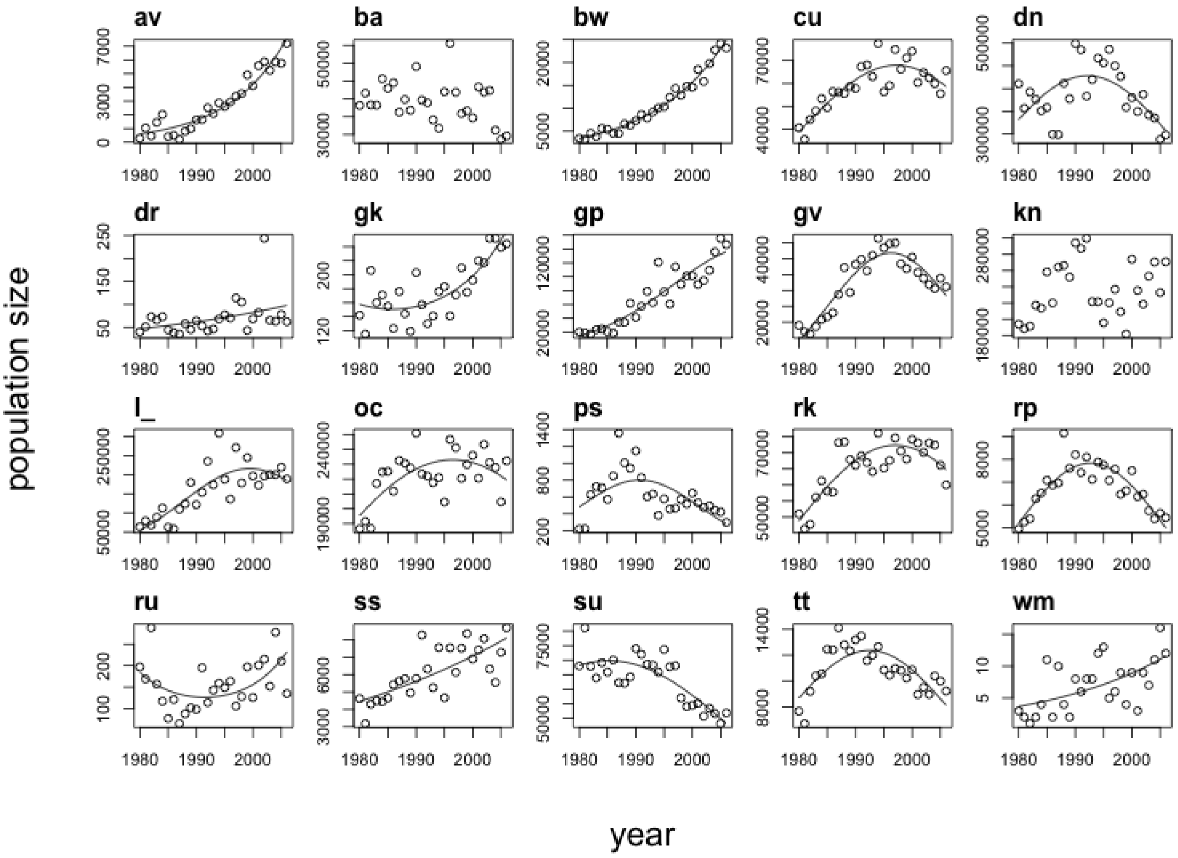

Figure 1. Temporal trends in wintering wader population size (*i.e.* total number of individuals per year) in Great Britain. Population size is calculated as the sum of the winter mean abundance across 83 coastal sites. Fitted lines represent generalised linear predictor models for annual trends in population size. Species codes may be found in Table 1.

Overall, site occupancy increased for all 20 species (*i.e.* the number of sites occupied at the end of the time period was overall greater than the number of sites occupied at the beginning of the time period) (Table 2b, year effect is positive for all the species). However, increases in occupancy have stopped for the majority of species (Table 2b, $year^2$ in the model is negative), and for species such as dunlin, grey plover, ringed plover, purple sandpiper, bar-tailed godwit and turnstone declines in occupancy were more pronounced since the early 90s (Figure 2).

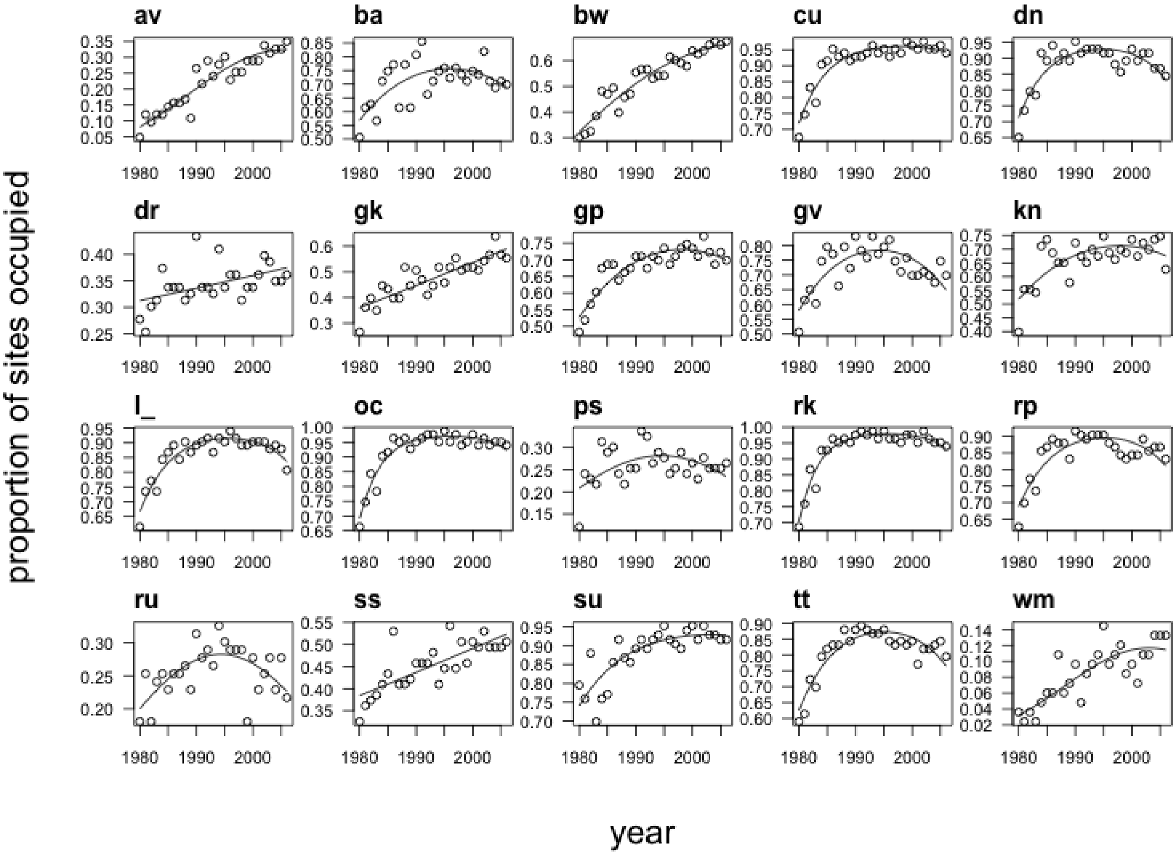

Figure 2. Trends in the variation of sites occupied by 20 species of wintering waders across 83 coastal sites in Great Britain. Fitted lines are the generalised linear model relationship. Species codes are provided in Table 1.

There was no significant correlation between annual wintering population sizes and site occupancy for dunlin, knot, oystercatcher, purple sandpiper and ruff (Table 2c). In contrast, for the majority of species (14) a significant positive correlation between population size and the number of estuaries occupied was found, and only for shelduck there was a (weakly) significant negative correlation (Table 2c), with site occupancy increasing with population declines in this species.

Changes in wintering wader community

On British estuaries between 1980/81 and 2006/07, there was a significant effect of the occurrence or absence of several species on changes in SES-FD (*i.e.* the changes in wader FD on individual estuaries; Table 3). The effect of the presence of avocet, spotted redshank, greenshank and shelduck on the variation in SES-FD was positive (intercept, Table 3). Thus, when any of these species were present in the community, SES-FD values tended to be less negative than when they were absent from the community. In other words, when any of these four species was present in a community, it was more functionally distinct than communities where they were absent, hence functional diversity tended to be less negative or closer to that expected by chance. In contrast, when any of the other nine species (species with negative estimates, Table 3) were present in the community, SES-FD values tended to be more negative than when these species were absent from the community. Hence, species within the community tended to be more similar than expected by chance when any of these nine species were present.

Table 2. Estimates of the annual changes in (a) population size and (b) site occupancy for each species in Great Britain, and (c) the Spearman's correlations between population size and site occupancy. Significance levels are coded as follows: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ and NS = not significant. Non-linear annual trends (Year^2) were explored in all models but are only included when significant. Species details are given in Table 1.

	Change in population:				**Correlation between population size and occupancy**
	(a) size		**(b) occupancy**		**(c) rho**
Species	**Year**	**Year^2**	**Year**	**Year^2**	
AV	0.096 (***)		10.02 (**)	-0.0025 (**)	0.88 (***)
BA	-0.006 (NS)		13.38 (**)	-0.0033 (**)	0.39 (*)
BW	0.076 (***)		5.94 (**)	-0.0015 (**)	0.95 (***)
CU	7.540 (***)	-0.0018 (***)	26.95 (***)	-0.0067 (***)	0.61 (***)
DN	6.895 (***)	-0.0017 (***)	30.29 (***)	-0.0076 (***)	0.32 (NS)
DR	0.028 (***)		0.010 (**)		0.39 (*)
GK	-5.421 (*)	0.0013 (*)	0.036 (***)		0.63 (***)
GP	9.476 (*)	-0.0023 (*)	10.75 (***)	-0.0027 (***)	0.66 (***)
GV	16.40 (***)	-0.0041 (***)	19.29 (***)	-0.0048 (***)	0.63 (***)
KN	0.004 (NS)		10.49 (**)	-0.0026 (**)	0.15 (NS)
L_	14.59 (***)	-0.0036 (***)	27.66 (***)	-0.0069 (***)	0.55 (**)
OC	2.615 (**)	-0.0006 (**)	41.61 (***)	-0.010 (***)	0.31 (NS)
PS	17.78 (**)	-0.0044 (**)	7.5 (*)	-0.0018 (*)	0.11 (NS)
RK	5.453 (***)	-0.0013 (***)	47.46 (***)	-0.012 (***)	0.45 (*)
RP	10.21 (***)	-0.0025 (***)	23.71 (***)	-0.0059 (***)	0.67 (***)
RU	-11.48 (*)	0.0028 (*)	8.75 (**)	-0.0022 (**)	-0.28 (NS)
SS	0.023 (***)		0.02 (***)		0.65 (***)
SU	3.413 (**)	-0.0008 (**)	10.95 (*)	-0.0027 (*)	-0.45 (*)
TT	9.116 (***)	-0.0022 (***)	24.82 (***)	-0.0062 (***)	0.71 (***)
WM	0.044 (**)		10.47 (*)	-0.0026 (*)	0.82 (***)

Table 3. Results of the minimum adequate linear mixed model of the influence of species presence/absence on changes in functional diversity (SES-FD). The parameter estimate of a given species is scaled relative to the intercept and indicates the effect of the presence of that species on SES with the influence of all the remaining species held constant. Species codes are given in Table 1.

		Estimate	**Std. Error**	**t value**	**p-value**
	(Intercept)	- 0.301	0.178	- 1.688	0.09
Presence of:	AV	0.192	0.048	3.960	**<0.0001**
	BA	- 0.257	0.044	- 5.818	**<0.0001**
	BW	- 0.115	0.039	- 2.915	**0.02**
	DR	0.142	0.039	3.635	**0.0002**
	GK	0.162	0.036	4.432	**<0.0001**
	GP	- 0.065	0.045	- 1.445	0.36
	GV	- 0.180	0.049	- 3.632	**0.0001**
	OC	- 0.239	0.158	- 1.510	**0.03**
	PS	- 0.071	0.043	- 1.623	0.07
	RP	- 0.225	0.064	- 3.515	**0.0002**
	RU	- 0.094	0.042	- 2.240	**0.007**
	SS	- 0.071	0.041	- 1.725	**0.008**
	SU	1.027	0.063	16.294	**<0.0001**

Species position in the ecomorphological (functional) space

Patterns of variation in wader functional traits are shown in Figure 3, with each species positioned in multidimensional functional space. Species placed close together share more similar functional trait states (*e.g.* the feeding techniques are similar, they feed on similar prey types and they display similar morphological characteristics) than species placed further apart, which tend to have more dissimilar functional trait states. Shelduck, avocet, spotted redshank and greenshank, species that had a positive estimate in Table 3, were positioned further apart from the rest of the species (top left of the ordination), indicating that they are more functionally distinct than the other species (Figure 3).

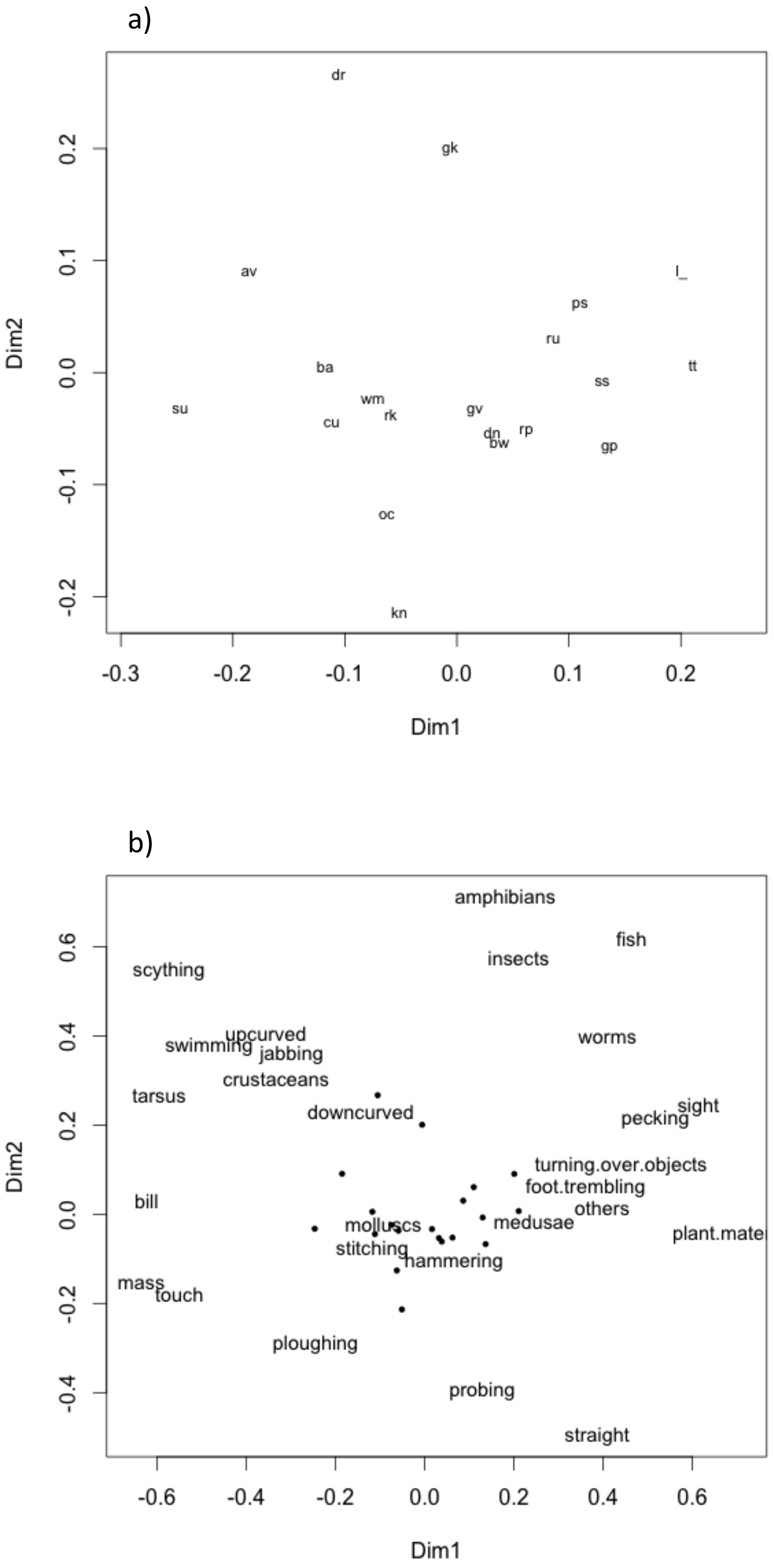

Figure 3: Principal Coordinate Analysis (PCoA) of the functional traits of 20 wintering wader species across British estuaries. For ease of interpretation, species scores are represented alone (a) and in relation with the functional traits (b). Species codes are provided in Table 1.

Discussion

The wintering population size and site occupancy of several wader species across British estuaries have undergone considerable changes, and the direction and magnitude of these changes are species-specific. These population changes are influencing changes in community composition (*i.e*. which species are present in the community), resulting in changes in functional diversity. Coexisting species are becoming more functionally complementary, and the structuring influence of species interactions is becoming stronger and/or abiotic factors are becoming weaker in ruling community assembly.

Changes in wintering wader population size and occupancy

The overall trend in the wintering population abundance of wader species in the UK has been one of increase over the last 40 years, and in particular from mid-1970s to late 1990s (Holt *et al*., 2011). However, since the late 1990s, the numbers of the majority of species have stabilised and for some species have fallen (Holt *et al*., 2011; Musgrove *et al*., 2011). Our study, based on a shorter time period and using mean winter abundances, also captures these trends. Of the 20 wintering species, only bar-tailed godwit, dunlin and shelduck experienced overall declines in numbers whereas the remaining species increased. But these increases are not always linear, and species such as curlew, grey plover, lapwing, oystercatcher, purple sandpiper, redshank, ringed plover and turnstone are experiencing recent declines after a period of increasing in numbers (Figure 1, Table 2a). It should be noted that abundance trends and the population estimates reported here may differ slightly from those already published, because the sites included here represent only the sites with most complete counts which are only a portion of the sites used to calculate the annual indices reported in WeBS (Holt *et al*., 2011) and the overwinter population estimates (Musgrove *et al*., 2011), which also include inland sites. However, the changes in overall population abundance patterns have not previously been related to changes in site occupancy and community structure.

As observed for many other taxa (*e.g*. Gaston *et al*., 2000), wader population sizes tend to be positively correlated with site occupancy, thus species with large population sizes such as redshank, oystercatcher and dunlin, tend to occupy a large number of estuaries, whereas rare species, such as spotted redshank and whimbrel, are present in fewer sites. This positive association seems also to extend to the changes in population size and site occupancy. For example, avocet and black-tailed godwit, two of the wader species that have greatly increased in numbers, have also occupied new sites. The increase in numbers is likely to result in increases in local abundance and consequent density-dependent effects may be a key mechanism facilitating winter recruitment or dispersal into new sites and establishing new local populations. Alternatively, changes in abundance and occupancy may occur independently, and it is important to note that not all the changes in populations and occupancy have been significant or positive for wader species across Britain.

Non-significant correlations between population size and wintering occupancy could indicate that changes in wintering population size may primarily be driven by changes in local abundances. For instance, constraints on the availability of suitable sites to colonize may mean that increasing species are more likely to increase in local abundance. Wader species are typically highly philopatric, returning every year to the same wintering site (Townshead, 1985; Burton, 2000), thus declining populations may have fewer individuals returning to the same estuary each year, resulting in lower local abundances but similar site occupancy. This might be the case for dunlin, as the decrease in numbers does not seem to vary with numbers of sites occupied, suggesting a reduction in local abundances, which could be attributed to shifts in wintering distribution to sites outside the UK (Austin & Rehfisch, 2005; Maclean *et al*., 2008) or to overall population declines at the flyway level. Interestingly, we also found a negative association between occupancy and population size in shelduck, which has undergone a significant decrease in population size over the last 30 years while its wintering occupancy has increased, indicating a likely redistribution of wintering sites and a reduction of local abundances.

Despite the wealth of scientific research evaluating factors underlying changes in population abundance (*e.g.* Rehfisch *et al*., 1997; Gill *et al*., 2007; Maclean *et al*., 2008; Amar *et al*., 2011), there is relatively little understanding of the consequences of changes in population size to changes in occupancy and local abundance. We have shown an association between changes in population size and wintering occupancy in waders but the contribution of changes in local abundances and/or changes in site occupancy to the overall population change remain unknown. Furthermore, we do not know (i) the carrying capacities of sites for local populations, before density-dependence effects begin to operate and (ii) the role of Allee effects (benefits for individuals of species from the presence of conspecifics) and thus the extinction risk associated with different population sizes. Further investigation into these aspects of population dynamics are needed since they are likely to aid in understanding the link between population trends and mechanisms, and consequently enable assessment of extinction risk and the likelihood of successful colonization events.

Changes in wintering wader communities

Changes in functional diversity are influenced by individual species in different ways and, of the 20 species included in this study, only 13 proved to have a statistically significant effect on the variation in community functional diversity. The level of redundancy or distinctiveness of functional traits contributed by each species is likely to explain differences between the magnitude and the direction of the effect of species presence/absence on functional diversity. Species with a positive effect – avocet, spotted redshank, greenshank and shelduck (Table 3) – appear to be more functionally distinct with respect to resource use, broadening the functional trait space when they are present in the community (Figure 3). In fact, these species are all particularly specialised for feeding in shallow standing water and forage by moving their bills from side to side (Cramp & Simmons, 1983; van de Kam *et al*., 2004), traits that are not shared by any of the other wintering species. Furthermore, these species can feed on fish and/or other aquatic invertebrates found in the water column (van de Kam *et al.*, 2004; BWPi, 2006), which again are not resources exploited by the other species. Avoiding niche overlap by being able to exploit different parts of the resource spectrum and to perform different functional roles within the community might thus explain why these species have been able to successfully establish local populations in new sites. Additionally, since these species were found in few estuaries, it seems that there may have been an under-utilisation of resources at the beginning of the time period or the type and abundance of resources available within estuaries have changed. Thus, observed increases in the overall FD of UK wintering communities may be a consequence of the expansion of the total niche space (new traits are incorporated into the community) and/or strengthening of the levels of niche partitioning (displacement of functionally similar species occurs when there is limited resource, resulting in communities with more complementary species) as previously suggested (chapter 1).

There was a significant negative effect on changes in FD of seven species (Table 3). In other words, when any of these species were present in a community, they contributed to species being more functionally similar than in communities where they were absent, hence lowering levels of FD than expected by chance. Thus, the addition of these species into these communities appears to add largely similar functional traits. These species tended to cluster within the functional space (Figure 3) since they feed on similar main prey types (*e.g*. worms, molluscs and crustaceans) using similar feeding techniques (*e.g*. probing or pecking). The similarity amongst species might be enhanced through the influence of environmental conditions. For instance, bar-tailed godwit and sanderling tend to occur on large sandy estuaries (Hill *et al.*, 1993), whilst the presence of golden plover in estuaries seems to be linked to winter weather severity (Rehfisch *et al*., 2004; Gillings & Fuller, 2009). These and other environmental conditions could be constraining the presence of these and other species, hence, acting as a filter and allowing only a specific and more similar set of functional traits to be present in a given community.

One of the advantages of FD as a measure of biodiversity is that, as well as representing the range of functional traits, it also expresses the extent of complementarity in resource use space, and thus, resource partitioning/niche differentiation amongst coexisting species (Petchey & Gaston, 2006; Petchey *et al*., 2007; Villéger, Mason & Mouillot, 2008). The ability of a species to colonise is partly constrained by the extent of the niche space available and by species interactions, in particular competition between species exploiting similar parts of the resource spectrum (MacArthur & Levins, 1967). Previous studies have examined the responses of wader numbers to environmental and anthropogenic changes such as shell-fishing (van Roomen *et al*., 2005; Atkinson *et al*., 2010), habitat loss (Burton *et al*., 2010), organic loading (Burton *et al*., 2005; Alves *et al.*, 2012) and more recently climate change has been suggested as a cause of changes in wintering wader distribution and abundance (Rehfisch *et al*., 2004; Austin & Rehfisch, 2005; Maclean *et al.,* 2008). However, the results of this study suggest that some of the changes in occupancy may be occurring through density dependent processes, species interactions, niche availability and suitability, while acknowledging that changes in population size are often correlated with changes in environmental conditions and these have to be suitable for a species to persist within a community. Understanding trait diversity and the functional role of each species within the community is an important topic that can improve our understanding of species interactions and co-existence and better inform conservation policy.

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Chapter three

Consequences of population change for the distribution of wintering waders on British estuaries

Abstract

Aim The population size of many European wintering waders is changing, with some species increasing and others declining. Given the statutory importance of maintaining these species in designated protected areas, it is necessary to understand the consequences of population change for local abundance and distribution, as this can help in assessing extinction/invasion risk and targeting conservation measures. Here, we explore patterns of change in local abundance and site occupancy of wintering wader species on estuaries throughout Great Britain over the last two decades, and investigate possible ecological correlates of these changes.

Methods We use national survey data (Wetland Bird Survey, WeBS) for 19 non-breeding waders in 83 estuaries between two time periods (1980/81-1984/85 and 2002/03-2006/07) to build Rank Occupancy-Abundance Profiles (ROAPs) for each species, in order to assess the consequences of population change for changes in local abundances and/or site occupancy. We also explore the variation in local abundance and distribution between species that differ in diet, social behaviour, location of breeding grounds and winter habitat.

Results Populations sizes of all 19 species were observed to fluctuate, with significant overall increases for nine species while none declined significantly. Although the number of estuaries occupied by some species has changed greatly, population changes have primarily resulted in changes in local abundances. Species that were initially more widespread showed smaller changes in local abundance and site occupancy than rare species. Only changes in local abundances were positively correlated with total population change. None of the ecological characteristics explored here proved to be significant in explaining the observed variation in local population size or distribution.

Main conclusions This study provides insights into the processes influencing changes in local abundance and range expansion during periods of population fluctuations. While large changes in site occupancy were apparent for a few species, changes in total wintering population size were typically manifested more in changes in local abundances. It appears that the mechanisms through which population change influence distribution are varied, but habitat availability and site fidelity, along with wader longevity may explain the observed patterns of change in occupancy and local abundances.

Keywords local abundance, population change, ROAP, site occupancy, species traits, waders

Introduction

Changes in community composition and structure can greatly influence the dynamics of an entire ecosystem, impacting its processes and functioning by altering, for instance, productivity, food webs, nutrient cycling and successional stages (Loreau *et al.*, 2002; Hooper *et al*., 2005). Shifts in community composition can result from changes in species' abundance and distribution, through changes in local abundance, colonization of new sites, local extinctions and/or range shifts. Therefore, understanding changes in community composition requires an understanding of the dynamics of species that co-exist, and particularly how changes in local abundance and regional occupancy are linked to processes acting at these two spatial scales.

The general (although not universal) positive association between abundance and occupancy (reviewed in Gaston *et al.*, 2000 and Holt *et al*., 2002) has allowed large scale population dynamics to be modelled as a function of local population dynamics, with the aim of predicting total population size and, more recently, extinction risk (Gaston & Fuller, 2007; Mace *et al*., 2008). Different ecological mechanisms have been put forward to explain the relationship between abundance and occupancy (Gaston *et al*., 2000; Gaston & Blackburn, 2000) and these can be grouped as: (i) range position, referring to the spatial position of species with respect to their geographical range, since species tend to decline in abundance and occupancy towards the edge of their ranges (Blackburn *et al*., 1999); (ii) resource availability, resulting from variation in abundance and variety of resources used (*e.g.* Brown, 1984; Gaston, Blackburn & Lawton, 1997) and in the availability of suitable habitat, since occupancy can depend on the amount of suitable resource or habitat (*e.g.* Holt *et al*., 1997; Freckleton *et al*., 2005); and (iii) population dynamics, concerning the possible consequences of population growth, colonization and extinction rates (*e.g*. Levins, 1970; Holt *et al*., 1997; Hanski, 2000). However, investigations of the processes underlying the abundance and occupancy relationship usually use the average local abundance across all occupied sites. This approach can result in either considerable overestimations of minimum local population size prior to extinction or in underestimations of the maximum local population size that can be supported by the available resources. Consequently, averaging local abundances across sites limits the capacity to understand and detect changes in the distribution of abundances across sites throughout species' ranges.

Changes in total population size must involve either changes in the average abundance at occupied sites and/or changes in total site occupancy (by means of gaining or losing local populations through local colonisation or extinction). These changes are often associated with changes in environmental conditions, such as habitat loss or degradation (Sutherland *et al*., 2012). However, there can be substantial variation between species in terms of the magnitude and direction of population change in response to such environmental changes. Species' responses are likely to be influenced by differences in species-specific traits related to life history and to other ecological characteristics such as dispersal and competitive ability, as particular traits are likely to respond differently to different environmental conditions. For instance, species with greater dispersal capacity and competitive ability may be more able to colonize new areas and establish viable populations and be less vulnerable to extinction (Hanski, 2000). However, the predictive capacity of such traits in this context has been recently argued to be limited for several taxonomic groups, including birds, odonates, alpine plants and mammals (Angert *et al*., 2011). However, there was some evidence that differences in species traits within those taxonomic groups were associated with variation in population changes with regard to range shifts, with some traits promoting faster range shifts than others (Angert *et al*., 2011).

Migratory wader species (Charadrii) use wetland habitats extensively during the non-breeding season, and these habitats face increasing anthropogenic pressures (*e.g*. land claim, disturbance and sea level rise). Recent studies have demonstrated that the composition and structure of wintering wader communities is currently changing (Godet *et al*., 2011; Mendez *et al*., 2012) as a result of variation in the demography of different wader populations (chapter 2). Population size estimates are available for the majority of wintering waders in northwest Europe (Delany *et al*., 2007; Musgrove *et al*., 2011), and changes in their abundance and distribution have been documented across this region (Maclean *et al*., 2008). However, it remains unclear how changes in population size are manifested as either changes in local abundance or site occupancy. In other words, whether increases or decreases in population size result in changes in local abundances within occupied sites, changes in distribution through colonization of new sites or local extinction, or both. Understanding the spatial structure of changes in local abundances for individual species and how it might vary among species can help to identify how site protection measures might also vary for those species. For instance, species for which population declines result in decreases in local abundances but not local extinctions may be managed differently from those declining in site occupancy resulting in a more restricted distribution.

Here we use abundance data for non-breeding waders across British estuaries to examine the extent to which overall changes in wintering population size have resulted in changes in local abundance and/or site occupancy. Changes in abundance and site occupancy of wader species are likely to depend on traits such as the extent of site-fidelity and other factors that constrain or facilitate dispersal, such as flocking and territoriality. Knowing which of these is more prevalent is important because it can influence how best to monitor populations, within and between sites. Similarly, the frequency of changes in population size will influence the probability of range change, and thus the need to consider sites beyond current ranges when planning conservation. In order to quantify the magnitude and direction of changes in wintering population abundance and distribution between two time periods (1980/81-1984/85 and 2002/03-2006/07) we use Rank Occupancy-Abundance Profiles (ROAPs; Collins *et al*., 2009). This approach provides a graphical representation of local abundances across all sites occupied by a given species and, thus, the total number of sites occupied. We quantify changes in local abundances and site occupancy in relation to overall population change for 19 study species. We then explore whether (i) changes in local abundance and site occupancy are more or less likely in species that are initially widespread or narrowly distributed, initially abundant or rare; (ii) social behaviour influences the probability of colonisation of new sites, with the expectation of non-flocking species having greater capacity to expand into new suitable habitat than flocking species; (iii) diet breadth influences the probability of changes in site occupancy, as a result of different rates of change across different species of the invertebrate community (*e.g.* shell-fishing activities could cause bivalve feeders to go locally extinct); and (iv) wintering habitat choice or breeding region influences patterns of population change, which could suggest differences among species in the effect of environmental pressures operating within wintering habitats, or in processes occurring across different breeding grounds.

Methods

Data collection

Several species of waterbirds winter in the UK, however, we restricted our analyses to 19 wintering species for which population trends are available and regularly assessed by Wetland Bird Survey (WeBS, Holt *et al*., 2011), a joint scheme of the British Trust for Ornithology (BTO), Royal Society for the Protection of Birds (RSPB) and Joint Nature Conservation Committee (JNCC), in association with the Wildfowl & Wetlands Trust (WWT). These species were also selected because of their high winter dependency on coastal wetlands, mainly estuarine habitats, which are very dynamic systems and prone to environmental and anthropogenic change (Davidson *et al*., 1991). All selected species are waders with the exception of shelduck *Tadorna tadorna*, which (as elsewhere, *e.g.* Clark & Prŷs-Jones, 1994) is included here because of its high dependence on estuaries during winter and its similarity in feeding ecology to waders, being also extremely reliant on intertidal invertebrate prey.

Under the WeBS monitoring scheme and its predecessor schemes, synchronized monthly counts are carried out at the UK's important wetlands on predetermined monthly dates (thus minimizing the likelihood of double-counting some individuals or missing others), and the resulting national population estimates for all species are published annually (Holt *et al*., 2011). Detailed information on the survey methodology, count accuracy and completeness are provided in Holt *et al*. (2011). We used count data for 83 British estuaries that have been systematically surveyed and for which the monthly coverage is considered to be complete between the winters of 1980/81 and 2006/07.

Winter mean abundance for each species at each site was calculated using counts from November to February, when the number of birds using a site more accurately reflects stable non-breeding population numbers.

Data Analysis

To compare population changes across time, a five-year mean abundance at each site was calculated for the periods 1980/81-1984/85 and 2002/03-2006/07, as this reduces the influence of any between-observer differences in counts. The five-year mean abundance for a given species in a particular estuary is thus considered as its local abundance.

Variation among population trends was firstly assessed using population growth indices, which provide a measure of population size on an arithmetic scale relative to one, and result from dividing the final population size by the initial population size. Thus, if an index is above unity, for example 1.3, means that the population has increased by 0.3 (*i.e*. 30%) and if it is below unity, for example 0.8, the population has decreased by 0.2 (*i.e*. 20%).

To understand the consequences of population change for local abundances and species distribution (*i.e.* site occupancy), we used Rank Occupancy-Abundance Profiles (ROAPs; Collins *et al.*, 2009). ROAP uses a graphical representation of abundances across space, displaying the distribution of local abundances and site occupancy. To generate a ROAP for a single species at a given time, all sites are ordered and ranked by the species local abundance (here using five year means, as described above), from the highest (site rank 1) to the lowest local abundance. The rank position of a given site is divided by the total number of sites (83) to determine the relative rank. This allows comparisons between species with different distributions (some species are present across the majority of British estuaries whereas others have a more restricted distribution). Species-specific ROAPs can then be generated by plotting the local abundance (y-axis) against the relative rank of the estuaries (x-axis) (Figure 1).

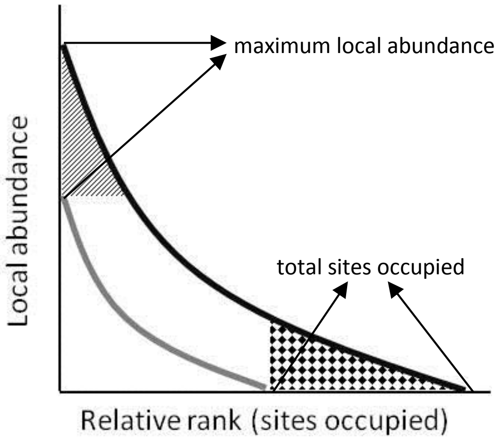

Figure 1. Species Rank Occupancy-Abundance Profiles (ROAPs) for two time periods, represented by the grey and black lines. Each ROAP shows the distribution of local abundances (y-axis) and the proportion of sites occupied (x-axis). Overall population change is the area between the two ROAPs (*D**). The filled triangles represent the changes in maximum local abundance (diagonal lines) and in site occupancy (diamonds). Changes in intermediate local abundance are represented by the unfilled space between ROAPs. Figure adapted from Collins (2009).

To test for differences between ROAPs at different time periods, we used the non-parametric statistic *D** (Collins *et al.*, 2009), calculated as the area between the two ROAPs or the difference in total population size between two time periods (Figure 1). Total population size was calculated as the sum of the local abundances across all estuaries for each time period (*i.e.* the area under each ROAP). Therefore, *D** represents the number of birds gained/lost between two time periods. We tested for statistical significance of *D** using a randomization protocol (Collins *et al.*, 2009). For each pair of ROAPs, we combined the dataset of each time period into one, and re-sampled the data 1000 times, randomly assigning each abundance to a time period without replacement, and calculated *D** for each randomization. This generates a statistical distribution of *D** values that could have been generated by chance alone, given the observed data. We compared the empirical *D** (increase or decrease) to the distribution generated from the randomizations and considered the results to be significant at $\alpha=0.05$

We then quantified the changes in local abundance and site occupancy resulting from changes in the overall population change for each species. First, we divided the area between ROAPs into different sectors according to where each ROAP intersects with the true axis (Figure 1) (Collins, 2009). Changes in site occupancy were assessed from the intersect between ROAPs on the x-axis (diamond-filled triangle in Figure 1) and calculated as the sum of individuals at sites where a species has colonized or gone locally extinct between the two time periods. Changes in local abundance were explored for both maximum and intermediate local abundance (Figure 1). Changes in maximum local abundance were quantified using the intersect between ROAPs and the y-axis, summing the populations at sites that, at the end of the time period, have higher/lower abundances than the maximum local abundance at the beginning of the time period (diagonal line-filled triangle in Figure 1). Changes in intermediate local abundances were calculated as the sum of local populations that have not been included in the other two changes. Finally, changes in local abundance and occupancy were transformed into proportions of the initial population. For example, to understand shifts in maximum local abundance between periods, we divided changes in maximum local abundance by *D**, and multiplied by the growth index previously calculated (% population change between 1980/81-1984/85 and 2002/03-2006/07), resulting in the proportionate amount by which the population had increased or decreased through changes in maximum abundance. The % change in site occupancy represents the % of the initial population that occurs in colonised sites or that was in sites from which the species has gone locally extinct.

We used Kruskal-Wallis tests to explore differences in population change (overall changes and the consequent changes in maximum and intermediate local abundances and site occupancy) of species grouped by diet, social behaviour, location of breeding grounds and winter habitat (Table 1). Using the proportion of prey in the species diet (Leopold *et al*., 2004 a, b; Gill *et al*., 2001b; Gillings & Sutherland, 2007), we classified species by their food preference: bivalves, worms, mixed (feed on both worms and bivalves) and other (when the main prey is neither bivalves nor worms). The social behaviour of species was classified into three broad categories: gregarious (from few individuals to <1000), highly gregarious (from 1000 to >10000 individuals) and not gregarious (from 1 to 30 individuals) (Birdlife, 2012). Location of the breeding grounds allowed the species to be classified into temperate, sub-arctic, arctic and high arctic (Delany *et al*., 2009). Finally, following Musgrove *et al*. (2011), we also classified species by their wintering habitat preference: estuaries, estuaries & inland, estuaries & non-estuarine, non-estuarine & inland, fresh water marshes & wet grassland, and non-estuarine (*e.g.* rocky shores).

We used the number of individuals rather than density as a measure of abundance because although the correlation between density and area was not statistically significant, there was a negative association such that small estuaries tend to have greater densities than large estuaries. Thus, in the ROAP approach, small estuaries with high density populations will be ranked high, whereas a large local population in a very big estuary may have a low density and thus be ranked low. Moreover, total numbers are more suitable in indicating real differences in local population sizes and population trends (*i.e*. it is more meaningful to say that a given population has lost 3000 individuals than 2 individuals per hectare). All analyses were conducted in R (R Development Core Team 2011).

Table 1. Species' diet, social behaviour, location of breeding grounds and winter habitat. The information sources are specified in the text.

Species	**Scientific name**	**Species code**	**Food preference**	**Social behaviour**	**Breeding grounds**	**Wintering habitat**
Avocet	*Recurvirostra avosetta*	av	worm	gregarious	Temperate	estuaries
Bar-tailed godwit	*Limosa lapponica*	ba	worm	highly gregarious	Arctic	estuaries
Black-tailed godwit	*Limosa limosa*	bw	bivalve	highly gregarious	Sub-arctic	estuaries, inland
Curlew	*Numenius arquata*	cu	mixed	not gregarious	Sub-arctic	estuaries, non-estuarine, inland
Dunlin	*Calidris alpina*	dn	worm	highly gregarious	Sub-arctic	estuaries
Spotted redshank	*Tringa erythropus*	dr	other	not gregarious	Sub-arctic	estuaries
Greenshank	*Tringa nebularia*	gk	other	not gregarious	Arctic	estuaries
Golden plover	*Pluvialis apricaria*	gp	other	gregarious	Sub-arctic	estuaries, inland
Grey plover	*Pluvialis squatarola*	gv	worm	not gregarious	Sub-arctic	estuaries
Knot	*Calidris canutus*	kn	bivalve	highly gregarious	Arctic	estuaries
Lapwing	*Vanellus vanellus*	l_	other	highly gregarious	Sub-arctic	estuaries, inland
Oystercatcher	*Haematopus ostralegus*	oc	bivalve	not gregarious	Sub-arctic	estuaries, inland
Purple sandpiper	*Calidris maritima*	ps	mixed	gregarious	Arctic	non-estuarine
Redshank	*Tringa totanus*	rk	mixed	gregarious	Temperate	estuaries, non-estuarine, inland
Ringed plover	*Charadrius hiaticula*	rp	worm	gregarious	Arctic	estuaries, non-estuarine, inland
Ruff	*Philomachus pugnax*	ru	other	highly gregarious	Sub-arctic	fresh water marshes, wet grassland
Sanderling	*Calidris alba*	ss	worm	gregarious	High-arctic	estuaries
Shelduck	*Tadorna tadorna*	su	other	highly gregarious	Sub-arctic	estuaries
Turnstone	*Arenaria interpres*	tt	other	gregarious	High-arctic	estuaries, non-estuarine

Results

Variation in population trends

The populations of waders using estuaries monitored by WeBS in the UK fluctuated by varying amounts between 1980/81-1984/85 and 2002/03-2006/07 (Figure 2). Five species have declined over this period, with purple sandpiper and shelduck suffering the greatest losses (both wintering populations declined by around 25%). Avocet, black-tailed godwit and golden plover experienced the greatest population increases, of 1689, 554 and 418% of the initial population, respectively (Table 2).

Of the 19 species analysed, nine showed statistically significant differences between ROAPs in 1980/81-1984/85 and 2001/02-2006/07 (Table 2, D^* test $p<0.05$). Populations of all these nine species had increased over this period (Figure 3). Black-tailed godwit showed the greatest increase in wintering site occupancy (25 new sites, with local abundances up to approximately 100 individuals), followed by avocet (15 new sites, with local abundances ranging from a few individuals to 200). Other species that also occupied new estuaries across Britain during this period were greenshank, golden plover and sanderling. Grey plover was the only species that showed a decrease in site occupancy, being present at five fewer sites in 2002/03-2006/07 than in 1980/81-1984/85 (Figure 3). Common species on British estuaries such as curlew, redshank and lapwing were present in at least 90% of the estuaries considered in the present study (Figure 3).

Consequences of population change for changes in local abundance and site occupancy

The changes in local abundance and wintering occupancy resulting from population changes varied among species. Overall, changes in wintering populations have largely resulted in changes in local abundances rather than changes in site occupancy. Only four species showed changes in site occupancy greater than 2% (Table 2, Figure 4). Of the species with statistically significant D^*, most of the population increase was manifest in increases in local abundances, both maximum and intermediate, rather than in site occupancy (Table 2). Wintering populations of avocet and black-tailed godwit increased in maximum local abundances by 829% and 215%, respectively between 1980/81-1984/85 and 2002/03-2006/07. For the remaining species, changes in intermediate local populations were greater than changes in maximum local abundance (*i.e.* the proportion of individuals gained at intermediate abundance populations is higher than the proportion of individuals gained through changes in maximum local abundance) (Table 2). Although the number of estuaries occupied by some species has changed greatly (*e.g.* black-tailed godwit and avocet), the local abundances in colonised sites were small in comparison to the increases in local abundances in occupied sites (Figures 3 & 4).

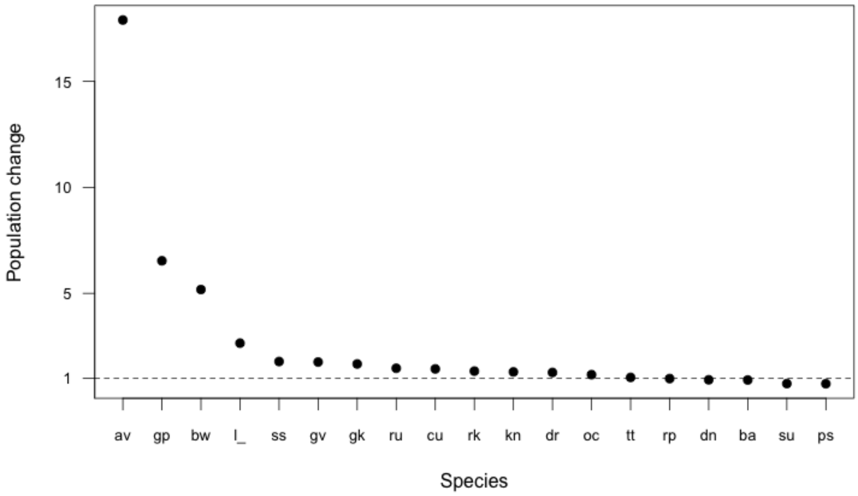

Figure 2. Population changes of wader species on British estuaries between 1980/81-1984/85 and 2002/03-2006/07 (y-axis is log-scaled). Population abundance at each time period is calculated as the sum of all local populations (mean winter abundance). Population changes are calculated in relation to the initial population abundance, thus population increases are above 1 (horizontal dashed line) and population decreases are below 1. Species are ordered by decreasing magnitude of population change. Species codes are provided in Table 1.

Table 2. Wintering wader population changes on British estuaries between 1980/81-1984/85 and 2002/03-2006/07. Initial population is the sum of all individuals across all sites. *D** is the difference in population abundance between the two time periods and represents the number of individuals lost or gained between time periods. The p values are derived using a randomization protocol by comparing empirical *D** with the random distribution of *D**. The percentage change is calculated in relation to the initial population abundance and indicates the total population change and the changes in maximum and intermediate local abundances and site occupancy. Species codes are provided in Table 1.

				% change of:			
Species code	**Initial population**	***D****	**p**	**total population**	**maximum abundance**	**Intermediate abundance**	**occupancy**
av	327	5525	**<0.001**	1690	829.05	636.39	224.85
ba	38092	-3322	0.37	-9	7.85	-16.58	0.005
bw	4060	16971	**<0.001**	418	214.67	187.16	16.15
cu	43422	18891	**0.009**	43	4.29	39.04	0.16
dn	357848	-27661	0.36	-8	1.13	-8.86	0
dr	41	11	0.20	27	-7.31	31.7	2.43
gk	136	92	**0.015**	67	19.63	44.36	2.90
gp	19329	107026	**<0.001**	554	274.75	278.79	0.15
gv	18297	13922	**0.005**	76	13.72	62.37	-0.01
kn	189824	55844	0.24	29	3.03	26.38	0
l_	76074	125535	**<0.001**	165	50.96	114.04	0
oc	196028	32350	0.29	16	7.01	9.48	0.0005
ps	557	-147	0.22	-26	-45.6	19.03	0
rk	51349	17027	**0.037**	33	3.36	29.78	0.005
rp	5757	-123	0.43	-2	3.634	-5.76	0
ru	120	56	0.24	47	16.66	30	0
ss	3979	3122	**0.035**	78	11.3	66.67	0.47
su	69160	-17859	0.11	-26	-29.79	3.95	0.01
tt	9331	329	0.41	4	0.39	3.12	0.01

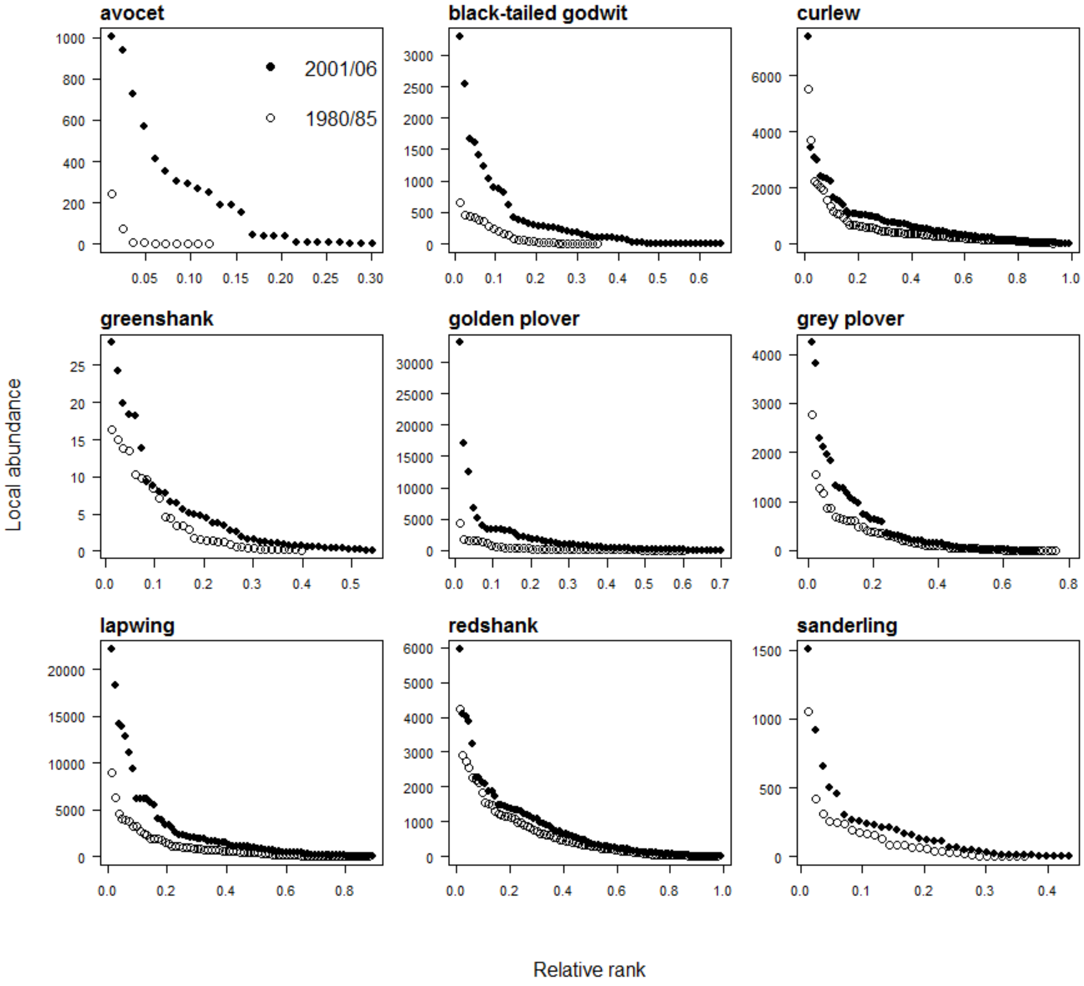

Figure 3. Rank occupancy-abundance profiles (ROAP) at two time periods, 1980/81-1984/85 (open circles) and 2002/03-2006/07 (filled circles), for all species that showed significant population changes (*D** - see table 2). Local abundance was measured as the five-year mean abundance for the two time periods at each estuary. Relative rank was calculated by dividing the rank order of estuaries by the total number of estuaries surveyed (n=83). Each estuary in which the species was present is represented by a single point. For ease of interpretation, estuaries where species were not present (local abundance=0) are not shown.

Correlates of population change

There was no significant correlation between changes in maximum or intermediate local abundance and initial population size (Figure 5 a, d). However, changes in site occupancy were negatively correlated with initial population size for species with significant change in population size (*D**) (Figure 5 g). Changes in maximum and intermediate local abundances and site occupancy were negatively correlated with initial population occupancy (Figure 5 b, e, h), but the correlation was only statistically significant for species with significant change in population size. So, among species with significant changes in population size, those that were initially rare have colonized more new sites.

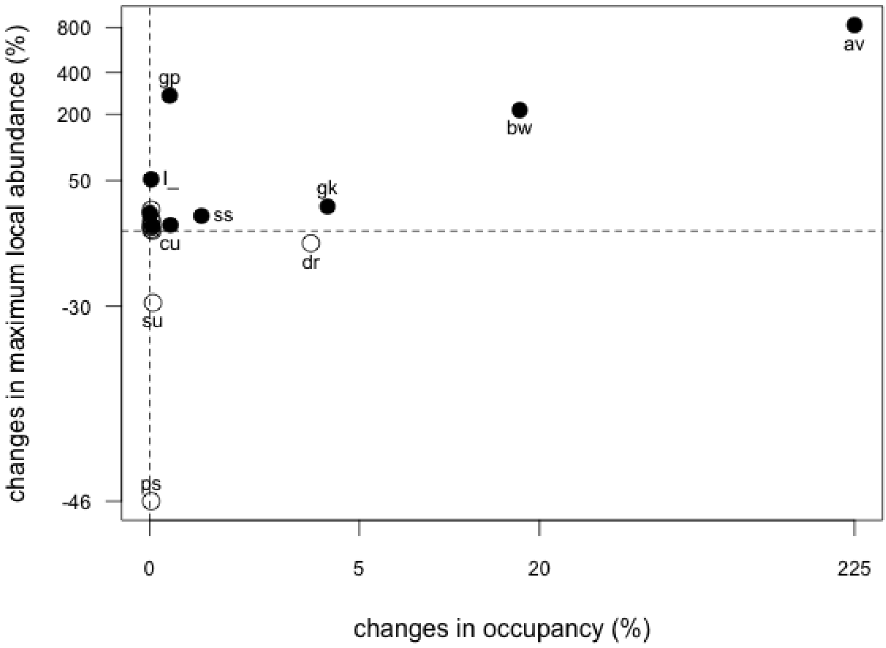

Figure 4. Relationship between changes in maximum local abundance and changes in site occupancy of 19 wader species on British estuaries. Changes are expressed as a proportion of initial population abundance. Both axes are $\log_{10}$-scaled. Dashed lines indicate the initial time period, hence species under the horizontal dashed line have decreased in maximum local abundance and species above the line have increased, and species to the left of the vertical dashed line have decreased in wintering occupancy and species on the right have increased. Species with significant *D** are shown in filled circles and species with non-significant *D** are shown in open circles. Species codes are provided in Table 1.

Changes in local abundances - maximum and intermediate - were significantly positively correlated with total population change; the greater the total population change the greater the change in local abundance (Figure 5 c, f). This correlation was consistent for analyses including all species and excluding the species showing non-significant *D**. On the other hand, there was no significant correlation between changes in site occupancy and total population change (Figure 5 i).

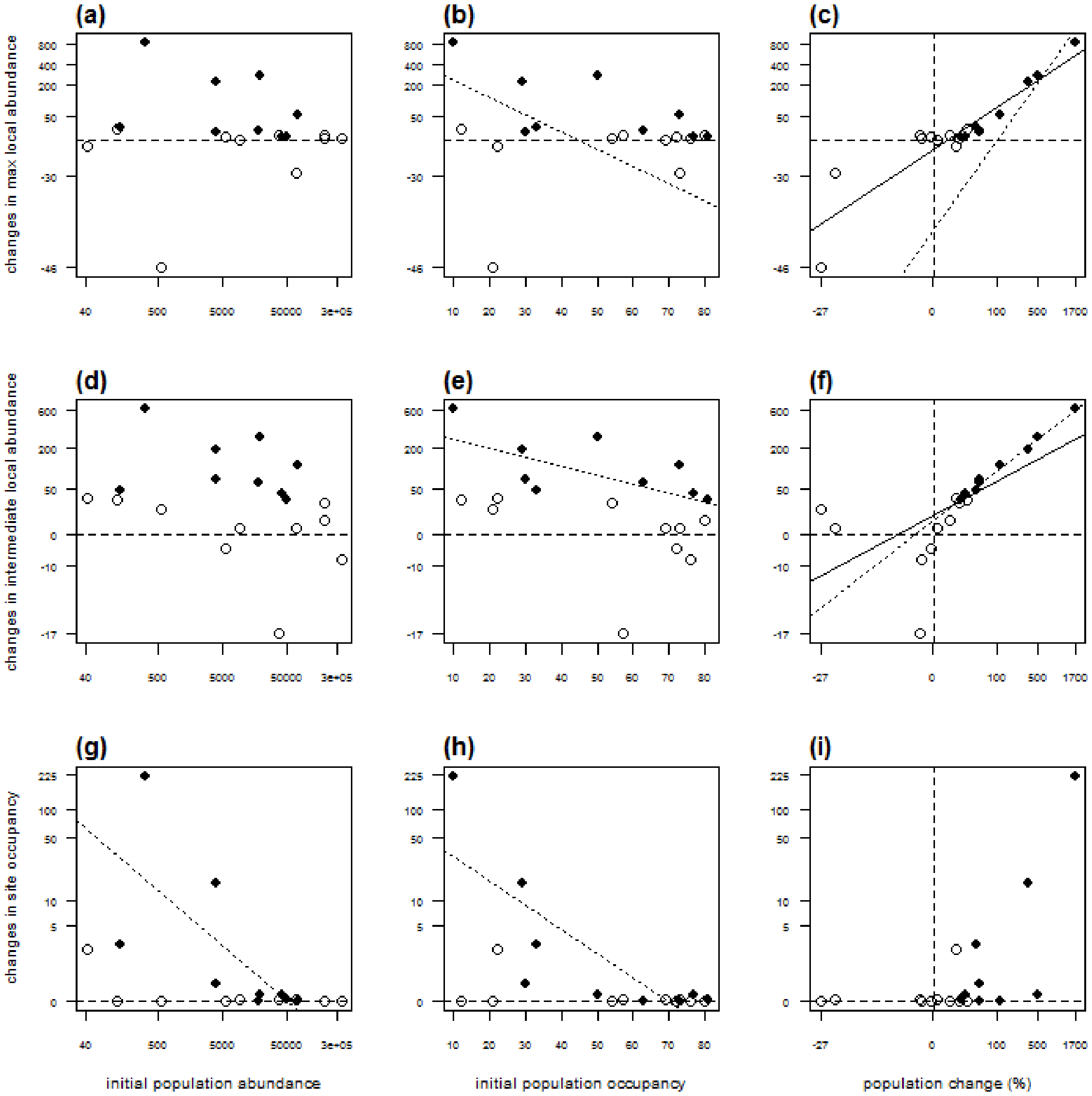

Figure 5. *Top row*: relationships between changes in maximum local abundance and (a) initial population abundance, (b) initial population occupancy (rho = -0.7, n = 9, p = 0.04) and (c) total population change (solid line, rho = 0.86, n = 19, p < 0.001; dotted line, rho = 0.93, n = 9, p < 0.001). *Middle row*: relation between changes in intermediate local abundance and (d) initial population abundance, (e) initial population occupancy (rho = -0.73, n = 9, p = 0.03) and (f) total population change (solid line, rho = 0.93, n = 19, p < 0.001; dotted line, rho = 1, n = 9, p < 0.001). *Bottom row*: relation between changes in site occupancy and (g) initial population abundance (rho = -0.7, n = 9, p = 0.03), (h) initial population occupancy (rho = -0.78, n = 9, p = 0.01) and (i) total population change. Black solid lines show the correlation when all the species are included, whilst dotted line show the correlation when only species with statistically significant change in *D**are analysed (filled circles). Open circles are species with no statistically significant change in D* (see table 2 for details).

There was no statistically significant difference between the overall population change of species with different dietary composition, social behaviour, breeding grounds and wintering habitat (Table 3). This pattern was also consistent when differences between these groups in maximum local abundances, intermediate local abundances and/or site occupancy were analysed (Table 3, Figure 6).

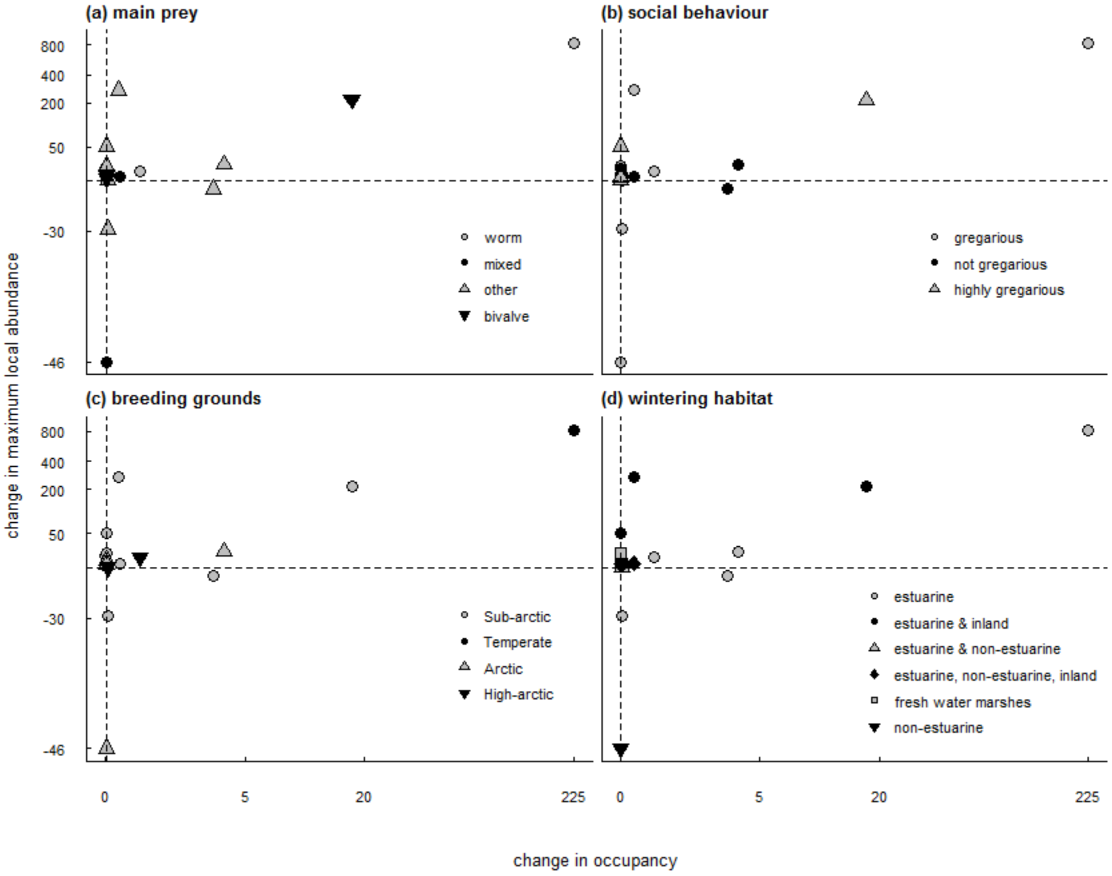

Figure 6. Variation in changes in local abundance and site occupancy between 1980/81-1984/85 and 2002/03-2006/07 of 19 wintering wader species, grouped by (a) the main prey type in their diet, (b) social behaviour, (c) breeding grounds and (d) wintering habitat.

Table 3. Variation in population change (overall changes and the consequent changes in maximum and intermediate local abundances and site occupancy) of species grouped by diet, social behaviour, location of breeding grounds and winter habitat (Kruskal-Wallis test).

	Dietary composition			**Social behaviour**			**Breeding grounds**			**Wintering habitat**		
Changes in:	**χ^2**	**df**	**p**	**χ^2**	**df**	**p**	**χ^2**	**df**	**p**	**χ^2**	**df**	**p**
Total size	0.88	3	0.83	0.36	2	0.83	3.83	3	0.28	5.94	5	0.31
Max. abundance	2.22	3	0.52	0.01	2	0.99	1.48	3	0.68	8.11	5	0.15
Interm. abundance	0.46	3	0.92	0.88	2	0.64	3.45	3	0.32	4.09	5	0.53
Site occupancy	0.59	3	0.89	1.25	2	0.53	2.69	3	0.44	2.35	5	0.79

Discussion

Consequences of population change for species distribution and local abundances

The overall abundance of wader species wintering on wetlands across Great Britain has increased over the last 40 years, and in particular during the mid-1970s to late 1990s (Holt *et al*., 2011). However, since then, the numbers of most species have stabilised and some have even decreased (Holt *et al*., 2011; Musgrove *et al*., 2011). Our analyses support the general trend in increasing population abundance for most species, and reveal that several species have also experienced changes in site occupancy, with all but one (grey plover) expanding their range within Britain. However, changes in occupancy were always accompanied by increases in local abundance (Figure 4), supporting the general pattern of positive abundance-occupancy relationships, and suggesting that many sites were not at maximum carrying capacity for these species at the start of the study (Goss-Custard *et al*., 2002). Colonisation of new sites is likely to be a density-dependent response to increases in local abundance. This process has already been described for wintering black-tailed godwits, which have undergone a significant increase in population size over the past 30 years and expanded into estuaries on the east coast of England (Gill *et al*., 2001a). However, the establishment and expansion of new populations will depend, among other things, on the number of suitable sites available and the amount of resources available within those sites (Gill *et al*., 2001a).

The extent of initial occupancy proved to be an important factor influencing patterns of change in local abundance and distribution of the wader species with significant population changes. Initially rare and narrowly distributed species (*e.g*. avocet) have been able to expand their ranges, whereas abundant and widespread species (*e.g.* lapwing) have not experienced changes in occupancy but have increased in local abundances. This pattern would be expected as widespread species were already present across the majority of suitable habitat, and thus the potential for colonisation of new sites in response to population increases was limited. Our results suggest that the expansion of some species into new sites may result from density-dependent pressures on resource use, as species that have expanded their range have also increased in local abundance within the previously occupied sites. Changes in site occupancy are likely to depend on the amount and distribution of suitable habitat, the distances over which individuals will disperse and the total number of potential dispersers in the population, resulting from intrinsic population growth (Freckleton *et al*., 2005). It is worth noting that it is likely that many of the common species may be expanding outside the range included here, for example into other estuarine sites across Europe (Maclean *et al*., 2008). Although the analyses used in this paper do not encompass the entire winter range of these species, the results suggest that, for declining populations, local declines will occur before local extinctions. Identifying overall population declines will thus require detailed surveys and monitoring of local winter population sizes on individual sites, such as the data used in this study.

Despite the large number of estuaries occupied by some of the wintering species (*e.g*. black-tailed godwit and avocet), the number of individuals gained through changes in site occupancy – resulting in the formation of new local populations – was small in relation to the number of individuals gained through changes in larger local abundances, as abundance increased at all local population sizes. As shown for other waterbird species (Jackson *et al*., 2004), site fidelity can strongly influence patterns of occupancy, particularly given the longevity of these bird species. Site choice by individuals may also be influenced by the performance and abundance of conspecifics, resulting in aggregations around areas of abundant resources (Doligez *et al*., 1999; Brown *et al*., 2000; Jackson *et al*., 2004). Thus, juvenile settlement decision may be influenced by the distribution of conspecifics, resulting in increased local abundances rather than colonisation of new sites.

Five out of the 19 species analysed decreased in number between 1980/81-1984/85 and 2001/02-2006/07 (bar-tailed godwit, dunlin, ringed plover, purple sandpiper and shelduck), although these changes were not statistically significant. Despite this decreasing tendency, no range contraction (*i.e.* local extinctions) occurred for these five species over that time period. Instead, the decreases in the wintering population size resulted solely in declines in local abundances, with either declines at maximum or intermediate local abundances. However, should populations continue to decline then local extinctions from sites with small local populations are inevitable, as small populations are most likely to be vulnerable to extinction (MacArthur & Wilson, 1967; Pimm *et al*., 1988; Lawton, 1993). The fact that the overall decline has not resulted in local extinctions for these five species might be because populations declines have not yet been sufficiently severe for local extinctions to occur, combined with the fact that we considered a time period of 26 years, which might also be insufficient to capture the effect of extinctions, given the longevity and site-faithfulness of waders. According to the extinction debt concept, local extinction of species may occur with delay following an environmental perturbation (Tilman *et al*., 1994) and it is expected that for long-lived species there would be a longer time lag between declines in local abundances and loss of site occupancy (reviewed in Kuussaari *et al*., 2009). The life-span of waders wintering in Great Britain ranges from around 7 to 40 years (BTO, 2012), and studies have shown that many wader species are faithful to their wintering sites both within and between winters (*e.g.* Burton & Evans, 1997; Burton, 2000 and reference therein). Thus, it is highly likely that small populations will persist at traditional wintering sites. All the declining species, with the exception of purple sandpiper, are widespread across Britain, so the persistence of small local populations may suggest that the biotic and/or abiotic pressures influencing the overall wintering population are acting differently across wintering sites, depressing the maximum and intermediate local abundances.

Potential drivers of variation in population trends in wintering waders

Differences in trends in the distribution and local abundance of wintering wader species in this study were not explained by any of the species-specific characteristics explored. We expected that social-behaviour might influence the probability of dispersal to new sites, resulting in gregarious species showing greater changes in local abundances rather than occupancy, and non-flocking species showing greater changes in occupancy than in local abundances. However, wintering waders are generally gregarious, and so there was limited variation in this trait with which to identify such an effect, and no statistical differences between groups of different levels of gregariousness were observed (Figure 6b). All of the wader species in this study are migratory, and thus their abundance and distribution may be affected by factors operating throughout the annual cycle, including wintering, breeding and migratory periods (Alves *et al*., in press). However, differences among species in wintering habitat type, main prey type or location of breeding grounds do not explain differences in trends in winter distribution and abundance (Figure 6). Between-species comparisons of this sort may not be capable of identifying these effects in this case due to the relatively limited variation in wader ecology. Identifying the role of these effects would probably therefore require within-species studies or inclusion of a wider range of species and sites (*e.g*. across Europe).

In conclusion, our study provides an insight into how local abundances vary across sites and how local abundance and site occupancy change in response to overall population change in wintering waders. While large changes in site occupancy have been described for some of the species included here, overall, changes in wintering wader populations have mostly resulted in changes in local abundance (at both maximum and intermediate population sizes). It appears that the mechanisms driving population changes are varied, but habitat availability and site fidelity, along with wader longevity may explain the strong tendency for local population abundance to change much more than site occupancy. Given the statutory importance of maintaining wader (and other waterbird) populations in designated protected areas under legislative frameworks such as the Birds Directive (2009/147/EC) and the Habitats Directive (92/43/EEC), it is important to maintain surveys for identifying the changes in local abundances and distribution that are likely to result from changes in the total population size. In the case of declining species, conservation plans should not be focused only on small populations since abundant local populations may suffer the greatest declines. Similarly, it is important to understand site occupancy of species to be able to assess whether there is potential for colonization of new sites by increasing species.

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Chapter four

Variations in functional diversity and structure of wintering wader communities along different environmental gradients in Great Britain

Abstract

Aim During the non-breeding season, British estuarine ecosystems support many populations of protected migratory wader species. The functional diversity of these wintering communities varies geographically and temporally. Understanding how wader community structure varies along different environmental gradients may indicate the processes that regulate the mechanisms by which communities are assembled. We used deviations of observed functional diversity from expected functional diversity (FD), which can reflect community assembly processes (limiting similarity and environmental filtering), to explore spatial variation in wader community structure in relation to environmental variables at a macro-spatial scale (estuarine morphology, climatic conditions and anthropogenic activities); and whether the magnitude and direction of annual changes in deviations of observed from expected FD relate to changes in climatic conditions or other environmental factors.

Methods We use national survey data (Wetland Bird Survey, WeBS) from the winters of 1980/81 to 2006/07 for 20 species to calculate annual values of the observed FD and expected FD in wader communities across 83 estuaries around the coast of Britain. We investigate how deviations of observed from expected FD for 44 communities relate to estuary morphology (estuary depth, tidal range and fetch), weather (minimum winter temperature and mean precipitation), shell-fishing activities (presence/absence), habitat structure (richness and heterogeneity) and location (latitude and longitude). We also investigate how the direction and magnitude of annual change in community functional diversity relates to estuary morphology, shell-fishing activities, weather and geographic location.

Results The model which best described the variation in deviations of observed from expected FD included longitude, fetch, tidal range, winter minimum temperature, estuary depth, and presence of shell-fishing activities, and these factors jointly explained 56% of the variation in observed minus expected FD. Communities tend to be more functionally similar than expected by chance further east and in estuaries with large tidal range and high fetch, and with shell-fishing activities. Conversely, communities tended to be more functionally diverse than expected by chance in warmer and deeper estuaries. Trends for wader communities to become more similar over time were detected on estuaries with greater depth and fetch (*i.e.* sandier), whereas communities in shallower estuaries with small fetch (*i.e.* muddier) have become more functionally diverse.

Main conclusions This study provides insights into how the mechanisms structuring wintering wader communities in Britain change along different estuarine and climatic gradients, by relaxing or increasing the effects of environmental filtering and competition, resulting in communities varying in functional diversity along those gradients. While we expected that increases in winter temperatures would relax environmental filtering effects, we did not find any association between the annual rate of change in observed minus expected FD and proportional changes and variability in climatic conditions. Instead, we found a modest but nevertheless significant negative relationship between the annual rate of change and both fetch and estuary depth.

Keywords community structure, competition, environmental filtering, environmental gradient, functional diversity, waders

Introduction

Over recent decades, there has been a growing interest in understanding ecological communities, and the mechanisms that determine species richness, as well as the identities and the abundances of species that can co-occur in the same location (*e.g*. Hutchinson, 1961; MacArthur, 1972). However, the relative importance of environmental factors, biological interactions, and random processes in determining the assembly and maintenance of ecological communities are still not fully understood (Leibold *et al*., 2004; McGill, 2010; Pavoine & Bonsall, 2011; Münkemüller *et al.*, 2012). In order to facilitate investigations into the role of species traits in community assembly and structure, a number of recent studies have developed and applied measures of trait dispersion, known as functional diversity (FD) metrics (*e.g.* Petchey & Gaston, 2002; Mason *et al*., 2005; Cornwell *et al*., 2006; Mouillot *et al*., 2007; Petchey *et al*., 2007; Algar *et al*., 2011; de Bello, 2012). Such studies have predominately focused on measuring differences between observed FD and FD expected under a null model (*i.e*. trait distribution expected by chance) as a means of providing evidence for or against the operation of non-neutral processes (Ricklefs & Travis, 1980; Mouillot *et al*., 2007; Petchey *et al*., 2007; Thompson *et al*., 2010; de Bello, 2012). Thus, environmental factors, acting as filters, should constrain specific traits to be present in the community (Cornwell *et al*., 2006), leading to a lower FD than expected by chance. Alternatively, biotic interactions are expected to result in competitive exclusion among species with similar traits, limiting the similarity amongst coexisting species, hence leading to a greater FD than expected by chance (*e.g.* Holdaway & Sparrow, 2006; Petchey *et al*., 2007; Thompson *et al*., 2010).

Across the relatively few studies that have investigated how FD varies along environmental gradients (de Bello 2006; Mayfield *et al*., 2006; Flynn *et al*., 2009; Gerisch *et al*., 2011), contrasting patterns have been found within and between systems. This might result from the variation in the relationship between FD and environmental variables as different mechanisms are thought to support the coexistence of functionally similar and distinct species along environmental gradients (de Bello 2006; Mayfield *et al.*, 2010). Given current rates of environmental change and biodiversity loss, and the importance of functional trait diversity to ecosystem functions and services (Díaz & Cabido, 2001; Grime 2001; Hooper *et al*., 2005; Petchey & Gaston, 2006; Díaz *et al*., 2007; Suding *et al*., 2008), it is necessary to understand the variation in the mechanisms that facilitate or constrain the coexistence of species along environmental gradients, in order to inform conservation strategies aimed at maintaining biological diversity and to monitor community responses to environmental change.

During the non-breeding season, migratory wader species (Charadrii) extensively use wetland habitats, which are recognised as being amongst the most productive ecosystems (Costanza *et* *al*., 1997) but also amongst the most vulnerable (CBD, 2012). The United Kingdom attracts a large number of wintering wader species due to its geographical position along one of the major flyways for Arctic and subarctic breeding species (the East Atlantic flyway), its relatively mild climate during winter (van de Kam *et al*., 2004), and its extensive areas of wetlands and associated estuarine systems. However, as with estuarine environments elsewhere, British intertidal habitat has been and continues to be under high anthropogenic pressure. Habitat loss resulting from land claim (Davidson *et al*., 1991), alteration of the physical structure or shape of the estuary, which determine both the quality and quantity of habitat available for waterbirds (Austin & Rehfisch 2003), developments within and near estuaries (Burton *et al.*, 2002), and alteration of the invertebrate community due to shell-fishing activities (Frid *et al*., 2000) are amongst the most common impacts in estuarine systems. The consequent vulnerability of both habitats and species has provided the impetus for national-scale monitoring of wader populations, allowing the assessment of population trends, the importance of individual sites for these populations (Holt *et al*., 2011) and, more recently, the assessment of community composition, structure and functional diversity (Hill *et al*., 1993; Atkinson *et al.*, 2010; Mendez *et al*., 2012).

The functional diversity and structure of wintering wader communities varies geographically across British estuaries (chapter 1). Although overall wader communities across UK tend to be more functionally similar than expected by chance, there is a regional variation in how communities assemble (Figure 1a). Wader communities in the south and southwest regions tend to be more functionally diverse than expected by chance, suggesting that species interactions may have a relatively strong influence in structuring the communities, whereas in the east and northwest, communities are less functionally diverse than expected, suggesting environmental filtering to be the strongest process structuring communities (Figure 1a). In the present study, we first investigate the influence of estuarine environmental conditions across sites on the distribution of wader functional traits, in order to facilitate interpretation about the overall community functional diversity and the environment, using RLQ analysis. Estuarine conditions also vary regionally, with the eastern estuaries tending to be muddier and typically experiencing colder and drier winter conditions than the rest of the country. We therefore go on to explore the spatial variation of community structure in relation to environmental variables, using estimates of the difference between observed and expected FD extracted from chapter 1 and environmental variables that also vary at these spatial scales. We also investigate whether or not shell-fishing may influence the functional diversity of wader communities. The presence of shell-fishing indicates a richness of mussels and cockles, prey items that are particularly favoured by some species (*e.g*. knot and oystercatcher), which may influence the wader community structure as may increase or decrease the functional traits present in the community. Furthermore, if the fishery is poorly regulated and there is overfishing, the FD of wader communities may be higher than expected by chance due to an increasing in competitive interactions for the limited resource.

Additionally, changes in both observed FD and in the difference between observed and expected FD have taken place over the last 30 years, with wader communities becoming less similar than expected through time, suggesting that levels of species interactions may have become stronger through time and/or that environmental filtering has become weaker (chapter 1). There have also been changes in environmental conditions over the same time. For instance, eastern estuaries are becoming generally warmer during winter, where winter minimum temperatures have increased over 2^{o}C. Changes in climatic conditions could relax environmental filters, allowing an influx of more functionally diverse species into the community, or replacement of functionally redundant species within the community, resulting in increases of functional diversity. However, the magnitude and direction of changes in FD are not equal amongst communities and, contrary to community structure, there is no clear regional pattern in variation in the rate of change in FD (Figure 1b). Thus, other factors may be also influencing the magnitude and direction of changes in community structure, such as reduction of habitat and resource availability, which could increase the strength of competitive interactions and exclude the most functionally similar species, resulting in increases in functional diversity. Using estimates of the rate of change of the difference between observed FD and expected FD extracted from chapter 1, we explore the temporal variation in community structure in relation to environmental conditions and shell-fishing activities.

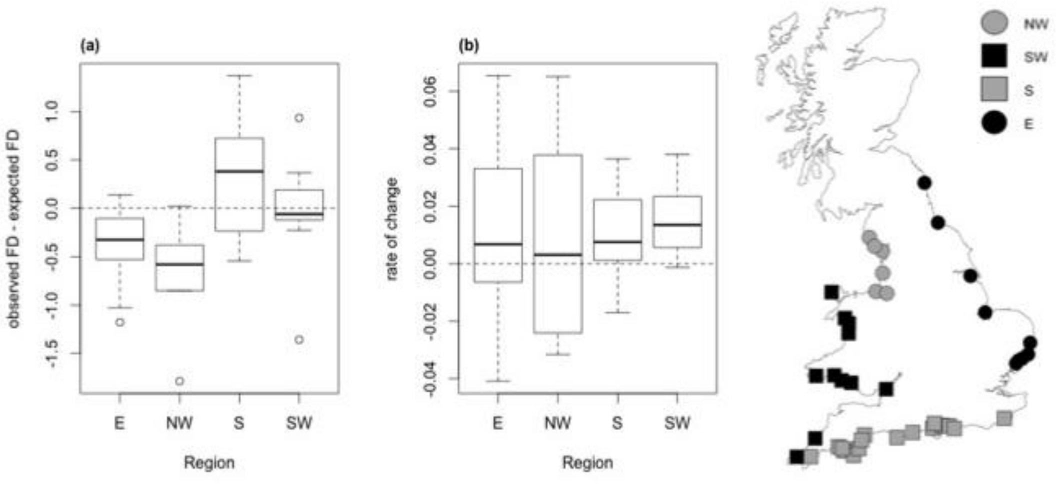

Figure 1: Regional variation in (a) observed FD – expected FD (intercept estimates of the linear mixed model reported in chapter 1), where negative values suggest stronger influence of environmental filtering and positive values suggest stronger influence of species interactions structuring communities; and (b) the rate of change in observed FD – expected FD (slope estimates of the linear mixed model reported in chapter 1), where positive values indicates communities becoming less similar throughout time and negative values indicates communities becoming more similar throughout time. The map displays the estuaries grouped within each region.

Methods

Wader functional diversity

We restricted our analysis to the same 20 wintering species included in chapter 1, which were selected based on their high winter dependency on estuaries and inter-tidal invertebrates. All selected species are waders with the exception of shelduck (*Tadorna tadorna*), which was included in this and previous community analyses as it has similar feeding ecology to waders and is also highly dependent on estuaries (*e.g.* Clark & Prys-Jones, 1994) (hereafter, waders refer to all the species in this study). Spotted redshank and whimbrel were also included although they are relatively scarce wintering species in the UK, with populations found only at a few sites. The majority of individuals of both species winter in Africa and a small proportion remain on some British estuaries during winter.

We used estimated values of deviations of observed from expected functional diversity extracted from chapter 1 to explore causes of geographic and temporal variation in wader community composition and structure. Deviations of observed from expected FD were calculated as (observed FD-expected FD)/standard deviation of expected FD (standardised effect size, SES; Gotelli & McCabe, 2002) for each wader community on each site each year. In order to calculate community FD, first a species by trait matrix was created. Seven trait types related to resource use were used, including morphological, behavioural and ecological traits (chapter 1, Table 2). Then, the entire species by trait matrix for all 20 species was converted into a distance matrix and this was then clustered to produce the functional dendrogram that describes the functional relationships between species (Petchey & Gaston, 2002, 2006). Gower distance was used throughout because it can deal with data-sets comprising continuous, ordinal and categorical traits (Gower, 1971; Pavoine *et al*., 2009). UPGMA clustering was used because it produced a dendrogram with the highest cophenetic correlation (c = 0.7). The regional FD (*i.e.* the FD for a community with all 20 species) was measured as the total branch length of the dendrogram and was used to standardize all measures of FD to vary between 0 and 1, where 0 occurs for single species communities and 1 for communities including all 20 species. Using presence/absence data on community composition (site x species matrix), the observed FD was measured as the sum of the branch lengths connecting all the species present in a given community. Expected functional diversity is calculated from the regional species pool (20 species), assembling random communities with the same number of species as the real community and the probability of inclusion weighted by the relative abundance.

In chapter 1, SES (deviation of observed from expected FD) was modelled as a function of year and estuary, with estuary as a random effect allowing each estuary to have a different rate of change through time. The statistical model was conducted using the *lmer* function of the *lme4* package (Bates *et al*., 2011) in R 2.12.2 (R Development Core Team, 2011). Here, we used the same model and extracted the intercept and slope estimates for each wader community using the *coef* function from the same package. SES intercept estimates coincided with the middle point of the time period of this study (year 1993/94) and we used them to understand the causes of geographical variation in wader functional diversity and community structure. Slope estimates were used to understand variation in the annual rates of changes across wader communities (magnitude and direction of change). Positive slopes indicate that species within a community are becoming less similar/more dissimilar through time. In contrast, negative slopes indicate that species within a community are becoming more similar/less dissimilar through time.

Estuary morphology and habitat data

We used information from 44 estuarine sites in England and Wales for which a comprehensive estuary morphology dataset is available. Burton *et al*. (2010) derived a range of morphological variables for these estuaries, following the previous work of Austin *et al.* (1996) and Rehfisch *et al.* (2000), using GIS shape-files of each estuary, defined by mean high and low water levels and corresponding with the estuary definitions used by WeBS. These included maximum and mean measurements of the area, length and width of the estuary, intertidal zone and estuary channels, and estuary depth (calculated as mean low tide channel width / mean estuary width). However, many of these variables were highly correlated ($p < 0.001$). To minimise the risk of collinearity between variables in the multivariate analysis, we used a subset of these variables for which the significance of their correlation with each other was $p > 0.05$. We included estuary depth, which was not strongly correlated with any other morphological variable (Burton *et al*., 2010). We extracted the mean spring tidal range (the height difference between low tide and high tide) of each estuary from the JNCC Inventory of UK Estuaries for southern, south- west, north-east, and north–west Britain (Buck, 1993a, 1993b, 1997a, 1997b).

We used the mean “fetch” of the estuary from Burton *et al*. (2010). Fetch reflects turbidity and the strength of wave action in the estuary: the higher the fetch value, the more turbid the water within the estuary becomes, influencing the deposition of sediments and consequently, the availability of invertebrate prey (Austin *et al*., 1996; Yates *et al.*, 1996). Thus, fetch is a good indicator of the sediments present within the estuary (high and low fetch are related to sandier and muddier sites, respectively). Fetch estimates were derived from GIS shape-files of estuary boundaries using the average distance perpendicular from the centre line of the intertidal area (*i.e.* the area encompassed between mean high and low water levels) on one side of the estuary to the centre line of the intertidal area on the opposite shore (adapted from Austin *et al*., 1996; Burton *et al*., 2010). Unfortunately, Scottish sites could not be included in the analysis because fetch values for those sites could not be calculated in the same way as for English and Welsh sites. This relates to the Ordnance Survey data and a different definition of high and low tide marks in Scotland to England and Wales: mean high/low water mark in England and Wales and mean high/low water spring tide mark in Scotland. Although the fetch and other estuary shape variables can be calculated for Scottish sites, they would not be comparable with English and Welsh sites due to these differences in measurements (Burton, pers. comm.).

Habitat data from Corine Land Cover Map 2000 of the UK (LCM2000, Fuller *et al.*, 2002) were overlaid with the shapefile of defined UK estuaries used by WeBS in order to extract habitat types and their areas within each estuary using ESRI ArcMap 10. LCM habitat classes were grouped by habitat types used by wader species as follows: littoral sediment (mud, sand, sand/mud with algae); supra-littoral sediment (shingle and dunes); rock; saltmarsh (grazed and ungrazed); and grasslands. We calculated habitat richness, as the total number of habitat types within the estuary, and habitat heterogeneity, as the diversity of habitat types taking into account habitat richness and habitat type area, using the Shannon-Wiener Index (Krebs, 1999; Oliver *et al.*, 2010).

Shell-fishery data

To assess whether shellfish harvesting activities are carried out in the estuary or not, we overlaid the UK estuaries boundary map with a map of bivalve mollusc harvesting area classification zones around England and Wales (GIS shape-file downloaded from www.magic.gov.uk) using ESRI ArcMap 10. There were 14 non-harvested estuaries and 30 harvested estuaries.

Climate data

We used 5-km resolution monthly data sets from 1980/81 to 2006/07 obtained from the British Met Office (www.metoffice.gov.uk) of the mean daily minimum temperature (monthly average of the daily lowest air temperature from 09:00 - 09:00, ^{o}C) and total precipitation (total precipitation amount during the month, mm). We overlaid these climate data with the UK estuaries boundary map and computed the area-weighted average monthly minimum temperature and precipitation for each of the 44 estuary sites. Then, we used data from November to February, the same winter months from which wintering communities are defined, to calculate winter weather indices. Minimum winter temperature was calculated as the lowest minimum temperature recorded during a given winter and was used as a proxy for winter severity. Other winter severity indices can provide a better fit in predicting wader survival and density (*e.g.* the number of consecutive days below freezing or snow cover ground), however, it should be noted that FD was calculated using presence/absence data, and thus, we believe that using the lowest minimum temperature recorded throughout the winter is a good proxy for winter severity in this analysis. Mean winter precipitation was calculated for each of the winter periods represented in the time series (1980/81-2006/07).

To understand the causes of variation in functional diversity and community structure, we calculated a five-year mean for each of the climate variables from winter 91/92 to 95/96, the central period in the overall time series considered. Using this mean rather than the values for the winter 93/94 (when SES intercepts are estimated) allows possible climatic differences between sequential winters at particular sites to be accounted for. To understand the differences amongst rates of change in deviations of observed from expected FD, we estimated the proportional change in minimum temperature and precipitation, calculated as the difference in climatic conditions between the end (five-year mean between winters 2001/02- 2005/06) and the beginning of the time period (five-year mean between winters 1980/81- 1984/85) divided by the climatic conditions at the end of the time period; and the variability (standard deviation) in climatic conditions across the whole time series for each estuary.

Data analysis

In order to explore the environmental drivers of functional diversity, we first investigated the association between functional traits and environmental conditions using RLQ analysis (Dolédec *et al.,* 1996). This approach allows the simultaneous ordination of three matrices (R-mode: site by environmental variables matrix, which contains the environmental characteristics at each site; Q-mode: site by species matrix, which contains the occurrence of species at each site; and L-link: species by trait matrix, which contains the functional traits of each species), in order to analyse relationships between species' traits and environment conditions, while accounting for species occurrence at sites (for detailed information see Dolédec *et al.,* 1996). The analysis was carried using the ade4 package (Dray & Dufour, 2007) in R 2.12.0 (R Core development team, 2011). First, individual ordination analyses were performed for each matrix: a correspondence analysis using the function *dudi.coa* for the site x species matrix; and a principal components analysis (PCA) for the other matrices using the function *dudi.hillsmith*, that allows mixing quantitative and categorical variables. Then, these ordinations were combined to perform the RLQ analysis using the *rlq* function. To test the significance of the relationship between traits and environment, we performed a Monte-Carlo permutation test with 1000 repetitions using *randtest.rlq* function.

We investigated deviations of observed from expected FD (SES) using multiple regression analysis to model SES intercept estimates for each estuary as a function of estuary morphology (estuary depth, tidal range and fetch), weather (minimum winter temperature and mean precipitation), presence/absence of shell-fishing activities, habitat (richness and heterogeneity), latitude and longitude. We specified an offset variable, intertidal area, to control for the area effect (*i.e.* larger estuaries can hold greater wader diversity, chapter 1). All morphological variables were $\log_{10}$ transformed prior to the analysis. We used a full model averaging approach to select the best combination of predictors, using the *AICcmodavg* package (Mazerolle, 2010). Models with delta AIC <6 were included for the calculation of the parameter estimates. Prior to the multivariate analysis, we checked for collinearity amongst predictors in the model; as all correlation coefficients were < 0.6, all variables were included. We also compared the explanatory power of the predictors and measured the relative importance of each of the predictors in the model using *calc.relimp* function within the relaimpo library (Grömping, 2006) in R 2.12.0 (R Core development team, 2011). Two methods were used to assess the relative importance of each of the predictors: (i) comparison of the amount of variance each predictor alone is able to explain (R^2 values from regression models with one predictor, method=first), and (ii) the R^2 contribution averaged over orderings among predictors (method= lmg).

We investigated the variation in the direction and magnitude of change in community functional diversity using SES slope estimates. We used multiple regression analysis, where SES slopes were modelled as a function of estuary morphology (estuary depth, tidal range, fetch), presence/absence of shell-fishing activities, weather (proportional change and standard deviation of both minimum temperature and mean precipitation), latitude and longitude, and intertidal area as a covariate. We followed the same steps as above described for model selection.

We assessed the extent to which spatial autocorrelation might influence all of our statistical models by plotting the residuals of the best-fit model using the Moran's I *correlog* function in the R package *ncf* (Bjornstad, 2009).

Results

Relationships between environmental conditions and functional traits

The first two axes of the RLQ accounted for 41% and 27%, respectively, of the total variance in the matrix that related the functional traits and environmental variables. The permutation test demonstrated a significant relationship between the environmental conditions and the species functional traits ($P = 0.0009$, Monte Carlo permutation test). The relationships between species functional traits and environmental conditions are shown in Figure 2, which provides a visual representation of where a given set of traits tends to occur. For instance, species with an up-curved bill, feeding on crustaceans by sweeping the bill through the upper surface of the mud or water (scything) tend to occur at estuaries at lower latitude and longitude, where the minimum winter temperature and precipitation are both high (warmer and wetter estuaries). Harvested and deeper estuaries tend to be dominated by species with a down-curved bill that probe or jab, are able to swim while feeding, and feed on worms. However, this does not necessarily mean that each species has to display all these traits, rather that those sites are characterized by the presence of those traits states, which could be displayed by more than one species.

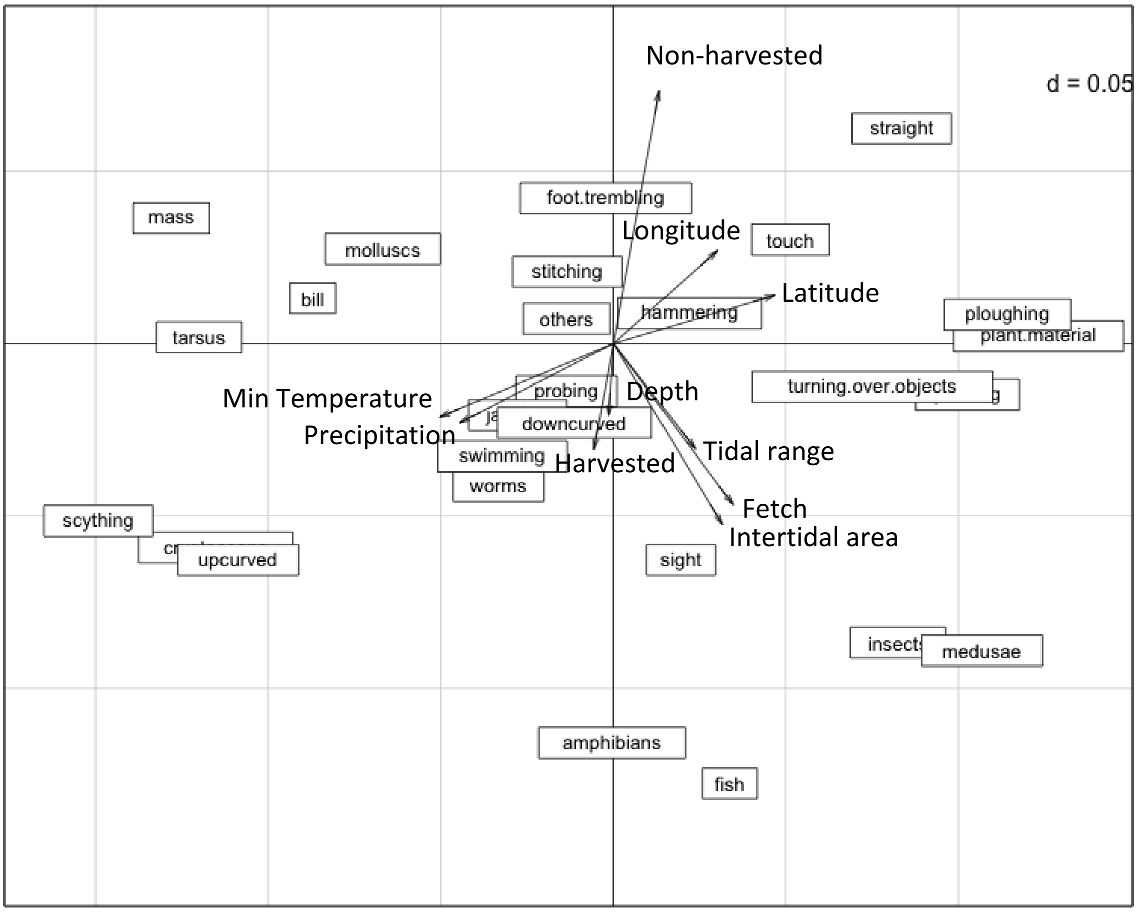

Figure 2. Relationship between environmental conditions and species functional traits along the first two RLQ axes, which explain 41% and 27% of the variation in wader functional traits on 44 UK estuaries. Arrows indicate environmental gradients. Traits are defined in chapter 1, Table 2.

Factors that determine variation in deviations of observed FD from expected FD (SES intercept)

Of all the variables analysed, longitude, fetch, tidal range, estuary depth, winter minimum temperature and whether or not shell-fishing activities take place within the estuary, provided the best-fit model and jointly explained 56% of the variation in SES intercepts (Table 1, Figure 3). SES intercept values tended to decrease with increasing longitude, fetch and tidal range (Table 2). Thus, communities tended to be more functionally similar than expected by chance further east and in estuaries with large tidal range and high fetch. On the other hand, SES values tended to be higher for estuaries with warmer minimum winter temperature and higher depth (*i.e.* communities were more functionally diverse than expected by chance). When the presence of shell-fishing was included in the multiple regression model, its influence in SES values was negative (Table 2). However, this effect was reversed when none of the other variables were included, where SES estimate values for harvested estuaries are higher than for the non-harvested (harvested = -0.03, p = 0.7; non-harvested = -0.2, p = 0.2). Thus, estuaries that are harvested tended to hold wader communities that are more functionally dissimilar than expected by chance. However, this difference was not statistically significant (F value=0.7, p=0.4).

Tidal range, longitude and winter minimum temperature were the most important variables in the model and their combination contributed 90% of the variance explained by the full model (R^2), using either of the methods to calculate the predictor's relative importance (Figure 4). Longitude, however, was one of the variables that was correlated with tidal range (r=-0.42, df=42, p=0.003) and winter minimum temperature (r=-0.57, df=42, p<0.0001). Thus, eastern estuaries tend to have smaller tidal ranges and also tend to be colder.

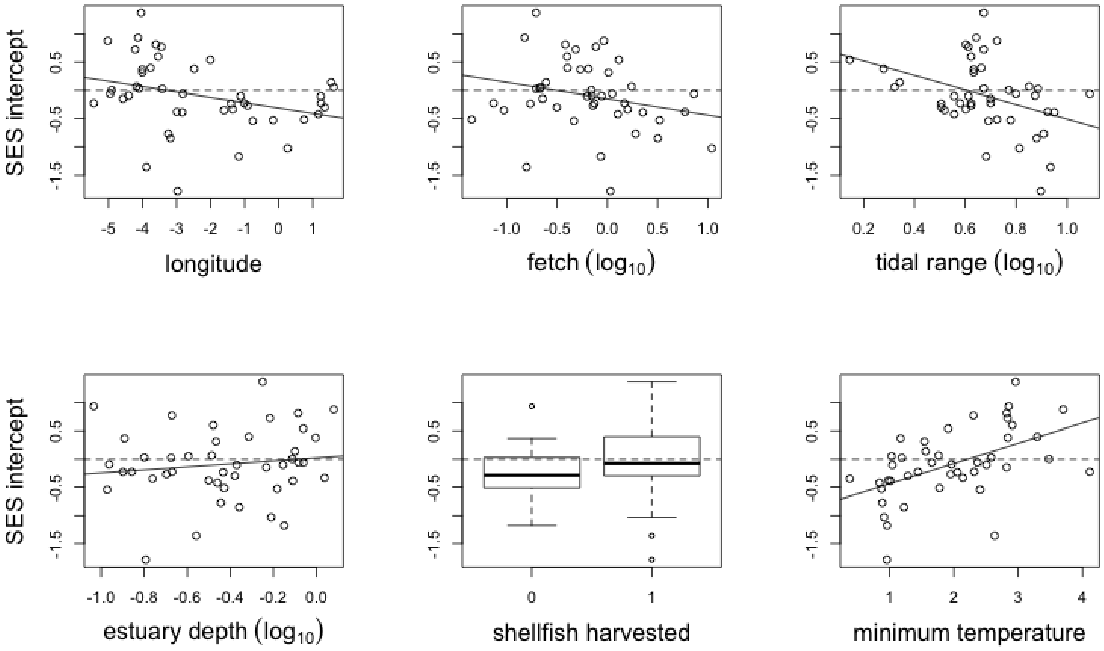

Figure 3: Variation in deviations of observed FD from expected FD (SES intercept) of wader communities and environmental variables on 44 UK estuaries. Fitted lines represent single linear predictor models for longitude (R^2 = 0.1, 42 df, p = 0.03), fetch (R^2 = 0.06, 42 df, p = 0.1), tidal range (R^2 = 0.15, 42 df, p = 0.009), estuary depth (R^2 = 0.01, 42 df, p = 0.4) and minimum winter temperature (R^2 = 0.26, 42 df, p = 0.0003). Shellfish harvested, 0 or 1 (absence [n=14]

and presence [n=30], respectively, of shellfish harvesting activities within estuary) (F=0.7, p=0.4).

Table 1: AIC values, Delta AIC, AIC weights, the cumulative AIC for each model where SES intercept was the response variable. Only models with Delta AIC < 6 are included in the table.

Parameters included in the model	AIC	Delta AIC	AIC Wt	Cum Wt
Fetch + Tidal range+ Depth + min Temp + Harvested + Long	69.32	0.00	0.29	0.29
Fetch + Tidal range+ Depth + min Temp + Long	69.74	0.42	0.24	0.53
Fetch + Tidal range+ min Temp + Long	69.82	0.50	0.23	0.76
Fetch + Tidal range+ Depth + min Temp + Harvested + Habitat Heterogeneity + Long	70.74	1.42	0.14	0.90
Fetch + Tidal range+ Depth + min Temp + Harvested + Habitat Heterogeneity + Habitat richness + Long	72.33	3.01	0.06	0.90
Fetch + Tidal range+ Depth + min Temp + Precipitation + Harvested + Habitat Heterogeneity + Habitat richness + Long	74.12	4.80	0.03	0.99

Table 2: Estimate values for the combination of predictors that best explain the variation in SES intercept. Model-average estimates and unconditional standard errors (as opposed to the conditional SE based on a single model) were obtained from the models in Table 1.

	Model-averaged estimate	**Unconditional SE**
Tidal range ($\log_{10}$)	-2.22	0.52
Fetch ($\log_{10}$)	-1.19	0.19
Estuary depth ($\log_{10}$)	0.40	0.28
Minimum temperature	0.20	0.12
Shellfish harvested	-0.25	0.18
Longitude	-0.16	0.05

Spatial autocorrelation was found to be absent from residuals of the best-fit models (Moran's I associated p-values > 0.05) for any lag-distance class within our data, with the exception of the second lag-distance (approx. 125km) where the Moran's I correlation is negative (-0.25) with a $p<0.05$ (Figure 5). However, the combination of spatial autocorrelation, being present only at the second lag-distance rather than at the more indicative, shortest lag-distance class, was interpreted as somewhat anomalous and non-problematic, and no further consideration was taken of it. Moreover, negative spatial autocorrelation is not readily addressed (Griffith, 2006).

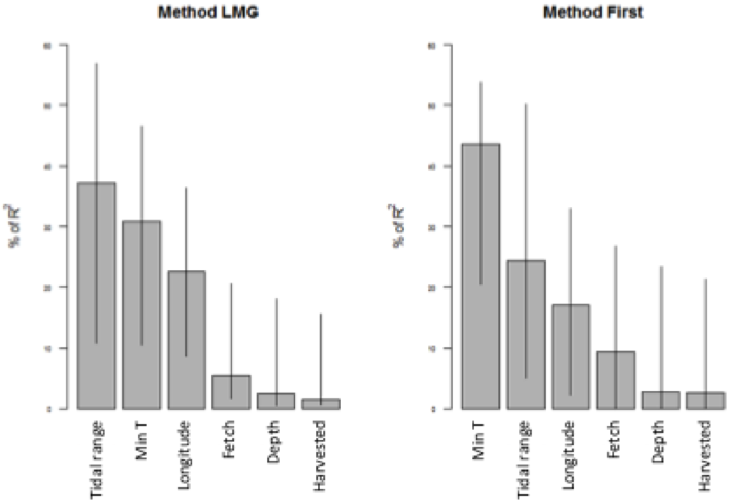

Figure 4: The relative importance of environmental predictors in determining the SES-Intercept (± 95% bootstrap confidence intervals). Relative importance is measured using the *LMG* method (left) the *First* method (right). In both cases, metrics are normalised so that their sum equals 100%.

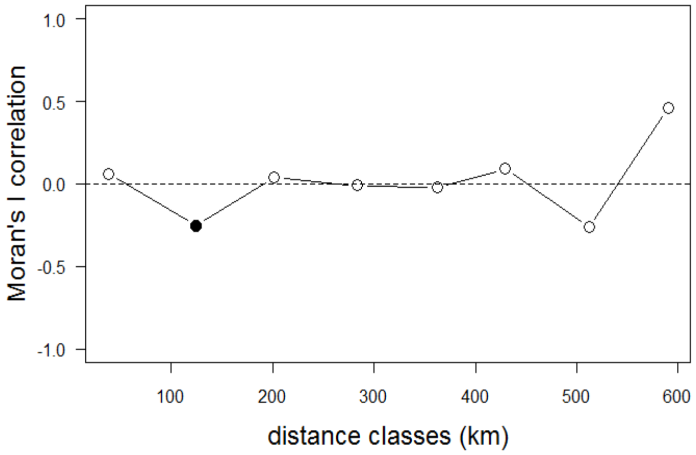

Figure 5. Moran's I correlogram for the residuals of the best model explaining the geographical variation of SES intercepts across wader communities. Significant spatial autocorrelation is indicated with filled circles.

Variation in the rate of change of deviations of observed FD from expected FD (SES slope)

The amount of variation in the direction and magnitude of changes in SES explained by the combination of fetch and estuary depth was rather modest but nevertheless significant ($R^2 = 0.13$, $p = 0.02$) (Figure 6). Both variables had negative estimates (Table 3), indicating that wader communities found in estuaries with greater fetch and depth have become more similar through time or little change was observed, whereas communities in shallower estuaries with small fetch have become more functionally diverse than expected by chance.

Spatial autocorrelation was found to be absent from residuals of the best-fit models for slope of SES (Moran's I associated p-values > 0.005) for any lag-distance class within our data.

Table 3. Estimate values for the combination of predictors that best explain the variation in SES Slope. Model-average estimates and unconditional standard errors were obtained from the models with Delta AIC < 6.

	Model-averaged estimate	**Unconditional SE**
Fetch ($\log_{10}$)	-0.01	0.01
Estuary depth ($\log_{10}$)	-0.02	0.01

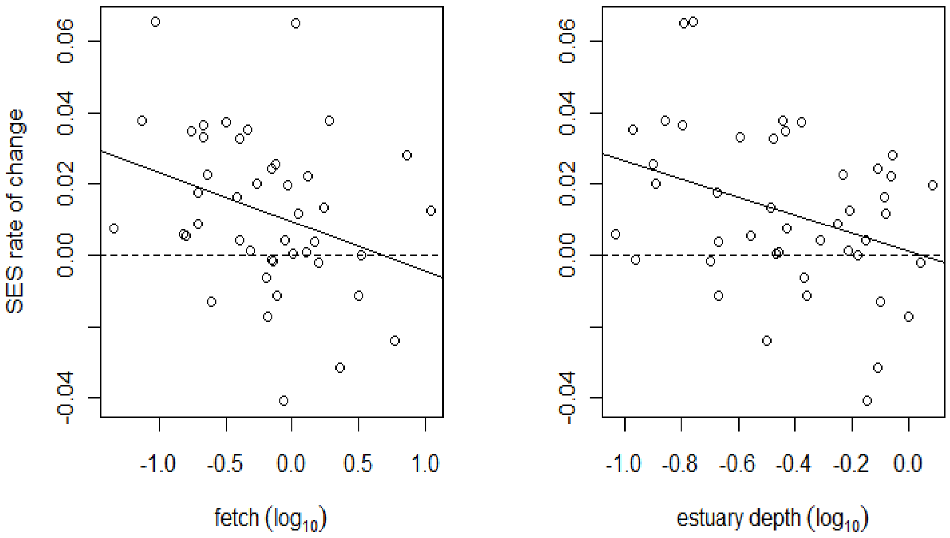

Figure 6. Variation in the rate of change of deviations of observed FD from expected FD (SES slope) in relation to estuarine morphological variables. Fitted lines represent single predictor models for (i) fetch (R^2 = 0.1, 42 df, p = 0.03) and (ii) estuary depth (R^2 = 0.1, 42 df, p = 0.02).

Discussion

Relationship between functional traits and environmental conditions

The RLQ analysis revealed a significant relationship between wader functional traits and environmental variables. The variation in functional traits is associated with a combination of estuarine morphological, climatic and anthropogenic variables (shell-fishing), suggesting that environmental conditions in estuaries influence the range of functional trait states represented within wader communities. However, even though environmental conditions vary across estuaries and may be associated with the presence of specific traits, there is no distinctive segregation of trait states along these environmental gradients, as the close proximity of the functional traits to the centre of the RLQ plot (Figure 2) indicates that a similar range of trait states tend to occur in a large number of estuaries. This is almost certainly due to the fact that the majority of the analysed species are widely distributed in the UK. Exceptions to this include avocet, black-tailed godwit, greenshank, ruff, spotted redshank and whimbrel, all of which have distributions that are more restricted to southern and western estuaries. In this study, these estuaries represent a disproportionate component of the total number of estuaries included in the analysis, making these species over-represented in our data set. Therefore it is possible that the segregation in functional traits along environmental gradients might be clearer if a larger number of coastal sites across the UK, and particularly Scotland, had been included. However, the number of estuarine communities included here is sufficient to show that the distribution of functional traits (*i.e*. functional diversity) is not uniform across communities (Mendez *et al*., 2012), with some communities being under-dispersed (species are more similar than expected by chance) and others being over-dispersed (species are less similar than expected by chance), possibly as a result of a stronger relative influence of environmental filtering and species interactions, respectively.

Geographic variation in community structure

Depending on how environmental variables affect the processes structuring wader communities, different functional trait distributions will result. Tidal range and minimum winter temperature turned out to be the factors that accounted for the largest proportion of the variance in the difference between observed and expected FD (*i.e*. SES intercept), followed by longitude and fetch (Figure 4). Although estuary depth and the presence/absence of shell-fisheries activities within the estuary improve the fit of the model, they explain very little of the variance in SES (Figure 3) and when they are removed from the model, the relative goodness of fit (AIC) changes only slightly (Table 1). Two models are considered to have the same weight in the data when the difference between their AIC is less than two (Burnham & Anderson, 2004). Thus, we will discuss the most important variables explaining the variance in community structure. However, it is worth mentioning that there was a tendency, albeit weak, for wader communities to be more similar when shell-fishing occurs in the estuary. Overfishing might increase the similarity by filtering out species that feed on bivalves and shifting towards communities dominated by worm-feeding species (Atkinson et al., 2010). Estuaries with shellfisheries are more likely to be dominated by worm feeders (Figure 2), which may increase the similarity amongst coexisting species. However, if shellfisheries are well regulated, they may have weaker effects on community structure than the overfished estuaries, resulting in a weak overall tendency for these communities to be more similar than expected by chance.

Tidal range, the vertical difference between low and high tide, varies greatly along the British coast (range from 1.4 metres to 12.3 metres). Twice a day, intertidal areas are exposed by the receding tide, and the period of exposure is determined by tidal levels (Wanink & Zwarts, 1993; and references therein). Generally, estuaries with greater tidal range can have their intertidal area exposed for longer periods of time, providing more foraging time to wader species. The foraging time available for waders will also depend on the interaction between tidal range and the distribution of invertebrates, as many invertebrate species are common at the mid-tide level and thus are available to waders for limited periods of time within each tidal cycle (Evans 1976). The decline in the difference between observed and expected FD with increasing tidal range (Table 2, Figure 3) could therefore reflect a relaxation of the effects of competition on estuaries with larger tidal ranges and greater foraging time. This is supported by the fact that decreases in the difference between observed and expected FD along this gradient are normally accompanied by an increase in species number (negative relationship between SES and species richness; Figure 4, chapter 1) suggesting more of an increase in species packing due to a relaxation of competition, rather than an increase in environmental filtering, which would occur if species numbers decreased along the gradient.

Conversely, winter minimum temperature has a positive effect on the difference between observed and expected FD (Table 2), with overdispersed communities associated with warmer sites, whereas underdispersed communities are associated with colder sites. In addition to direct effects on the survival of waders, severe weather conditions can have indirect effects by decreasing the availability of their invertebrate prey. Many intertidal invertebrates move or burrow deeper into the sediment in cold conditions, becoming inaccessible for short-billed waders (Evans, 1976). There is a tendency for long-billed waders to occur more frequently in estuaries where winter temperature and precipitation are higher (Figure 2). Furthermore, deep living invertebrates, such as Arenicola marina - a common wader prey species - become less active and come to the surface less frequently at low temperatures, hence are less accessible to birds (Evans, 1976). Thus, low temperature seems to strengthen environmental filtering effects, favouring a limited range of trait states and reducing the spread of ecological strategies, whereas higher temperatures seem to widen the filter, allowing more varied trait states to be present in communities. Although estuaries in the south-west are generally warmer than on the east coast, due to differences in estuarine morphology and tidal influence, east coast estuaries are also generally muddier than those on the west coast. Under the limiting similarity principle (MacArthur & Levins, 1967), we would expect an increase in competition between species that are more similar in exploiting the available resource when the latter becomes limiting. Consequently, the negative effect of fetch (greater fetch, indicates greater turbidity associated with sandier sediments) on the difference between observed and expected FD may indicate an increase in competition effects on sandier estuaries, if invertebrate population here are more limited in abundance and availability. Invertebrate abundance and availability to foraging waders is influenced by sediment particle size (Quammen 1982; Yates *et al.*, 1993; Rehfisch 1994), and is generally relatively higher in estuaries that have muddy sediments (Austin & Rehfisch, 2003). Thus, despite south-western warmer temperatures potentially relaxing environmental filters and allowing more trait states to be present, sediment type may limit the similarity amongst those trait states.

Despite the variance explained by climatic and physical conditions of the estuary, longitude still accounted for a large amount of the variance in the difference between observed and expected FD (Figure 4). This might be due to other factors that happen to be correlated with longitude and have not been accounted for. However, longitude was previously shown to be significantly associated with the composition and functional diversity of wader communities (Hill *et al*., 1993; Rehfisch *et al*., 1997; Mendez *et al*., 2012), with the latter decreasing when moving from west to east. Longitude could be acting as a proxy for proximity to species migratory routes and position within wintering distributional ranges. As discussed above, wader distribution can be influenced by food availability and climate. However, species breeding to the northwest of the UK are also more likely to winter on western estuaries, whereas those breeding to the northeast of the UK may occur more on eastern estuaries (Wernham *et al.*, 2002). As the UK also represents the edge of the wintering ranges of a number of species (*e.g*. avocet), their distribution among estuaries may be more restricted than for other species (*e.g*. oystercatcher) for which the UK represents the centre of their wintering ranges. Longitude may therefore represent both an ecological gradient of local environmental differences that influence wader communities among estuaries (*e.g*. temperature) and a spatial gradient of dispersal/migratory limitation.

Variation in the rate of change of community structure

Overall, over the last 30 years, wader communities on British estuaries have become functionally more dissimilar than expected by chance, suggesting that the levels of niche partitioning may have become stronger through time and/or environmental filtering has become weaker (Mendez *et al*., 2012). However, not all communities are changing at the same rate, and some are even losing functional diversity (Figure 1). Given the effect of temperature on community structure (discussed above), increases in winter temperatures might be expected to relax or widen environmental filtering effects. Thus, estuaries experiencing the greatest climatic changes may also experience the greatest changes in community structure. However, we did not find any association between the annual rate of change in observed minus expected FD and proportional changes or variability in climatic conditions. Instead, we found a modest but nevertheless significant negative relationship between the annual rate of change of SES and both fetch and estuary depth, with negative changes in SES being associated with estuaries with greater depth and more turbid waters. This may imply that environmental filters have become stronger and/or competition has become weaker in structuring communities at sandier sites, whereas the reverse may occur in muddy estuaries. Some species that favour sandy estuaries (*e.g*. bar-tailed godwit and knot) are undergoing shifts in their distribution across north-west Europe (Maclean *et al*., 2008). Thus, if the abundance and presence of such species are decreasing at sandier sites, then the competitive interactions (for the less abundant resource in sandy sediments) may also be reduced. At the same time, expanding species such as avocet and black-tailed godwit, may be favouring muddy estuaries and contributing to intensifying competitive interactions between coexisting species. Furthermore, changes in wave action, currents and tide may influence the type of intertidal sediment (Yates *et al*., 1996), leading to either more sand or more mud which will in turn affect the abundance and distribution of invertebrates. As a consequence of these estuarine morphological and physical changes, the influence of environmental filters on community structure may become stronger or weaker if sediment becomes sandier or muddier, respectively.

Ecosystems worldwide are being altered by human activities. Hence, we need to assess the relative importance of abiotic and biotic processes for community structure, and how these might be affected by environmental change, in order to understand the processes by which communities are sustained. The present study investigates differences between observed and expected FD increasing our understanding of changes in wader community structure along different environmental gradients and pointing to likely processes driving changes in the relative strength of the mechanisms by which communities are assembled. We highlight the need to understand the potential importance of functional traits for specific ecosystem functions, as waders are among the top predators in estuarine systems. Changes in the processes structuring communities can lead to changes in the distribution of functional trait states and hence, changes in estuarine ecological functions.

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Chapter 5

Co-occurrence patterns of wintering wader species foraging in the intertidal area of British estuaries

Abstract

Aim Many migratory wader species use estuarine wetlands during the non-breeding season and these habitats face increasing anthropogenic pressures. Wader species throughout the world are currently facing population declines, which raises concerns about the management and conservation of the estuarine systems upon which they depend. In order to improve management and design targeted conservation strategies, it is necessary to understand the distribution of birds within estuaries, both within and between species. Here, we apply a co-occurrence index and null model analysis to investigate co-occurrence patterns of wintering wader species that feed in the intertidal area of different estuaries across Great Britain, and assess whether species co-occurrence is associated with functional similarity or dissimilarity in order to identify the processes driving species co-existence.

Methods We use low tide counts (WeBS Low Tide Counts) for 17 wintering wader species from eight estuaries across Great Britain to examine patterns of spatial distribution within and between species. We test for (1) evidence of non-random patterns of co-occurrence and (2) relationship between species' co-occurrence and species' functional differences.

Results Locally abundant species tend to be widespread across the intertidal area of estuaries, whereas rare species tend to be narrowly distributed. However, distribution patterns were significantly non-random for only a few species on specific estuaries. On five of the eight estuaries, non-random patterns of species co-occurrence were detected and there is a tendency, though statistically non-significant, for functionally dissimilar species to segregate within estuaries more than functionally similar species, which tend to aggregate.

Main conclusions The distribution of species abundances within estuaries varies within and between species, suggesting that the distribution of species abundances is influenced by the operation of local-scale processes. Furthermore, this study suggests that species co-occurrence patterns were likely to be driven by species' habitat affinities, because there was a tendency of functionally similar species to aggregate. We discuss the potential drivers underlying these patterns and the importance of identifying these drivers for the better management of estuarine systems.

Keywords functional dissimilarity, species co-occurrence, species distribution, waders

Introduction

Understanding the processes underlying the co-existence of species and hence contributing to the maintenance of levels of diversity of natural communities is a major research topic for ecologists and conservationists. Recent advances in null model analysis have provided a means of detecting the presence of non-random patterns of species co-occurrence. This is achieved by comparing observed data with a null reference distribution constructed by reshuffling sample data in a random procedure, in order to test whether observed patterns differ significantly from null expectations (Gotelli, 2000). For example, recent meta-analyses carried out on a large number of communities from different taxa and using different null models demonstrated that non-random patterns are common across the majority of taxa studied and indicated that species co-occurrence was often lower than expected by chance, suggesting that species within natural communities were often segregated (Gotelli & McCabe, 2002; Ulrich & Gotelli, 2010). However, the demonstration of non-random patterns in species co-occurrence does not explicitly establish the mechanisms by which such patterns have emerged (Connor & Simberloff, 1979; Stone & Roberts, 1992; Gotelli, 2000), and it is likely that these might result from a number of alternative processes operating singly or in combination.

Non-random patterns of species co-occurrence can result from interspecific competition for limited resources (Diamond, 1975), from environmental differences across habitats, where species that are not adapted to specific environmental condition cannot occur (*i.e.* environmental filtering, Zobel, 1997; Peres-Neto, 2004), from stochastic processes (Ulrich 2004) or from differences in habitat histories (*e.g.* historical contingency or differences in disturbance histories within sites) (Badano *et al*., 2005). These processes are not mutually exclusive and might operate simultaneously (Mouillot *et al*., 2007; de Bello *et al*., 2006). For example, low water availability, a stressful environmental condition, will select in favour of drought resistant species, but it may also cause an intensification of competitive interactions between drought resistant species with similar water acquiring traits, as a result of limiting resources. Furthermore, the relative importance of the processes structuring communities may vary along environmental gradients (Callaway & Walker, 1997; de Bello *et al*., 2006; Maltez-Mouroa *et al*., 2010) and with spatial scale, with communities being assembled through the influence of a combination of mechanisms, some operating at large spatial scales and others at finer scales (Anderson *et al*., 1981; Gotelli & Ellison, 2002; Sanders *et al*., 2007). Therefore, understanding the mechanisms by which natural communities are assembled, and their relative importance in community structure, is currently a matter of great debate in community ecology and is likely to inform management interventions for the maintenance of biodiversity under current pressures of global environmental change.

Patterns of species co-existence are normally assessed using species-based (spatial dispersion) or trait-based (trait dispersion) approaches to determine whether species aggregate or segregate spatially or whether species traits converge (traits are more similar) or diverge (traits are more different) relative to null expectations. Species-based approaches use co-occurrence indices, which are single metrics that summarise the co-occurrence pattern in a presence-absence matrix (Gotelli, 2000), with the most commonly used indices being the 'Checker' index (Diamond, 1975) and the C-Score (Stone & Roberts, 1990). All co-occurrence indices identify levels of species' spatial segregation, which is often attributed to competition effects or habitat variability (*e.g*. Diamond, 1975, Sanders *et al*., 2007), or aggregation of species, which is attributed to habitat variability and, in some cases, to species facilitation (Callaway & Walker, 1997; Dullinger *et al*., 2007). However, these indices lack information about species ecology and, as indicated by Diamond (1975), the coexistence of organisms with differing traits or differing trait values can be among the key factors influencing co-existence of species within communities. Trait-based approaches incorporate this information in terms of functional traits, and focus on the similarity/dissimilarity of functional traits within communities. Trait dispersion indices, known as functional diversity indices, detect trait divergence and convergence (*e.g.* Petchey & Gaston, 2002; Mason *et al*., 2005; Cornwell *et al*., 2006; Mouillot *et al*., 2007; Petchey *et al*., 2007; Algar *et al*., 2011; de Bello, 2012). Trait divergence is often attributed to limiting similarity, where species within communities have different/complementary functional traits, which allow them to exploit different parts of the resource spectrum and hence, reduce competition amongst species (Petchey & Gaston, 2002). Conversely, trait convergence is attributed to environmental filtering, where species within communities share similar functional traits since they experience a common set of environmental pressures or stresses (Cornwell *et al*., 2006). Despite species and trait-based approaches sharing a common goal, it remains unknown whether a relationship between spatial aggregation/segregation and trait convergence/divergence exists.

In this study, we apply a co-occurrence index and null model analysis to investigate co-occurrence patterns of wintering wader species foraging in the intertidal areas of different estuaries across Great Britain, and assess whether species co-occurrence is associated with functional similarity or dissimilarity. Migratory wader species (Charadrii) mostly use estuarine wetlands during the non-breeding season and these habitats face increasing anthropogenic pressures (*e.g*. land claim, disturbance and sea level rise; Sutherland *et al*., 2012). Many wader species are currently facing declines in their global population (Stroud *et al.*, 2006), which raises concerns about the management and conservation of the estuarine systems upon which they depend. In order to improve management and design targeted conservation interventions, it is necessary to understand the distribution of birds within estuaries, both within species (as the individuals of some species might disperse across all available intertidal area whereas those of others may cluster in particular areas) and between species (since co-existing species might segregate or aggregate within estuaries). This information can also help in identifying important intertidal foraging areas for waders and key factors determining foraging site selection when species distribution patterns are associated with environmental factors.

Here, we use low tide counts (WeBS Low Tide Counts) for 17 wintering wader species from eight estuaries across Great Britain to examine patterns of spatial distribution within and between species. We examine whether co-occurrence patterns differ from null expectations and whether these differ across sites. We then examine the relationship between species pairwise co-occurrence patterns with pairwise functional differences and test whether (1) co-occurring species tend to be more functionally dissimilar (dashed line, Figure 1), due to competition effects; (2) co-occurring species tend to be more functionally similar (solid line, Figure 1), due to environmental filtering; or (3) co-occurrence patterns are not related to the ecology (traits) of the species (dotted line, Figure 1), due to random processes.

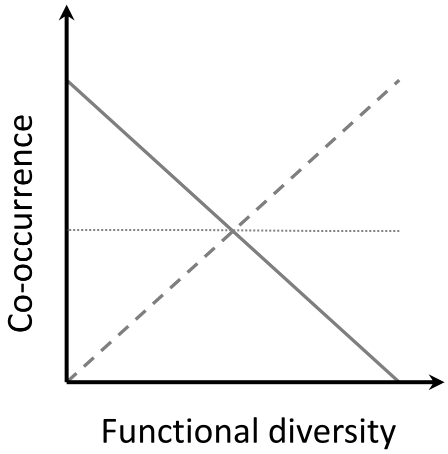

Figure 1. Possible relationships between species co-occurrence and functional diversity. Solid line indicates a negative relationship suggesting that co-occurring species tend to be more functionally similar. Dashed line indicates a positive relationship, suggesting that co-occurring species tend to be more functionally diverse. Dotted line indicates no relationship, arising from random processes of species assembly.

Methods

Study sites and species selection

The study was carried out using survey data from eight estuaries across England and Wales (Figure 2). These estuaries were selected because they have good coverage of Low Tide Counts (see section below). They are representative of other estuaries across Britain in relation to the abundance of wintering wader species, as they can hold both internationally and nationally important wintering populations of species listed in Table 1. Each estuary is divided into sectors of the intertidal habitat within estuaries, each of which can be counted by a single person in a reasonable amount of time during a low tide period.

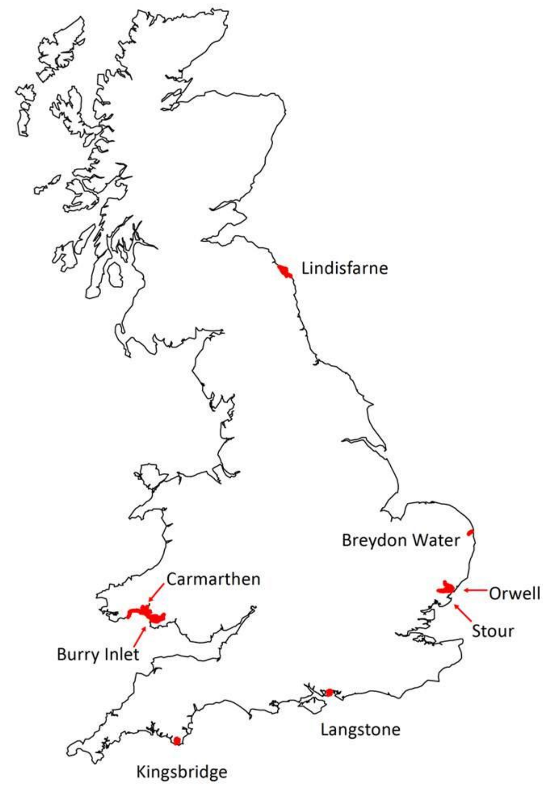

Figure 2. Distribution of the eight estuaries selected for this study, encompassing the coastal areas of Britain and Wales.

Seventeen wintering species of waterbirds were selected because of their high winter dependency on estuaries which are very dynamic systems and prone to environmental and anthropogenic change (Davidson *et al.*, 1991). All species are waders with the exception of shelduck *Tadorna tadorna* which (as elsewhere, *e.g.* Clark & Prŷs-Jones, 1994; Mendez *et al.*,

2012) is included here as it is highly dependent on estuaries as feeding areas during winter, and has a similar feeding ecology to waders being particularly reliant on intertidal invertebrate prey.

WeBS Low Tide Counts

The WeBS Low Tide Counts (LTC) scheme is designed to survey the distribution of feeding waterbirds over the intertidal area of a given estuary in order to assess the relative importance of feeding areas for wintering populations (Holt *et al.*, 2011). This scheme has taken place throughout the majority of the UK estuaries since the winter 1992/93. Due to the fact that many of the LTC are carried out by the same volunteers that participate in the Core Counts (another surveying scheme run by WeBS), WeBS LTC aim to cover most of the UK estuaries once every six years, but more frequent counts are made for several sites. On all sites, co-ordinated monthly counts of waterbirds are made from November to February on pre-established sectors of the intertidal area, in the period two hours either side of low tide (Holt *et al*., 2011). Count accuracy is provided by the counter, assessing the count as complete (‘OK’) or incomplete (‘LOW’). Detailed information on the survey type, methodology and count accuracy are provided in Holt *et al*., (2011).

Species traits

Waders display a remarkably high level of behavioural and morphological variation, particularly with regards to their feeding apparatus and feeding ecology (Burton, 1974). This results in variation in the types of prey that are exploited. Seven trait types were chosen to capture this key aspect of variation among waders that directly relates to their capacity to exploit food resources (Table 2, chapter 1). Similar combinations of traits have already been used in other studies of avian functional diversity (*e.g.* Petchey *et al*., 2007, Mendez *et al*., 2012). Trait values were obtained from the BTO data base (BTO, 2012) and from The Birds of the Western Palaearctic on interactive DVD-ROM (2006), using information for populations that occur in UK whenever possible. Mean trait values for species were used for continuous traits, while diet components, foraging methods and traits involved in prey location were divided into independent binary traits, as these are not mutually exclusive (Petchey *et al*., 2007). A species by trait matrix for all 17 species was generated.

Assessing species’ distribution within estuaries

We used WeBS LTC from the winter 2005/06 for all the estuaries, with the exception of Burry Inlet and Carmarthen Bay, for which data from 2005/06 were unavailable and data from 2006/07 were used instead. Sectors with no species recorded were not included in the analysis.

We calculated the mean number of individuals of each species present for each estuary sector over the winter, from November to February. As the number of sectors varies across sites, the local occupancy of each species within each estuary was calculated as the proportion of sectors occupied, thus the number of sectors where the species was present divided by the total number of sectors. For each species, the local abundance within estuaries was calculated as the sum of the abundances across sectors. We used generalised linear mixed models with binomial error distribution and logit link function to model the variation in occupancy using the *lmer* function of the *lme4* package (Bates *et al*., 2011) in R (2.12.2, R Development Core Team, 2011). Occupancy was modelled as a function of local abundance, species and the interaction between local abundance and species, fitted as fixed effects, and site fitted as a categorical random effect to account for possible variation introduced by each estuary. Local abundance was log-transformed prior to the analysis. The significance of the random structure was assessed using log-likelihood, and the significance of the fixed structure was assessed by comparing models applying maximum likelihood.

Table 1. The 17 species of wintering waterbirds included in the study

Code	Common name	Scientific name
av	Avocet	*Recurvirostra avosetta*
ba	Bar-tailed godwit	*Limosa laponica*
bw	Black-tailed godwit	*Limosa limosa*
cu	Curlew	*Numenius arquata*
dn	Dunlin	*Calidris alpina*
dr	Spotted redshank	*Tringa erythropus*
gk	Greenshank	*Tringa nebularia*
gp	Golden plover	*Pluvialis apricaria*
gv	Grey plover	*Pluvialis squatarola*
kn	Knot	*Calidris canutus*
l_	Lapwing	*Vanellus vanellus*
oc	Oystercatcher	*Haematopus ostralegus*
rk	Redshank	*Tringa totanus*
rp	Ringed plover	*Charadrius hiaticula*
ss	Sanderling	*Calidris alba*
su	Shelduck	*Tadorna tadorna*
tt	Turnstone	*Arenaria interpres*

To examine the spatial variation in local abundances and examine how species distribute within the intertidal area (whether species segregate, aggregate or their distribution is random within the estuary), we used the global Moran's I test, within the *ape* library (Paradis, Claude & Strimmer, 2004) in R. Moran's I tests the statistical significance of the degree of clustering across a region (spatial autocorrelation). Moran's I ranges from -1, which indicates dispersion, to 1 which indicates clustering. However, if Moran's I is not significant, then the spatial distribution of abundances within estuaries is random.

Assessing species co-occurrence patterns

Species data were organized as a presence-absence distribution matrix for each estuary, where rows were estuary sectors and columns were species. A co-occurrence index, the Stone and Roberts' (1990) C-score was calculated from the species matrix for each estuary and compared to a frequency distribution produced by the C-scores of the random matrices to quantify the degree of species co-occurrence within estuaries. The C-Score is negatively correlated to species co-occurrence and commonly used as a measure of species segregation. If the C-score from the original matrix lies within the 95% frequency distribution of the randomized matrices, there is no evidence for deterministic processes influencing species co-occurrence, whereas if the index lies outside the 95% confidence limits of randomized matrices, this indicates that these processes may be operating.

C-score measures the average number of checkerboard units (CU) for all species pair combinations within the site. CU is any submatrix of the form

$$\begin{array}{lcccccl} & \text{Species A} & \text{Species B} & & \text{Species A} & \text{Species B} & \\ \text{Sector 1} & 1 & 0 & & 0 & 1 & \text{Sector 1} \\ & & & \text{or} & & & \\ \text{Sector 2} & 0 & 1 & & 1 & 0 & \text{Sector 2} \end{array}$$

in which one species occurs on sector 1 but not on sector 2, whereas the other is on sector 2 but not on sector 1 (Stone & Roberts, 1990). Thus, when all sector pairs within an estuary are taken into account, the total CUs for a species pair combination are calculated as the sum of all CUs formed by these species. For example, considering an estuary with ten sectors and the following distribution of two species,

	Species A	Species B
Sector 1	1	0
Sector 2	0	1
Sector 3	1	0
Sector 4	0	1
Sector 5	**1**	**1**
Sector 6	1	0
Sector 7	**0**	**0**
Sector 8	**1**	**1**
Sector 9	1	0
Sector 10	**1**	**1**

the index is calculated by removing the co-occurrences and co-absences (sectors in bold - which do not contribute to the index), and multiplying together the number of events when a species is present given the absence of the other. Thus, in the example above we obtain a score of 4 x 2 = 8 CUs (species A occurs in 4 sectors where species B do not occur, and species B occurs in 2 sectors where species A do not occur). The C-score for a particular estuary is defined as the mean number of CUs per species-pair from the community.

As the number of sectors varied across estuaries and since there was a need to compare results across estuaries, we used the standardised effect size for C-score values ($SES_{C\text{-score}}$), calculated as (observed C-score – mean of simulated random C-score) / standard deviation of simulated C-score (for detailed statistical properties of this measure see Gotelli, 2000 and Gotelli & Rohde, 2002). $SES_{C\text{-score}}$ measures the deviation from random expectations that are centred around a mean of zero. Thus, a negative $SES_{C\text{-score}}$ indicates that the observed C-score is lower than randomised expectations, suggesting that species pairs are co-occurring more than expected by chance, hence, species tend to aggregate. In contrast, positive $SES_{C\text{-score}}$ indicates segregation of species within the community, *i.e.* pairs of species tend to co-occur less than expected by chance.

To detect significant co-occurrence between species' pairs, we created random communities for each estuary under different null models that incorporate only the occurrence features (species richness of sectors and species frequencies in the estuary) of the original species (presence/absence) distribution matrix. First, we used a 'fixed-fixed' null model (hereafter referred to as FF), where species frequencies (column totals) and species richness across sectors (row totals) from the species distribution matrix are maintained constant in the random communities (Gotelli, 2000), making it suitable for data recorded across heterogenous environments (Rooney, 2008). However, the differential power for detecting aggregation is low for FF null models, which tend to reveal segregation patterns (Sfenthourakis *et al*., 2006; Azeria *et al*., 2012). To back-up for comparison of co-occurrence patterns, we also used a 'fixed-equiprobable' null model (hereafter referred to as FE), where only species frequencies from the species matrix are held constant and thus, sectors are considered to be colonized with equal probability (Gotelli, 2000). Contrary to FF null models, FE null models tend to have greater differential power for detecting aggregation (Gotelli & Graves, 1996; Azeria *et al*., 2012). For each estuary, 1000 random matrices were created for each null model, using the function *permatfull*, a wrapper for the *commsimulator*, in the *vegan* R- package (Oksanen *et al*., 2011).

We calculated $SES_{C\text{-score}}$ under these two models to detect significant non-random patterns of co-occurrence and compare the outcome between null models. The significance for the observed C-score for each community was tested by comparing the observed C-score of each estuary with the C-score of the simulated random communities. Statistically significant patterns are indicated when the observed C-scores lie outside the 95% confidence interval of the C-scores of the simulated matrices. In addition, to identify the species pairs that contributed the most to the co-occurrence patterns at each estuary, we calculated the average of CU for each pairwise combination of species. To explore overall co-occurrence patterns across estuaries, we calculated the average of CU for each pairwise combination of species for estuaries that show significant segregation or aggregation patterns, but excluding the species that were not present in all the estuaries. For instance, if three estuaries showed significant species aggregation, we calculated the average of CUs for all the pairwise combinations common across the three estuaries, excluding those pair combinations that were not present across all of them, to identify which pairwise combinations contributed the most to the overall segregation pattern.

Associations between species co-occurrence and functional diversity

In order to estimate the functional dissimilarity between species, we performed a principal coordinate analysis (PCoA), using a Gower distance matrix calculated from the species x trait matrix and comprising the 17 species. The PCoA positions each species within multidimensional functional trait space, determined by the combination of functional trait states of each species. The PCoA was performed using the function *pcoa* from the R-package *ape* (Paradis *et al*., 2004).

To assess whether species co-occurrence correlates with functional dissimilarity, we performed a Mantel test. We used the pairwise matrix that reflects functional dissimilarities (same as for the PCoA) and the pairwise matrix of co-occurrence. For the latter, we average the CU of each species pair across estuaries.

Results

Distribution of wader local population within estuaries

Avocet, greenshank and spotted redshank are rare species within our data set, only occurring at two or three of the eight estuaries. The other species are present in at least 75% of the estuaries. An average of six species across all the estuaries was recorded (mean ± SD, 6.32 ± 2.18). Stour and Langstone had the highest mean species richness across all the sectors surveyed (10.02 ± 2.33, 9 ± 1.41, respectively), whereas Burry Inlet, Kingsbridge and Lindisfarne held on average the lowest number of species across all sectors (3.90 ± 1.99, 4.33 ± 1.93, 4.83 ± 2.65, respectively).

Wintering wader populations feeding on the intertidal area of British estuaries showed variation in their local occupancies (the proportion of intertidal area occupied) (Figure 3), and the effect of species' local abundances on species local occupancy (the proportion of intertidal area occupied) varied amongst species (the interaction term was Pr(>|Chisq|) = 0.0004 in the model where occupancy was modelled as a function of abundance, species and the interaction between local abundance and species, df=35). A positive association between species local abundance and local occupancy was observed for the majority of species (Figure 3). Thus, abundant species tend to be widespread across the intertidal area, whereas less abundant species tend to be present in fewer areas of the estuary. However, for curlew, knot and shelduck the relationship between local abundance and local occupancy was reversed (Figure 3).

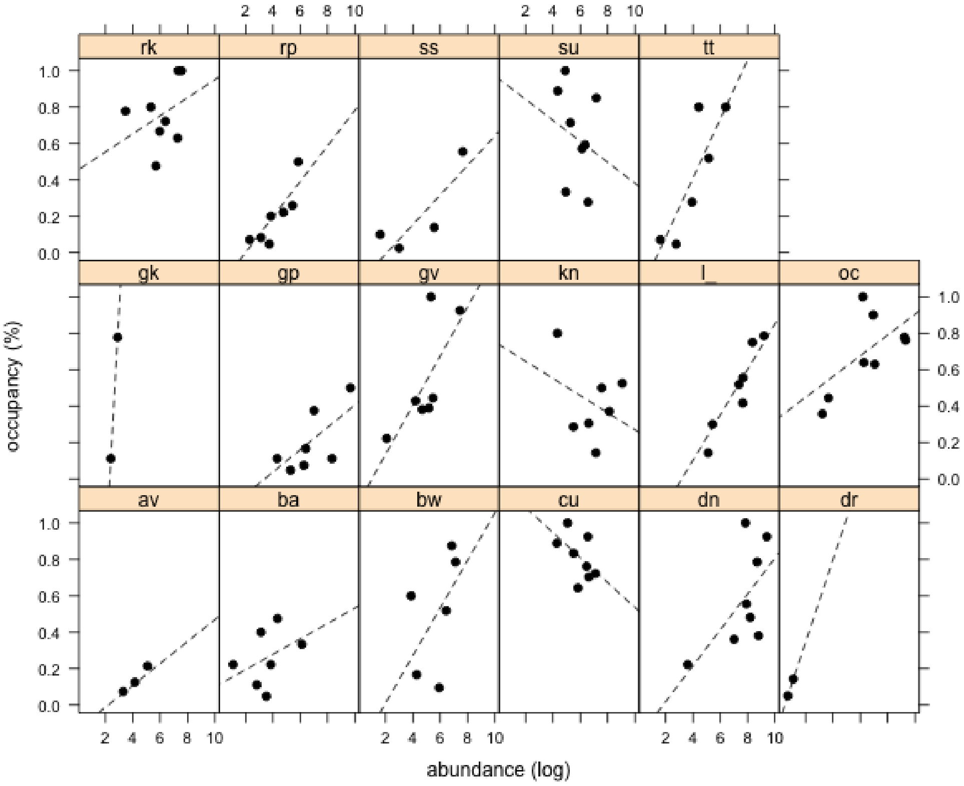

Figure 3. Relationship between local abundance and local occupancy (proportion of sectors occupied within estuaries) of 17 wintering wader species in Britain. Each point represents the local abundance and local occupancy at one estuary. The dashed lines are the generalised linear mixed model relationships between local occupancy, local abundance and species, accounting for estuary variation. Species codes are given in Table 1.

Overall, species showed a random distribution within estuaries, but with a tendency for dispersion of their abundances (Moran's $I < 0$, $P > 0.1$). However, the distribution of species abundances within the intertidal habitat varied within and between species across estuaries (Figure 4), with some species showing significant aggregation patterns at certain estuaries (Table 2), whereas ringed plover at Breydon Water (Moran's I = -0.063, P = 0.03) and Burry Inlet (Moran's I = -0.05, P = 0.02), sanderling at Stour (Moran's I = -0.013, P = 0.002) and golden plover at Kingsbridge (Moran's I = -0.09, P = 0.02) showed significant spatial dispersion at those sites.

Table 2. Moran's I estimates for the distribution of abundances of species that showed an aggregated spatial distribution of abundances within estuaries. Species codes are given in Table 1.

Species	Estuary	Moran's I	P-value
bw	Stour	0.086	0.001
cu	Carmarthen	0.128	0.001
dn	Stour	0.046	0.04
dn	Breydon	0.064	0.03
dn	Carmarthen	0.051	0.02
gk	Carmarthen	0.039	0.0003
gp	Carmarthen	0.08	0.0001
gv	Stour	0.066	0.002
gv	Carmarthen	0.09	0.001
kn	Stour	0.069	0.007
kn	Orwell	0.078	0.02
l_	Burry	0.135	0.003
rk	Orwell	0.097	0.01
rk	Breydon	0.192	0.005
rk	Carmarthen	0.082	0.008

Species co-occurrence patterns

The community level C-scores were variable across estuaries. Under the FE null model, which consider all sectors as having the same probability of being used by species, significant aggregation patterns were observed at four estuaries (Table 3). Orwell and Stour presented the highest levels of aggregation (Table 3). Under the FF null model, where species' total abundances within the estuary and richness within sectors are held constant, the $SES_{C\text{-score}}$ at Lindisfarne and Breydon communities indicated a significant segregation pattern (Table 3), suggesting that species feeding at those sites tend to disperse across the intertidal-area. Communities at Langstone, Burry Inlet and Carmarthen Bay showed non-significant patterns under both of the null models (Table 3), suggesting that feeding communities are randomly distributed.

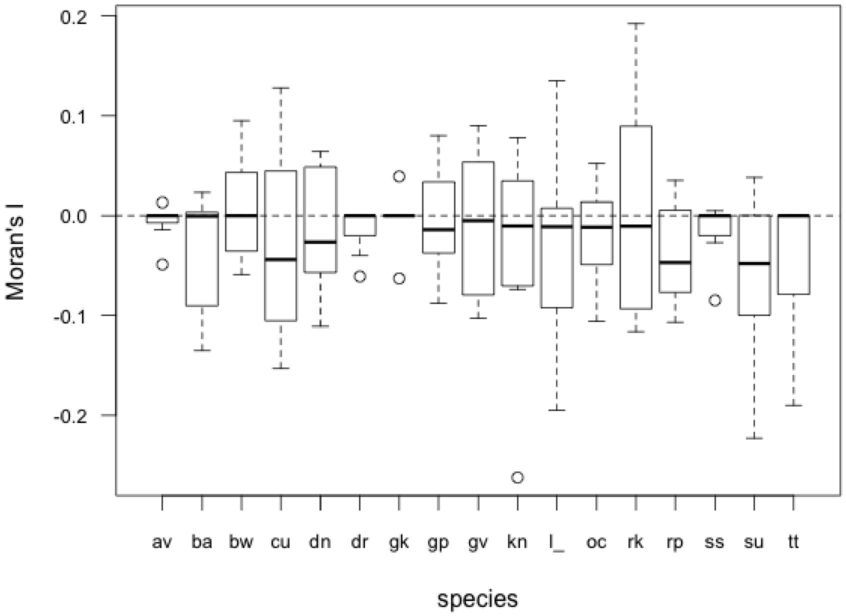

Figure 4. Moran's I estimates for the spatial distribution of species abundances within eight British estuaries. Negative Moran's I values indicate dispersed spatial distribution whereas positive values indicate clustered spatial distribution. Species codes are given in Table 1.

The species pairs that contributed the most to the overall segregation patterns were ringed plover combined with knot or turnstone, and turnstone combined with golden plover, knot or shelduck (Table 4). However, when estuaries that showed significant species' segregation were analysed separately (Lindisfarne and Breydon), other species pairs that are unique to those sites had a higher contribution to the community mean C-score, such as ringed plover and turnstone combined with other species (mean C-Score ± SD, 0.88 ± 0.28, 0.88 ± 0.28, respectively) at both estuaries, but also combinations of species with avocet (1 ± 0) and spotted redshank (1 ± 0) in Breydon, and combinations with sanderling (0.80 ± 0.12) in Lindisfarne. In contrast, combinations of species together with dunlin or bar-tailed godwit contributed the most to the overall aggregation patterns observed across British estuaries (Table 4). However, when estuaries are analysed independently, if avocet or black-tailed godwit were present in the estuary, they contributed the most to the aggregation pattern when combined with other species (avocet together with any species has a mean C-Score of 0.23 ± 0.34, and black-tailed godwit of 0.24 ± 0.16).

Table 3. Standarized effect sizes (SES) for C-Scores under two null models, fixed-fixed (FF) and fixed-equiprobable (FE) for wintering wader communities across eight different estuaries (see "Methods" for differences in the null-models). Statistically significant patterns are indicated when the observed C-Score lies within the tails of the distribution outside the 95% limits of the C-Scores values of the simulated matrices. Significant values are in bold. Positive values indicate segregated distribution whereas negative values indicate aggregated.

	SES $_{\text{C-Score}}$	
	FF null model	FE null model
Lindisfarne (n_{sectors}= 36)	**2.604**	**-4.355**
Stour (n_{sectors}= 40)	-0.334	**-6.340**
Orwell (n_{sectors}= 27)	2.613	**-11.102**
Breydon (n_{sectors}= 14)	**4.412**	-1.590
Langstone (n_{sectors}= 10)	0.166	-0.452
Kingsbridge (n_{sectors}= 9)	-1.116	**-3.890**
Burry Inlet (n_{sectors}= 21)	1.949	-1.743
Carmarthen(n_{sectors}= 18)	-0.596	-2.2413

The position in functional space of the species pairs that contributed the most to the segregation and aggregation patterns are shown in Figure 5. Although not statistically significant, there is a weak association between functional diversity and species co-occurrence (Mantel-statistic r = 0.18, p=0.06). Thus, there is a tendency for functionally dissimilar species to segregate more than functionally similar species, which tend to aggregate (Figure 5).

Table 4. Species pairs with the highest contribution to the mean C-score values for the co-occurrence patterns observed across British estuaries. Only species pairs with significant co-occurrence patterns on more than one estuary are shown. Mean and SD are given for the combination of all species pairs. Species codes are given in Table 1.

Co-occurrence pattern	Species pair	C-Score
Segregated	rp-kn, rp-tt	0.80 ± 0.002
	tt-gp, tt-kn, tt-su, tt-rp	0.73 ± 0.05
Aggregated	dn-cu, dn-ba, dn-oc	0.069 ± 0.03
	ba-dn, ba-cu, ba- oc	0.061 ± 0.02

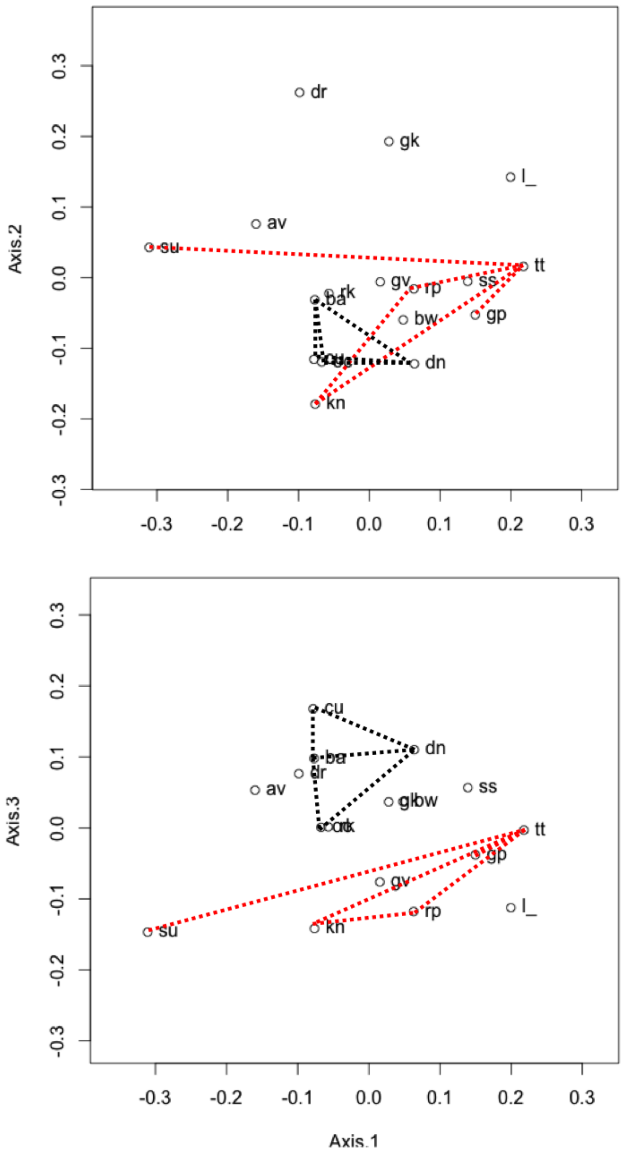

Figure 5. Position of the 17 species of wintering wader in functional (ecomorphological) space from the Principal Coordinate Analysis (PCoA). Axis 1, axis 2 and axis 3 are displayed. Red lines represent the position of the species pairs that contribute the most to segregation patterns and black lines represent the species pairs that contribute the most to aggregation patterns across estuaries. Species codes are given in Table 1.

Discussion

Distribution of local wader species' abundances within estuaries

In agreement with the general abundance-occupancy relationship (*e.g.* Gaston *et al.*, 2000), we found that the majority of wader species included in this study showed a positive association between their local abundances and the proportion of intertidal habitat occupied. Thus, locally abundant species, such as redshank and oystercatcher, tended to occupy a larger proportion of the intertidal habitat, whereas rare species, such as avocet and ringed plover, tended to be narrowly distributed within an estuary. However, shelduck, knot and curlew did not show positive abundance-occupancy associations. The negative association predicted by the model for the abundance of knot and its occupancy is likely to be driven by the one estuary where knot has low abundance and is present in a high proportion of the intertidal area (Figure 3). If that estuary is not considered, a positive association appears for the other six estuaries. Curlew and shelduck are amongst the most abundant and widespread species across and within Britain estuaries (Holt *et al.*, 2011). The lack of a positive association for these species might be due to lack of suitable sectors (habitat) within some estuaries, reducing the occupancy at higher local abundances.

Overall, species abundances were distributed randomly within estuaries. Some species, however, showed significant non-random patterns across different sites. Thus, species distribute differently within estuaries and the same species might aggregate in one estuary but randomly distribute in another. The lack of consistency in the spatial distribution of foraging wintering waders within estuaries suggests that the distribution of abundances is influenced by the operation of local-scale processes, such as distribution of abundance and quality of invertebrate prey across estuaries and location and availability of roosting sites. Most wader species show high levels of prey specialization (Burton, 1974; van de Kam *et al.*, 2004) and, consequently, their distribution within estuaries will be influenced by the distribution of their prey, which in turn is influenced by sediment type (Yates *et al.*, 1996). Although we do not have sediment type or prey data available at the sector level for the estuaries included here, it is likely that each estuary will have idiosyncratic habitat configurations (*i.e.* different combinations of sediment types), influencing the prey distribution and ultimately, wader distribution. Furthermore, it has been shown that the location of roosting sites is very important for the distribution of foraging waders, with bird density declining with distance from their roost (Dias *et al.*, 2006), probably as a result of strategies to minimize the energy expenditure between foraging and roosting sites (Luís *et al.*, 2001; Rogers, 2003). In addition, the pattern of use of intertidal areas for some species can result from a trade-off between the distance from roosting sites and the quality of foraging locations (van Gils *et al.*, 2006) or safe feeding grounds (Rogers *et al.*, 2006). Thus, if location and availability of roosting grounds for each species varies across sites, then different distribution of wader species across estuaries can be expected. One way to test the variation in availability of roost sites across estuaries may be to explore the sector-level variation in WeBS Core Counts, where birds are counted while roosting, as estuaries with few roosting locations may have birds clustered in fewer sectors during high tide roosts.

Knowledge of how birds distribute within estuaries is of major importance for conservation planning of estuaries, because, as suggested here, different local processes may influence their distribution. Moran's *I* test has provided an overview of the spatial distribution of waders within eight British estuaries, but it does not address the question of whether a clustered abundance is concentrated into one or several parts of the intertidal area or whether abundance is dispersed evenly or unevenly across the intertidal area. A more spatially explicitly approach will be needed in order to address which estuarine sector/s are the most intensively used by species.

Patterns of wader co-occurrence within and across estuaries

Of the eight wader communities examined in this study, five showed significant co-occurrence patterns. However, the direction of co-occurrence (segregation or aggregation) varied across sites, with two sites showing significant segregation and four sites showing significant species aggregation. For one of these sites, Lindisfarne, co-occurrence was significant under both null models, and showed significant segregation and aggregation of species pairs. It is possible that C-score, as with other community level indices, may be sensitive to the inclusion of rare species (*e.g*. ringed plover), emphasizing different aspects of co-occurrence patterns of the same distribution matrix under the two null models (*e.g*. Stone & Roberts, 1992; Azeria *et al*., 2009). Further analysis on how rare species may affect the differential power of different null models for detecting aggregation or segregation patterns would be useful for drawing concise conclusions on such patterns. We can, however, conclude that non-random patterns of species co-occurrence can be detected across British estuaries. Overall, species that contribute the most to segregation patterns were species pairs' that occupied different parts of the functional space (Figure 5, red lines). For example, turnstone, one of the species that contributes the most to the pattern, has a unique foraging technique of using its bill to overturn stones, shells and other items, allowing exploitation of resources unavailable to other species. In contrast, species that contribute the most to aggregation patterns were species' pairs that occupied similar distribution within the functional space (Figure 5, black lines). For instance, bar-tailed godwit, one of the species that contributed most to aggregation effects, feeds on all types of benthic animals, small prey pecked from the surface and larger ones taken from deep in the sediment. Such generalism is likely to result in species sharing similar functional trait values, hence positioning them within similar functional space.

Following previous findings on the influence of environmental filtering on wader community structure (chapter 1), this study suggests that species' co-occurrence patterns were likely to be driven by species' habitat affinities. As discussed, there was a tendency for functionally similar species to aggregate, whereas functionally dissimilar species tended to segregate within estuaries. Several studies have suggested that the aggregation of species can arise due to species having similar habitat affinities (*e.g.* Jackson *et al.*, 1992; Peres-Neto *et al.*, 2001; Azeria *et al.*, 2009), and that habitats and their complexity may change the nature of interspecific interactions and their influence on co-occurrence patterns (Hughes & Grabowski, 2006; Azeria *et al.*, 2009). By incorporating functional differences among co-occurring species, our study reinforces these findings because aggregation patterns were associated with species that are functionally similar being situated closer within their functional space (Figure 5). In estuarine systems, waders often co-occur across habitats of varying complexity, and the interaction between sediment type and prey will determine the variation in species distribution within estuaries and consequently species pairwise co-occurrence (as discussed above). In addition, other factors have been shown to be highly influential on the distribution of birds within estuaries. For example, Granadeiro *et al.* (2007) showed the exposure period, the mud content of the sediment and the presence of shell banks strongly influenced the distribution of foraging wader species in the Tagus estuary. These types of habitat attributes may be causing functionally similar species to spatially aggregate within estuaries, in order to be able to exploit the resources available under certain environmental conditions. However, the relationship was statistically non-significant, and we suggest incorporating more species and estuaries in order to more rigorously test the relationship, since only 17 species and 8 estuaries comprised our data set. Nevertheless, there is a tendency that is in accordance with the previous findings concerning the importance of environmental filters. Species interactions, in particular competition, may also be important structuring wader communities. However, is highly likely to operate at relatively finer spatial scales, for example among individuals foraging within the same sector.

In summary, species distribute differently within estuaries, with functionally similar species tending to aggregate within the intertidal area. This pattern varies between estuaries. We suggest that these patterns are strongly influenced by habitat filtering effects, and that interspecific interactions may be operating at finer scales (*e.g.* within the same habitat type). Combining co-occurrence with functional diversity analysis could contribute to a better understanding of the mechanisms underpinning the role of environmental and biotic filters in the assembly of natural communities. Studies like the one presented here provide evidence for the importance of environmental conditions, in particular habitat characteristics, in influencing the distribution and co-occurrence of species within estuaries.

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Conclusions

Conclusions

Migratory waders, and other migratory species, migrate annually between breeding and non-breeding grounds. Many migratory wader species depend on the intertidal area of estuaries for feeding during the non-breeding season, using these habitats as wintering area or as stop-over sites during migration. However, many estuaries around the world are under intense pressure from human impacts (Sutherland *et al*., 2012), greatly influencing the composition of wintering wader communities to the extent that some species are suffering national and global population declines (Sutherland *et al*., 2012). Understanding of the mechanisms by which estuaries sustain wintering wader communities, and the environmental and anthropogenic influences upon these, can greatly improve the conservation and management of estuarine systems across the world. This thesis uses national-scale datasets to explore spatial and temporal variation in the composition and structure of wintering wader communities across the UK, and presents one of the few large-scale studies of wader communities for this area and possibly the world. For the first time, morphological, behavioural and ecological characteristics of wading bird species are used to estimate the functional diversity of wader community, and to investigate the factors determining wader community composition and the functional ecological significance of their community structures. The work presented in this thesis provides evidence that wintering wader community composition and structure is spatially variable across British estuaries, and that changes in both observed functional diversity (FD) and in the difference between observed and expected FD (SES-FD) have taken place over the last three decades (chapter 1).

The variation in observed FD is driven primarily by variation in the number of species present in the community. Normally, measures of FD that do not account for species abundances (as in this study) are naturally correlated with species richness (Schleuter *et al*., 2010). In this study, wintering wader FD shows a strong correlation with species richness ($R^2 = 0.9$, $p < 0.0001$), providing relatively little evidence of functional redundancy among the 20 wader species included here. Early work on the effects of species richness on FD suggested a linear increase in FD with species richness (Díaz & Cabido, 2001), indicating that species' traits are equally complementary, and hence, contributing equally when species are added into communities (Petchey & Gaston, 2002). Subsequently, asymptotic and quadratic relationships between species richness and functional diversity have been described (Mayfield *et al*., 2005; Mason *et al*., 2008; Villéger *et al*., 2010). The asymptotic relationship can occur when functional diversity saturates at high levels of species richness due to functional redundancy amongst species. In contrast, quadratic relationships can arise when the amount of functional space occupied does not increase proportionally with species richness, because environmental conditions that are conducive for species-rich communities might lead to the presence of many redundant species due to niche specialization (Mason *et al*., 2008; Villéger *et al*., 2010). It is possible that the levels of species richness represented in this study are too limited to encompass the ranges in diversity at which asymptotic or quadratic phases of these relationships might be evident. It would be interesting to increase the species pool to examine whether (1) wader species are highly complementary at all levels of species richness, (2) high levels of wader functional diversity saturates at higher levels of species richness (asymptotic relationship), or (3) communities with high level of species include high levels of redundancy due to niche specialization, resulting in levels of functional diversity lower than communities with an intermediate number of species (quadratic relationship). However, it is highly likely that increasing the species pool would not result in a quadratic relationship, as waders present a high level of complementarity in morphological and behavioural traits through their evolutionary adaptations for the exploitation of prey of different morphology, shape, size and burrowing depth within the intertidal sediment (Burton, 1974; van de Kam *et al*., 2004).

To control for the effect of species richness on the observed patterns of functional diversity, I used null models because the comparison between observed patterns and null expectations allows us to test for non-random patterns which may reflect the underlying mechanisms that structure community assembly (Gotelli, 2000; Mouillot *et al*., 2007; Thompson *et al*., 2010). I thus focused on understanding variation in observed minus expected FD (SES), and for the rest of the conclusions, will focus on variation in SES and the possible consequences for community structure.

Spatial variation in wintering wader communities' structure

Overall, species within wintering wader communities are more functionally similar than expected by chance, reinforcing the role of environmental conditions in shaping communities. However, species interactions appear to be having a stronger influence on some communities around Britain (chapter 1), suggesting that the relative strength of these processes may vary along environmental gradients. The analysis presented in chapter 4 showed that environmental factors, such as tidal range and minimum temperature, accounted for a large proportion (~70%) of the variation in community structure across Britain (Figure 4, chapter 4). The increase in functional diversity (SES) along the temperature gradient may be evidence of a widening of the filter, allowing more varied trait states to be present in communities, whereas low minimum temperatures appeared to strengthen environmental filtering effects perhaps due to a lack of sets of traits for persisting under very cold conditions. Severe weather conditions can influence the distribution of birds, through mortality (Clark, 2009) and through changes in prey abundance and distribution within the sediment (Esselink & Zwarts, 1989).

Thus, species that could reach the deep prey would be favoured in relation to species that cannot reach the prey. Our results also indicate a relaxation in the intensity of competition in estuaries with larger tidal ranges as this was also accompanied by an increase in species richness, suggesting in turn an increase in the aggregation of species with more similar traits in these estuaries. However, the links between species' spatial distribution and similarity/dissimilarity of their functional traits still remains unclear (Stubbs & Wilson, 2004). Understanding how community processes vary along environmental gradients contributes to the knowledge-base needed to predict and determine changes in community composition due to changes in environmental conditions. For instance, reductions in tidal ranges may be likely to increase competitive effects resulting in communities with more complementary traits.

In chapter 5, I attempted to test the relationship between species' spatial distribution within an estuary and functional diversity using a subset of estuaries for which low tide counts were available. Although the relationship was not significant, there was a tendency for functionally similar species to aggregate, whereas functionally dissimilar species tended to segregate within estuaries. These results highlighted even more the importance of environmental filters on structuring wader communities. These sets of results do not exclude the occurrence of competition effects on the distribution of species and community patterns. However, limiting similarity is likely to operate at relatively fine spatial and/or temporal scales, and the spatial scale used here might be too broad in order to capture its influence on co-occurrence patterns, as we consider the entire winter period and subsections of estuaries that are delimited for counts but are not necessarily of relevance for birds. Despite the small number of estuaries included in this study, it provided an opportunity to explore these associations and opened up a field for further research on understanding links between spatial distribution and functional diversity of foraging species.

Changes in wader wintering distribution community structure

The analyses reported in chapter 2 identified changes in wintering occupancy across Britain for many of the wintering wader species and related these population changes to changes in community functional diversity and structure. As discussed, levels of redundancy/distinctiveness of functional traits contributed by each species will correlate with the variation in functional diversity. Thus, our results showed that species that contribute positively to functional diversity (*i.e.* making communities more functionally diverse) are species that are more functionally distinctive within multivariate functional trait space, and have also expanded their wintering ranges. The colonization of new sites is likely to be a density-dependent response to increases in local abundances (chapter 3) and the establishment and expansion of new local populations will depend, among other things, on the number of suitable sites available and the amount of resources available within those sites (Gill *et al.*, 2001). Furthermore, avoiding niche overlap by being able to exploit different parts of the resource spectrum and perform different functional roles within the community might thus explain why these species have been able to successfully establish local populations in new sites. A combination of both effects, increased competition by the presence of new species in the communities and/or reduction of prey availability, and relaxation of environmental filters by changes in environmental conditions allowing more species to be present in communities, are thus likely to explain the observed changes in functional diversity.

Changes in the distribution of non-breeding waders have been studied within the UK and across Europe in relation to climate change (Rehfisch *et al.*, 2004; Austin & Rehfisch, 2005; Maclean *et al.*, 2008). These studies have shown that the overall winter distribution of some species may have shifted in a northeasterly direction. However, we found no association between the magnitude and direction of changes in functional diversity and climate. Instead, we found a modest but nevertheless significant relationship between the rate of change of functional diversity (SES) with estuary fetch and estuary depth (chapter 4). Fetch reflects turbidity and the strength of wave action in the estuary and, hence, is a good indicator of the sediments present within the estuary. Thus, the negative relationship suggests that species within communities at sandier estuaries are becoming much functionally similar than species within communities at muddier estuaries, which are becoming more functionally diverse. With these results, the question becomes “why are wintering wader communities at different habitat types changing in different ways?”. The increasing wintering temperatures may have direct impacts on waders through reductions of mortality events and indirect impacts through changes in the abundance, distribution and accessibility of invertebrate prey (Gill, 2012 and references therein). For instance, some mollusc species that have metabolic systems adapted to cold temperatures reduce their body conditions and breeding success with increases in winter temperature (Beukema, 1992). The burrowing depth of the ragworm (*H. diversicolor*), a common prey amongst waders, can also increase when sea temperatures are low (Esselink & Zwarts, 1989), becoming out of reach for some wader species. Thus, it is likely that invertebrate communities in different habitats may be affected in different ways by changes in environmental conditions. Further work on understanding the mechanisms that are driving variation in changes in functional diversity and wader community composition and the interplay between habitat and climate are required.

Species’ responses to changes in environmental conditions may not correspond to the responses of the community as a whole. For example, shifts in species’ distributions can dissociate important species interactions if other species within the community do not respond in a similar way (Walther *et al*., 2002; Schweiger *et al*., 2008). Increases in winter temperatures across UK might be expected to relax environmental filtering effects, allowing more wader species with different functional traits to be present in communities. However, Figure 1 suggests a non-linear relationship between community structure (SES FD) and winter minimum temperature. Such a trend suggests that at low and high winter minimum temperatures, communities are less functionally diverse than expected by chance. As such, environmental filters seem to be strengthening at the extremes of winter temperature range. On the other hand, temperatures in the middle of the wintering range seem to relax those environmental filters and/or increase competitive interactions, resulting in communities around an intermediate temperature that are more functionally diverse than expected by chance. The mechanisms by which this pattern may arise are not fully understood, but it is highly likely that, as mentioned before, changes in winter temperatures may impact birds directly (*e.g*. by reducing high mortality from very cold winters or not being able to thermoregulate properly with warmer temperature as they are adapted to colder temperatures) or indirectly through changes in prey behaviour, abundance and distribution. Further analysis needs to be carried out in order to gain greater insight into how wintering wader community structure may be responding to changes in climatic conditions. Such an analysis could follow a similar approach to that in Godet *et al*. (2011), where they used a community temperature index to relate long-term changes in the composition of wader communities in France with climate change. The community temperature index was derived from the temperature index of each species present in the community weighted by their abundances. The species' temperature index corresponds to the mean temperature within the wintering range of each species. They found a change in wader community composition towards species associated with higher temperatures, but consequences for community structure were not explored. Thus, it would be very interesting to test for associations between community temperature indices and community structure to further understanding of community responses to environmental change.

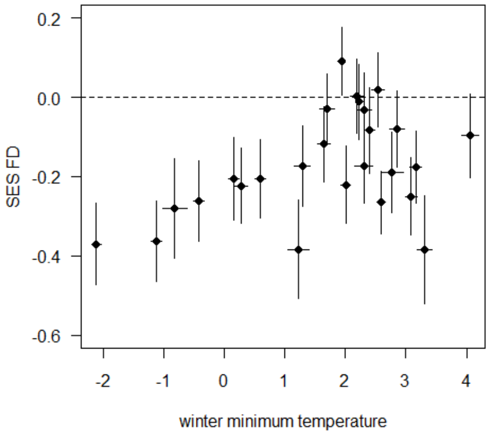

Figure 1. Relationship between SES functional diversity (comparison between observed and expected FD) and the winter minimum temperature. Filled circles represents the average of functional diversity and winter minimum temperature for a given year. Data from winter 1980/81 to 2006/07 are used. Standard errors are provided.

Implications for conservation management

The increasing loss and degradation of wetland systems has been widespread and is currently seen as a major conservation issue. Wetlands support vast numbers of waders and waterfowl many of which are solely dependent on this habitat during the non-breeding season. As this habitat decreases in quality many species face an increasing level of threat (Meyers 1990, 1993; Goss-Custard *et al*., 1997). Motivated by the need to mitigate the negative impacts of habitat loss and degradation, many wetland restoration projects have been implemented across the world (*e.g*. Pethick 2002; Nakamura *et al*., 2006). However, despite increasing the amount of habitat available for wintering waterbirds (Armitage *et al*., 2007), these projects do not necessarily lead to the re-establishment of communities as, in some cases, many species remain absent from the restored wetland or their relative abundances change (Brawley *et al*., 1998; Melvin & Webb, 1998; Li *et al*., 2011). These alterations in community composition and structure can disrupt the ecological functions performed by a given set of species (Hughes *et al*., 2003). Waders, situated at the top of the estuarine food web, are among the main predators of the invertebrate community and therefore likely to strongly influencing the entire ecosystem. In fact, top predators are known to greatly influence ecosystem-level processes. For example, Hughes (1994) described how the reduced abundances of herbivorous fishes and high mortality of grazing sea urchins in early 1980s most likely caused the switch from coral to algal-dominated reefs around Jamaica. Removing herbivorous species from the system also removed the control of algal growth and reduced the resilience of these ecosystems (Hughes 1994). However, Hamilton *et al*. (2006) did not find evidence for a top-down trophic cascade on an estuarine trophic web composed by semipalmated sandpipers, *Calidris pusilla* (top), the amphipod *Corophium volutator* (middle), and benthic diatoms (bottom), which secrete a substance that helps to bind the sediment together and contributes to the stability of the mudflat. Despite birds exerting a top-down effect by reducing *Corophium* densities, there were no increases of diatom densities, because snails found in the intertidal area compensated for changes caused by shorebirds and fed on the diatoms. Both examples highlight the importance of understanding how structural properties of communities are related to the ecological functions performed by each species within the community. Our study provides the basis for understanding the functional role played by each species within wintering wader communities. We have shown that there is little evidence for redundancy amongst wintering wader species in the way they use resources across UK estuaries, as the species are taxonomically distinct and exhibit complementary ecological functions within the assemblage. Therefore, if wintering communities in UK needed restoration following the extinction of certain species, functionally equivalent species may not be available to replace them.

In order to conserve the present integrity of wader communities and ecosystem functioning, the implementation of habitat and community restoration is required to compensate for the loss of intertidal areas. The capacity to restore communities is challenging but much progress has been made over the last decade. One of the greatest current challenges in wader ecology and conservation is to protect and understand populations along the Asia-Pacific flyway. Land claim is currently a major problem in eastern Asian wetlands, particularly in the Yellow Sea region (Sutherland *et al*., 2012), a keystone site for waders during the non-breeding season. Intertidal habitat loss has led to the decline of 19 species that use the Yellow Sea as non-breeding grounds and to the concentration of the remaining populations in a few remaining areas while planning for further development in that region continues (Sutherland *et al*. 2012). Because these changes may be irreversible, understanding the functional role of species using the Yellow Sea may help in predicting changes in functional diversity and in estimating levels of redundancy. For example, losing functionally distinctive species will cause a relatively large decrease in functional diversity (*e.g*. this might be the case if the spoon-billed sandpiper *Eurynorhynchus pygmeus* goes extinct) whereas loss of functionally similar species will have little effect on functional diversity. Studies like the ones presented in this thesis can provide the basis for understanding wader community structure and composition around the world, and can help to develop ideas for better conservation management, particularly on sites were biodiversity is changing rapidly.

Future directions

The findings reported in this thesis represent only a subset of the wintering ranges of 20 wader species, and suggest that, even within this subset, wintering community structure varies along gradients, increasing or relaxing the effects of species interactions and/or environmental filtering. Changes to wader communities are likely to result from estuarine development that affects the estuarine morphology and other environmental variables, which may alter the strength of the mechanism structuring communities. Data on prey availability should be assessed on different estuaries across the UK to explore the influence of competition upon communities.

Future work, including analysis at the flyway level and global scale, would enhance our understanding of the processes determining community structure and how they vary along environmental gradients. If data are available, comparing breeding and non-breeding season functional diversity would allow for the testing of differences across the annual cycle and the examination of possible factors that can drive differences within and between seasons. It is well known that the behaviour and ecology of waders changes between seasons. For instance, many gregarious species in winter become extremely territorial during the breeding season. How these changes in behaviour and ecology affect community processes remains unknown. Despite the many remaining gaps in our knowledge of population and community level dynamics, studies like this one provide a chance to develop our understanding and steer a path towards the protection and conservation of these species and biodiversity in general.

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Appendix

Appendix

Appendix 1. Description of the foraging methods used to calculate functional diversity.

Foraging method	**Definition**
1. Pecking	Striking or biting with its beak with the beak touching the substrate
2. Probing	Bill partly or fully inserted in the substrate in search of prey
3. Jabbing	Poking rapidly or quickly at a prey item.
4. Stitching	Making rapid movement as stitches producing a particular pattern. Often done in a dense flock.
5. Ploughing	Turning over the upper layer of the substrate and bringing prey to the surface
6. Scything	Sweeping the bill quickly through the upper surface layer of the mud or water
7. Foot trembling	Placing one foot on the sediment, slightly forward of the other, and vibrating it up and down to disturb invertebrates hidden in the substrate.
8. Turning over objects	Moving and rotating objects in search of prey
9. Hammering	Hitting or beating repeatedly with the bill to open bivalves
10. Swimming	Swimming in the water column while foraging.

Appendix 2. The functional relationships among 20 wader species that winter in British estuaries. The dendrogram is produced by hierarchical clustering using UPGMA algorithm of the distance matrix calculated from the functional traits of species. Horizontal distance represents separation in trait space, vertical distance is for clarity.