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Changes in habitat suitability for three declining *Anatidae* species in saltmarshes on the Mersey estuary, North-West England.

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Abstract

Saltmarshes are areas of coastal grassland that are regularly flooded by seawater. They support a large number of resident and migratory bird species, both overwintering and breeding. The Mersey Estuary Site of Special Scientific Interest (SSSI) is situated in North West England and it supports nationally significant numbers of overwintering wildfowl and waders. Decline of three overwintering bird species' populations (pintail, teal and wigeon) were more marked than national trends, so changes in local factors were believed to play a part. The aim of this study was to determine whether habitat suitability for the three target species changed between 2002 and 2012 in saltmarshes on the Mersey estuary.

One habitat suitability model per species was built using a variety of source data (elevation, vegetation and macroinvertebrate surveys, aerial photography, questionnaires) and expert judgment to evaluate the relative importance of factors. Models uncertainty was estimated using "bounding maps" representing the most extreme plausible scenarios for each factor contributing more than 10% to the total value of the habitat suitability index.

Saltmarsh area decreased between 2002 and 2012 in the Mersey Estuary, reducing available habitat for all three target species. Vast areas of pioneer zone disappeared during the study period, especially affecting species like pintail, which preferentially feed on pioneer zone species. Evidence suggested that although recreational disturbance is likely to be an issue in parts of the study area, its intensity did not change notably during the study period. Wildfowling, however, significantly affected the suitability of the study site for all species. The western part of the site had no shooting disturbance in 2002 but by 2012 a clay-pigeon shooting club had opened nearby. Although this activity does not cause direct damage to birds, the shooting noise is likely to make birds avoid the area. In addition, wigeon was also negatively affected by the increased abundance of an invasive bird species in the eastern part of the study site.

The observed decline in pintail, teal and wigeon numbers overwintering in the Mersey estuary could only partly be explained by habitat changes. While suitable habitat for pintail drastically decreased and could fully explain this species' decline, the decrease in suitable area for teal and wigeon was not as marked as the decline in bird numbers. For these two species other factors may be involved, such as habitat improvements in nearby estuaries or changes in land use in the area functionally linked to the Mersey saltmarshes. The possible management measures identified by this project include altering the Mersey estuary dredging regime to reverse saltmarsh erosion and addressing the lack of a wildfowling sanctuary area in the study site.

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List of abbreviations:

AHP = Analytic Hierarchy Process

ASCII = American Standard Code for Information Interchange

BTO = British Trust for Ornithology

DSM = Digital Surface Model

DTM = Digital Terrain Model

GAM = Generalised Additive Model

GLM = Generalised Linear Model

GPS = Global Positioning System

HAT = Highest Astronomical Tide

LiDAR = Light Detection and Ranging

MHWN = Mean High Water Neaps

MHW = Mean High Water

MLWS = Mean Low Water Springs

ODN = Ordnance Datum Newlyn

RMSE = Root Mean Square Deviation

SAC = Special Area of Conservation

SSSI = Site of Special Scientific Interest

SPA = Special Protection Area

TSS = True Skill Statistic

WeBS = Wetland Bird Survey

1. Introduction

Saltmarshes are areas of coastal grassland that are regularly flooded by seawater. They support a large number of resident and migratory bird species, both overwintering and breeding. During high tides, they are a refuge for birds feeding on adjacent mudflats. They can also be used as breeding sites for waders, gulls and terns and as a source of food for passerine birds. In winter, grazed saltmarshes are used as feeding grounds by large flocks of wild ducks and geese (McMullan, 2008).

The Mersey Estuary Site of Special Scientific Interest (SSSI) is situated in North West England, very close to the city of Liverpool. The saltmarsh within the SSSI extends for approximately 700 hectares and it supports nationally significant numbers of overwintering wildfowl and waders (Natural England, 1981). Many of the protected bird species have declined in numbers more markedly on the Mersey estuary than they have at the regional or national level (Frost et al., 2016). Local factors are therefore partly responsible for the decline of teal, pintail and wigeon populations. Potential local factors that have been highlighted as possible determinants for changes in bird populations are changes in saltmarsh extent or zonation, grazing levels (Norris et al., 1998), food availability (Hua et al., 2012), disturbance (Hua et al., 2012) as well as competition and overgrazing by Canada goose (Rehfisch et al. 2010).

Since the 1970s, habitat suitability indices (HSI) have been crucial to wildlife habitat evaluation, and habitat suitability maps are routinely used to guide land management and conservation decisions (Lauver et al., 2002). The HSI models usually estimate the level of habitat suitability as an HSI score ranging from 0 to 1, with 0 representing poor habitat and 1 being an area meeting all the species' habitat requirements (US Fish and Wildlife Service, 1981). Outputs of HSI models can predict the spatio-temporal variation of bird habitat conditions and GIS technology has the capability of integrating a variety of spatial data and automatizing their analysis (Church, 2002).

Habitat requirements of the three species target of this study are well-known: they mostly feed on plants, need areas near water to feed and roost, prefer short swards to spot nearby predators and are sensitive to human disturbance from wildfowler or recreational users. Protected sites in England need to meet a number of species-specific criteria, such as those summarised above, to be considered in favourable condition (Kirby et al., 2000). However, habitat suitability models have rarely been used in British protected sites designated for overwintering birds, and only occasionally to look into how habitat influences the distribution of breeding bird species (Norris et al., 1998).

No habitat suitability models exist to assess how changes in British saltmarsh habitat could affect populations of teal, pintail or wigeon. In addition, spatial patterns within sites are not usually examined, as models are produced on a regional or even larger scale. A spatially explicit HSI model produced using GIS would help to determine which of the numerous factors affecting the target species distribution have been driving the observed decline in bird populations. Mapping habitat suitability in the SSSI would also highlight which parts of the saltmarsh are high quality and should be protected, and which areas have deteriorated between 2002 and 2012 (when data for most factors of interest was collected) and should be the object of conservation measures aimed at reversing their decline.

The overall project aim is to determine in which areas of the study site habitat suitability for pintail, teal and wigeon has changed between 2002 and 2012 in saltmarshes on the Mersey estuary (NW England). Specific objectives are:

1) To determine whether **saltmarsh extent** decreased between 2002 and 2012 and which areas of the site have been lost to erosion. Anthropogenic activities have influenced sediment dynamics in the Mersey Estuary for centuries, and over the last 40 years sediment inputs in the middle estuary have decreased (Blott et al., 2006). This is likely to have increased saltmarsh erosion rates during the study period, however recent changes in saltmarsh extent in the study area have not been quantified.

2) To determine in which areas of the study site **food availability** for birds changed between 2002 and 2012. This could be due to changes in saltmarsh zonation following increased saltmarsh erosion rates. For example, saltmarsh pioneer zones are particularly sensitive to erosion and its *Salicornia*-dominated vegetation is an important food source for all the target species of this study, especially pintail (Ferns, 1992). In addition, benthic macroinvertebrate populations are likely to have changed significantly between 2002 and 2012 thanks to improved water quality in the estuary (Jones, 2006).

3) To determine in which areas of the study site **habitat characteristics** affecting habitat suitability for the three target species (i.e. distance to open water, slope, sward height and grazing levels) changed between 2002 and 2012. It is possible distance to open water and slope have changed between 2002 and 2012 following changes in the estuary's sediment dynamics, while changes in saltmarsh management and increased abundance of the invasive Canada goose may have driven changes in grazing level and sward height of the saltmarsh (Davidson et al., 2017).

4) To determine in which areas of the study site **disturbance** by wildfowlers, recreational saltmarsh users and the invasive Canada goose (*Branta canadensis*) increased and caused displacement of overwintering birds. Canada goose populations have increased across the UK in the study period (Calbrade et al., 2010; RSPB, 2017) and human population in the region surrounding the study area has increased significantly between 2002 and 2012 (Office for National Statistics, 2011), leading to potential increases in

recreational and wildfowling disturbance for birds overwintering in the Mersey estuary saltmarshes.

5) To determine the **spatial distribution of suitable areas** for all target species in the study site and to analyse how these changed between 2002 and 2012 by building species-specific habitat suitability models. Areas of saltmarsh that have remained highly suitable to the target species could be prioritised for conservation measures, while those parts of the saltmarsh that have deteriorated between 2002 and 2012 could be targeted with improvement measures.

The project will inform management of the Mersey Estuary SSSI and, to the best of my knowledge, will be the first study to quantify saltmarsh habitat suitability for overwintering birds in the UK taking into account food availability and disturbance by larger birds. This approach could therefore help to determine saltmarsh habitat suitability for wading birds for the rest of the UK and Western Europe. In addition, examining the relative importance of food availability, habitat and disturbance in influencing habitat suitability changes will inform the development of specific conservation measures for the estuary.

2. Literature review

2.1 Saltmarsh definition, classification and ecology

Saltmarshes are intertidal habitats that occur in sheltered parts of the coastline such as bays and estuaries, where deposited fine sediment is stable enough to allow vegetation to grow (Boorman, 2003). They are found at slightly higher elevations than mudflats, meaning that they flood less often and the velocity of flood water is lower. Saltmarshes are found in temperate and high latitudes, while mangroves can be found at corresponding elevations in tropical and subtropical regions.

It is estimated that saltmarshes cover approximately 140 million hectares worldwide (Duarte et al., 2008), but their extent has reduced dramatically over the last 200-300 years because of anthropogenic pressures (Lotze et al., 2006). In England, saltmarshes declined in extent during the 20th century, but there is evidence that this decline has slowed down (Baylis et al., 2011). This could be partly due to conservation efforts such as coastal realignment and managed retreat schemes (Parker et al., 2004).

A saltmarsh is generally formed by vegetation areas interspersed with a network of branched and normally blind-ended creeks (Allen, 2000). Saltmarsh vegetation changes depending on elevation, and the plant species present in a certain area of a saltmarsh can be predicted, to an extent, by its elevation (Figure 1). These zones, however, are not usually distinct, but they blend into each other as there is a gradual transition from one zone to another.

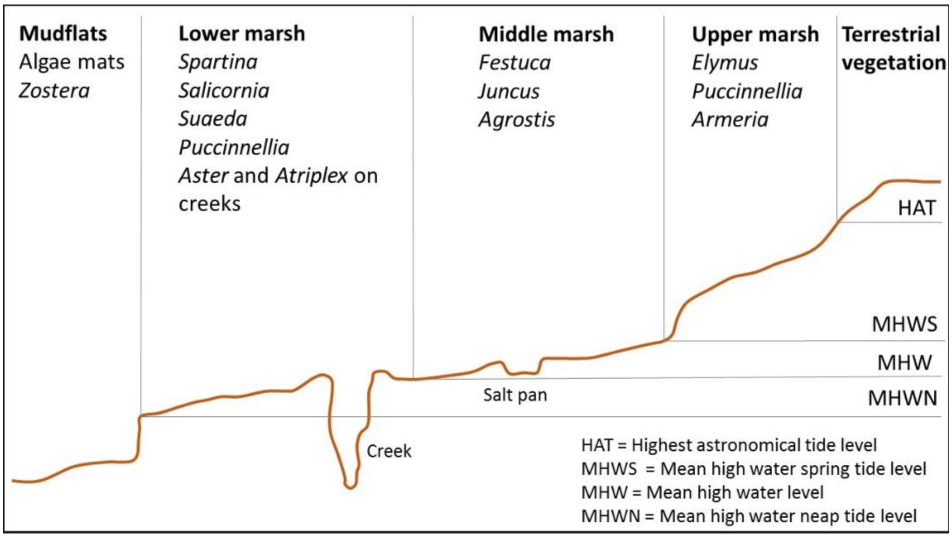

Figure 1. Typical saltmarsh profile.

Various classification methods have been used for saltmarsh; for this project, the UK Environment Agency's classification system was used because it identifies different plant communities found in saltmarshes but also reflects what habitats can be identified using aerial imagery (Hambridge & Phelan, 2014). This classification's categories are:

a) Pioneer: the area flooded by most tides, except the lowest neaps (Boorman, 2003). Here tidal inundation is more frequent and sediment less stable. The most common plant in this zone is *Salicornia*. Other species in this zone include *Puccinellia* (especially in the North-West of England; Adnitt et al., 2007), *Sueda*, *Halimione* and *Limonium*.
b) *Spartina*: *Spartina alterniflora* was introduced to the UK over a century ago and hybridised with the native *Spartina maritima* to produce the hybrid *Spartina anglica*. *S. anglica* spread rapidly thanks to its fast growth rate, high fecundity and aggressive colonisation (Benham, 1990). This species was also extensively planted in British saltmarshes for its ability to stabilise soft sediments (Hubbard & Stebbings, 1967). However, there are concerns on its impacts on wildfowl populations because it leads to roosting and feeding habitat loss (Davidson et al., 1991).
c) Mid-low marsh: this zone is only covered by spring tides (Boorman, 2003). Plant diversity is therefore typically much higher than in the pioneer and *Spartina* zones. Some species from the pioneer zone, especially *Puccinellia*, can still be present. Other common species in this zone are *Halimione*, *Festuca*, *Atriplex*, *Sueda* and *Limonium*.
d) Upper marsh: this zone is only covered by the highest spring tides (Boorman, 2003). Vegetation cover is usually dense and plant diversity is similar to that of mid-low marsh. Common species include *Agrostis*, *Festuca*, *Elytrigia* and *Juncus*.
e) Reedbeds: *Phragmites* beds are only found in brackish waters in the upper parts of estuaries and are usually confined to mid-low marsh areas (Adnitt et al., 2007).

Changes in saltmarsh extent over time and its zonation are determined by a number of physical, chemical and biological factors. Relevant physical factors include tides, waves and water velocity. Vertical tidal ranges in UK estuaries are typically around 4-5 metres, while on the open coast they are approximately 3 m. The tidal regime controls salinity, organic matter content, sediment deposition and soil waterlogging. All these factors determine which plant species will be able to grow in a specific area of saltmarsh (Boorman, 2003). Waves and water velocity are connected, as waves increase water velocity and do not allow fine sediment to settle and form a saltmarsh.

Nutrients are not considered a factor that significantly influences saltmarsh zonation, as saltmarsh plants have nutrient requirements that are similar to those of non-halophile species (Boorman et al., 2001). Rather, the most important chemical factor for saltmarsh zonation is salinity itself. The most halophile plant species are able to survive in the pioneer and *Spartina* zones, but they are outcompeted by other species in the upper zones of the saltmarsh (Hambridge & Phelan, 2014). As elevation increases, biological factors such as competition become more important. Another key biological factor is the distance to other saltmarshes, as saltmarsh plant diaspores do not tend to travel for long distances in water (Parker et al., 2004; Wolters et al., 2005).

2.2 Importance of and threats to saltmarsh habitat

Saltmarshes provide important and valuable ecosystem services, such as protecting coastal areas from erosion (Ranwell, 1981), reducing water pollution, capturing and storing carbon dioxide (Millennium Ecosystem Assessment, 2005) and contributing to nutrient cycles (Foster et al., 2013). In particular, they are essential for overwintering birds, who depend from saltmarshes and mudflats for food and roosting (McMullan, 2008). As a consequence, saltmarshes are often protected by national and international legislation, including the Habitat and Species Regulations 2017.

Saltmarshes are threatened by human activities both directly and indirectly. Coastal areas worldwide are developing rapidly, with approximately 3 billion people living within 200 km of the coastline, and population in coastal areas growing faster than those inland (Cohen, 1995). Habitat loss and degradation following dredging, housing or commercial development and agriculture have significantly reduced the extent of British saltmarshes over the last decades (Lotze et al., 2006). Resource over-exploitation is also a major threat to many estuarine ecosystems (Millenium Ecosystem Assessment, 2005).

Furthermore, invasive non-native species are a bigger threat than in terrestrial ecosystems because juveniles are transported long distances by water currents. Once established, invasive species are generally very hard or prohibitively expensive to eradicate (Eno et al., 1997). All coastal habitats, including saltmarsh, are threatened by climate change in several ways, including “coastal squeeze”. This is when intertidal habitats are prevented from migrating landwards following sea level rise because their landward edge is fixed due to hard structures such as flood defence walls or roads (Pontee, 2013).

2.3 Target bird species ecology and habitat requirements

Northern pintail (*Anas acuta*, Figure 2A), Eurasian teal (*Anas crecca*, Figure 2B) and Eurasian wigeon (*Mareca penelope*, Figure 2C) are three species of duck common and widespread in Eurasia and North America. They are migratory species and move southwards in autumn from northern breeding grounds (Stroud et al., 2001). In the UK, teal overwinter in inland or coastal wetlands, while pintail and wigeon are mostly found in coastal wetlands (Stroud et al., 2001). The majority of individuals of these species overwintering in Great Britain come from Iceland, Scandinavia and Russia (Owen et al., 1986). Very few pintail and wigeon breed in Britain (Owen et al., 1986), while teal overwintering populations contain migrating and locally breeding birds (Batten et al., 1990).

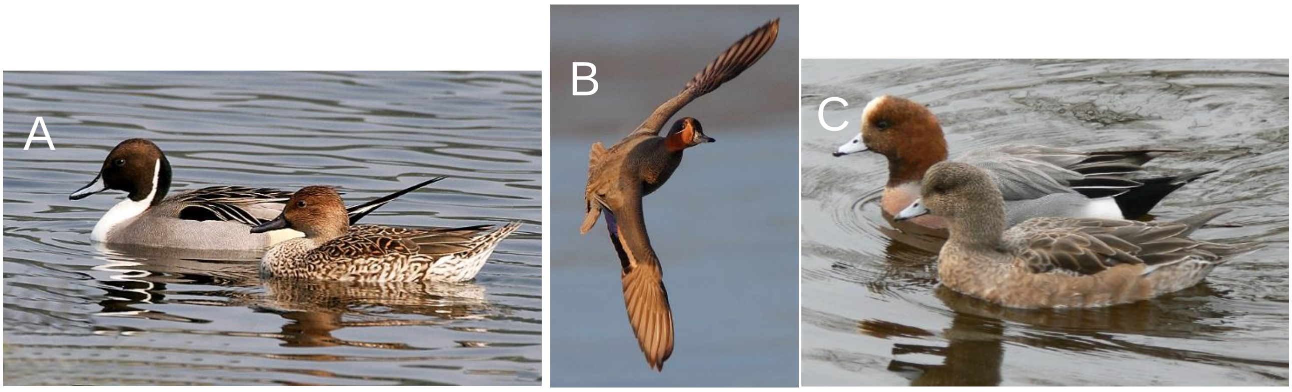

Figure 2. (A) Male (left) and female (right) pintail; (B) Male teal in flight; (C) Male (back) and female (front) wigeon. © Creative Commons CC BY-SA 2.0

Pintails concentrate in large number in a smaller number of sites than the other two species, with the main overwintering sites found in the North-West of England and on the Welsh coast (Scott & Rose, 1996, Pollitt et al., 2000). Fluctuating counts of overwintering pintail between years suggest low site fidelity (Colhoun, 2000; Pollitt et al., 2000). Overwintering wigeon also tend to congregate in large groups and move rapidly from an area when the conditions are no longer suitable (Stroud et al., 2001). Teal are highly susceptible to severe winters, when they often disperse to areas further south than their usual wintering grounds (Ridgill & Fox, 1990). Similarly, wigeon overwintering populations can shift southwards or exhibit high mortality rates during particularly cold winters (Stroud et al., 2001).

Although all three species belong to the family *Anatidae*, each species has fairly specific requirements when overwintering in a saltmarsh habitat. Individuals of all three species feed on plant seeds, leaves and - to a lesser extent - macroinvertebrates living in mud and sandflats, especially the snail *Hydrobia ulvae* (Kirby et al., 2000). The proportion of invertebrates in the diet is lower in overwintering birds but increases during the breeding season (Dessborn et al., 2011).

Pintail show a strong preference for *Salicornia* seeds (Ferns, 1992), while the two other species are more adaptable when it comes to selecting food sources. Teal's favourite foods are *Atriplex portulacoides* and *Salicornia* spp. seeds (Ferns, 1992). Wigeon is a very adaptable species, as it was mostly feeding on the seagrass *Zostera* in the UK until the 1930s, when *Zostera* started to decrease in abundance in British waters. This species has since redistributed into different habitats, widening the range of plants on which it feeds (Owen & Williams, 1976). In saltmarshes, wigeon is known to preferentially feed on the grass *Puccinellia maritima* rather than other grasses such as *Agrostis stolonifera* (Owen, 1973).

All Anseriformes are aquatic birds and select areas near water to feed and roost (Tang et al., 2016). Proximity to open water is therefore an important factor for all the three species targeted by this study. Pintail and teal need areas with shallow water (<25 cm) for feeding (Kirby et al., 2000) and teal often roost in or near shallow ponds and pans

(Hsu et al., 2014). In addition, several studies found that teal prefer areas with low slope for feeding and roosting (Genard & Lescourret, 1992; Hsu et al., 2014).

Another critical factor for all three species when selecting suitable habitat is sward height: all species prefer short swards in order to be able to spot nearby predators. Wigeon prefer very short sward (<5 cm) in their feeding areas, while teal and pintail do not require such short swards. However, they prefer vegetation to be shorter than 20 cm (Kirby et al., 2000). Saltmarshes are often managed using livestock grazing, most commonly by cattle (Gedan et al., 2009). Grazing influences sward height, but also influences waterfowl distribution by increasing plant diversity. As a result, long-term grazing has been shown to increase bird abundances in saltmarshes, although excessive grazing levels can negatively affect waterfowl by creating bare soil patches following excessive trampling (Davidson et al., 2017).

Estuaries are an important habitat for large populations of overwintering water birds, but they are also a hotspot of economical and recreational human activities. Human disturbance to waterfowl is therefore to be expected in this environment. The most common human activities in saltmarshes have been described as wildfowling, angling, bird and wildlife watching, military, port and construction activities (Davidson & Rothwell, 1993). Walkers and dog walkers are less common on saltmarshes (Davidson & Rothwell, 1993), as walkers mostly keep to shoreline footpaths or beaches above the high water mark (Liley et al., 2011).

New military, port or construction activities between 2002 and 2012 on the Mersey estuary have been far enough from the saltmarshes examined in this project (>1 km) not to be a source of disturbance for local bird populations. For the three species studied here, the 'alert distance' (the distance between the disturbance source and the animal at the point where the animal changes its behaviour) ranges from 200 to 1000 metres (Laursen et al., 2005). In addition, anglers do not commonly fish in the area. The two main sources of human disturbance on the saltmarshes in the study area are therefore considered to be wildfowling and recreational disturbance, defined as the collective impact of walkers, dog walkers and bird/wildlife watchers (Liley et al., 2017). Dog walkers can be very disruptive to wildfowl, especially when the dogs are off-lead (Liley et al., 2017).

Disturbance can impact overwintering birds in several ways, including:

- Temporary or chronic displacement of birds from otherwise suitable habitat (Burton et al., 2002a; Burton et al., 2002b; Liley & Sutherland, 2007);
- Reduced food intake rates because the birds feed in areas with suboptimal food availability (Bright et al., 2003, Yasue`, 2005);
- Increased energy expenditure because of birds flying away from disturbance (Nolet et al., 2002);
- Direct mortality, such as killing by wildfowlers or predation by dogs (Liley & Sutherland, 2007).

Birds can still survive when exposed to chronic disturbance, but the suitability of part or all of a site will be reduced. In this situation, disturbance can be considered equivalent to habitat loss (Sutherland, 2007).

Among the species targeted in this project, a recent study (Liley et al., 2017) found that wigeon is the species most sensitive to recreational disturbance, with approximately 40% of individuals exposed to disturbance showing some kind of behavioural response. In contrast, only about 20% of pintail and 7% of teal individuals exposed to disturbance exhibited any response. In the study area for this project, Hale Bank has a lower number of visitors compared to other sites in the Mersey estuary, however low numbers of observed birds suggest recreational disturbance is significant at the site (Liley et al., 2017). On the other hand, Ince and Stanlow Bank on the southern bank of the estuary have consistently low levels of recreational disturbance thanks to the Manchester Ship Canal, which prevents public access to that part of saltmarsh.

Wildfowling is widespread throughout Europe, where it is known to affect waterfowl directly through killing and indirectly through disturbance (Nichols, 1991). Some wildfowl species, such as wigeon and teal, will avoid an area completely if wildfowlers operate there (Madsen, 1994; Bregnballe et al., 2004). During the hunting season, pintails in California were spending their days in areas with lower quality food and switched to nocturnal feeding (Casazza et al., 2012). In fact, wildfowling can disturb birds unless shootings are several weeks apart (Fox & Madsen, 1997). Wildfowling is therefore likely to affect all three target species more severely than recreational disturbance.

Not all disturbance to overwintering birds is directly caused by humans. Canada goose (*Brenta canadensis*) was introduced to the UK in the late 17th century and is currently widespread throughout the country (Watola et al., 1996). This species can drive away other duck species (Giles, 1992) and compete with wigeon for grazing (Hughes & Watson, 1986).

2.4 Mapping of saltmarsh extent and zonation

There are many different methods to determine saltmarsh vegetation distribution, while relatively few studies dealt with determining saltmarsh extent. In the UK, the Environment Agency regularly assesses the extent and zonation of all English saltmarshes using a standard methodology based on analyst's interpretation of aerial imagery combined with elevation data (Baylis et al., 2011). Saltmarshes do not exist above Highest Astronomical Tide (HAT) and Mean High Water Neap (MHWN) levels (Boorman, 2003; Balke et al., 2016). Visual analysis can therefore be aided by Lidar-derived contour lines showing where these two elevation levels occur in the study site.

Recently, a method for unsupervised detection of saltmarsh extent was developed by Goodwin et al. (2018). This method is based on the principle that mature saltmarshes usually occur on relatively flat platforms delimited by subvertical scarps, and their extent can therefore be determined analysing slope patterns in Lidar-derived elevation data. Its accuracy is very high (> 90% for resolutions up to 3 metres; Goodwin et al., 2018) and comparable to that of the more labour-intensive methodology used by the Environment Agency (> 96%; Baylis et al., 2011). However, pioneer zones are not easily identified using the unsupervised method because they occur on the accreting part of saltmarshes, which have a slope very similar to that of the tidal flats immediately below them (Goodwin et al., 2018).

Saltmarsh zonation can be determined using three broad types of methodologies: These are plant surveys, manual interpretation of aerial imagery and predictive models that use remote sensing and/or edaphic variables. Plant surveys are extremely labour-intensive, as they involve collecting large amounts of field data. Their accuracy is extremely high for accessible areas, but in saltmarshes part of the survey area will often be inaccessible to surveyors because of e.g. large creeks.

In the UK, the Environment Agency uses a semi-automated method for determining saltmarsh zonation. After a preliminary selection of vegetated saltmarsh areas, a grid is superimposed to the aerial imagery in the selected area and each grid point is assigned to a saltmarsh zone (see section 1 for a description of the zones). The total percentage of points consistently classified using this method is > 90%, and the accuracy can be improved further using ground-truthing surveys (Hambridge & Phelan, 2014).

Predictive models using both edaphic (e.g. soil water content, soil redox potential) and remote sensing (e.g. elevation, distance from HAT, NDVI) variables can be used successfully to determine saltmarsh zonation. The best of these models have total accuracies ranging between 70 and 90% (Hladik & Alber, 2014; McGruer, 2017; Sun et al., 2018) and models using remote sensing variables are generally more accurate and less labour-intensive (Hladik & Alber, 2014). A recent study predicted saltmarsh zonation in the Ribble Estuary (North-West England) with up to 87% overall accuracy, however none of the pioneer zone points were correctly classified (McGruer, 2017). On the other hand, the Environment Agency methodology consistently classified approximately 58% of pioneer data points in two areas of the Humber Estuary (Hambridge & Phelan, 2014).

2.5 Habitat suitability models

Habitat models and predictive distribution maps have become widely used for wildlife conservation and protected sites management over the last 40 years (Guisan & Zimmerman, 2000; Roxworthy et al., 2003; Jeganathan et al., 2004; Johnson & Gillingham, 2004). Habitat suitability models can be classified as deductive or inductive based on the approach they use (Corsi et al., 2000). Deductive models define habitat suitability based on known species ecological requirements, while inductive (or empirical) models are based on the analysis of species distribution data (Vogiatzakis, 2003).

Ideally, presence/absence data for the species of interest are needed in order to correlate species presence to environmental variables and produce an empirical habitat suitability model, although presence-only data are often used (Zaniewski et al., 2002). Models using presence-only data are effective for predicting species distribution for many species and regions (Elith et al., 2006; Hirzel et al., 2006). However, species distribution data are often expensive and time-consuming to collect. Furthermore, a species usually does not occupy the whole habitat with suitable environmental conditions (termed its fundamental niche; Hutchinson, 1957), but only a subset of it, its realised niche (Brown and Lomolino, 1998). Results of empirical suitability models therefore tend to underestimate the area of suitable habitat for the target species (Phillips et al., 2006).

For presence/absence data, a range of habitat suitability models have been developed, most commonly using logistic regression methods such as GAMs (Hastie & Tibshirani, 1990) and GLMs (McCullagh & Nelder, 1989). For presence-only data, some methods use pseudo-absences to adapt presence/absence models such as GAMs and GLMs to presence-only data (Elith et al., 2006). Other models, such as BIOCLIM, are specifically built to deal with presence-only data (Busby, 1991).

When species distribution information is not available, it is possible to use deductive models based on expert judgment and/or literature searches (Store & Kangas, 2001). Empirical models generally perform better than deductive models when estimating species richness (Pearce et al., 2001), however the two modelling approaches have similar accuracy when predicting single species distribution (Di Febbraro et al., 2018). Deductive models based on literature searches can be more accurate than those based on expert judgment because peer-reviewed papers often derive from statistically analysed data and are therefore more objective than experts' memory and experience (Clevenger et al., 2002).

Using expert knowledge in habitat suitability modelling requires methods for transforming expert judgment into numerical forms. One approach is using multi-criteria evaluation (MCE), which produce a suitability index based on a combination of multiple criteria (Nijkamp et al., 1990). Weighted linear summation, an additive technique based on the multi-attribute utility theory, is the best-known MCE technique (Berry, 1993). Weighted linear summation is a technique by which criteria scores are standardised and the total score is calculated by multiplying each criterion score by its weight and summing the results (Store & Kangas, 2001). Criteria weight can be consistently calculated using the analytic hierarchy process (AHP), which produces criteria weights and makes criteria of different kinds commensurable (Saaty, 1980).

Both deductive and empirical models' accuracy is affected by various types of errors, e.g. error in data sources or variability in expert opinion. Model accuracy can be tested by validation, sensitivity analysis or uncertainty analysis (Johnson & Gillingham, 2004). Validation is only possible when species distribution data are available, while sensitivity and uncertainty analysis can be carried out without field data (Rothley, 2001). Sensitivity and uncertainty analysis quantify the variability in model predictions due to errors and variability in input data, therefore improving confidence in the model results (Regan et al., 2002). Expert-based habitat models accuracy is rarely assessed because they are normally used when species distribution data are not available and validation not possible, but when sensitivity analyses are carried out they show that model estimates can change by up to 85% due to variability in expert opinion (Johnson & Gillingham, 2004).

3. Study area

3.1 Physical characteristics

The Mersey Estuary is situated in Merseyside, North West England, close to the city of Liverpool. The estuary is 50 km long from its tidal limit at Warrington, with a catchment of 4500 km^2. It is traditionally divided into four sections (Figure 3):

- The upper tidal estuary, a narrow section extending from Warrington to Runcorn;
- The middle estuary, a large open basin characterised by extensive intertidal flats and channels and an area of accretion for sediments imported from the coast;
- The Narrows, the mouth of the estuary which reaches depths of 20m and has strong currents (spring tide currents > 2.5m/s) that prevent the accumulation of sediments;
- The outer estuary, which extends from the mouth of the estuary to Formby Point and Dove Point and consists of large area of intertidal sand banks.

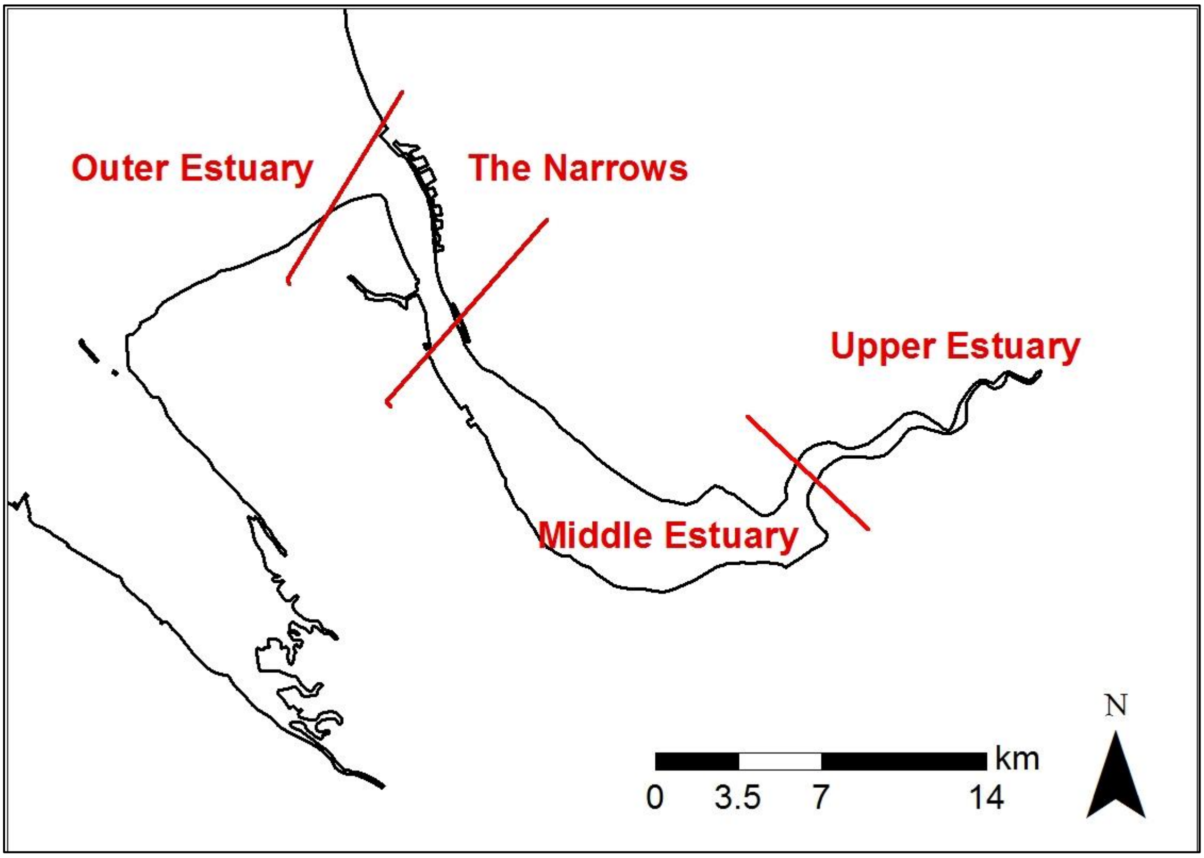

Figure 3. The tidal Mersey estuary and its zones.

Spatial changes in the sedimentology of the estuary are observed in response to changes in the flow regime. Along the estuarine gradient the substratum is typically composed of medium sand in the Narrows, fine sand in the inner estuary, very fine sand upstream of Hale and silt/clay deposited in slow flowing regions at the estuary margins, especially at Frodsham Score, Ince and Stanlow Bank.

Another characteristic of the Mersey is the limited water exchange between the estuary and the coast (Cole and Whitelaw, 2001). In addition, there is a net influx of sediment from the coast to the inner estuary, which creates large expanses of intertidal flats in this area (Halcrow, 2013). A survey of sediment-living invertebrates from 2001 showed that invertebrates in the estuary followed a typical pattern for estuarine areas with habitats of relatively species-poor communities over large areas, particular the sand flats and tide swept channels, but richer communities and more abundant waterfowl prey resources in the settled depositional areas and mudflat habitats (Scott, 2002).

Following high levels of pollution since the 1930s low invertebrate species diversity has historically been observed, but in subsequent years invertebrate diversity has improved. This is believed to have contributed to a dramatic increase in bird numbers during the 1970s (Scott, 2002). The Mersey estuary, however, remains one of the most contaminated estuaries in the UK (Allen et al., 2001).

3.2 Conservation importance

The Mersey estuary is of great conservation importance and several protected sites can be found in the area (Figure 4). The Inner Mersey estuary has been classified as a Special Protection Area (SPA) under Article 4.2 of the EU Birds Directive. This SPA covers the intertidal habitats of the estuary (from mean high and mean low water marks) between Runcorn Bridge to the east and Bromborough to the west and also includes some land not covered by tidal waters (English Nature, 2004). This area qualifies for SPA status because it supports internationally important populations of regularly occurring migratory (wintering) species. The qualifying species are dunlin *(Calidris alpina)*, redshank *(Tringa totanus)*, pintail (*Anas acuta*), shelduck (*Tadorna tadorna*), teal (*Anas crecca*), black-tailed godwit (*Limosa limosa islandica*) and golden plover (*Pluvialis apricaria*). The Mersey estuary also qualifies for SPA status because it regularly supports over 20,000 wintering waterfowl (English Nature, 2004).

In addition to its SPA status the Inner Mersey area is also designated as an internationally important wetland site (Ramsar site) under the Ramsar Convention and is a Site of Special Scientific Interest (SSSI) under the Wildlife and Countryside Act 1981. Bird species that are designated as SSSI features but not as SPA features are curlew (*Numenius arquata*) and wigeon (*Anas penelope*), while black-tailed godwit is a SPA feature only.

The Mersey Narrows and the North Wirral foreshore are also a SSSI and a SPA because they regularly support at least 20,000 waterfowl including overwintering populations of redshank and turnstone (*Arenaria interpres*).

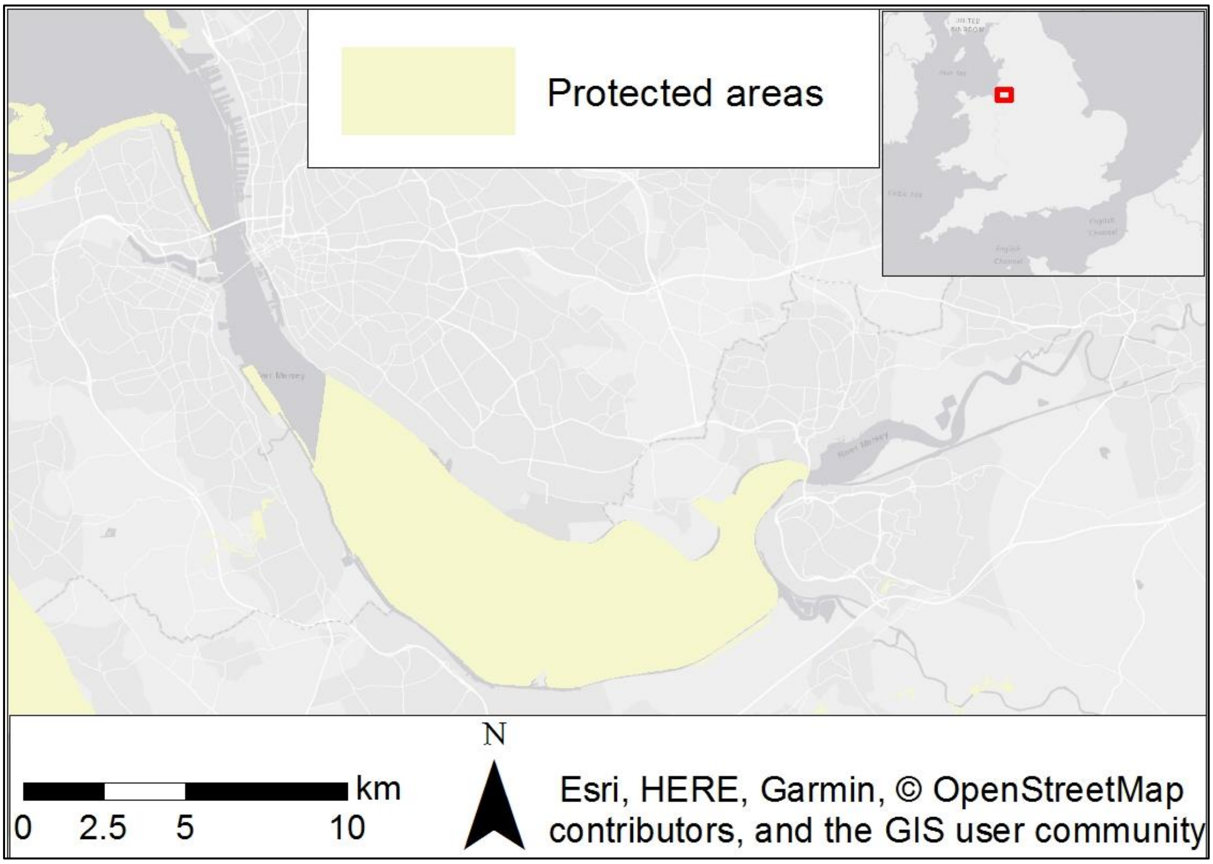

Figure 4. The Mersey Estuary SSSI/SPA/Ramsar and the Mersey Narrows and North Wirral Foreshore SSSI/SPA/Ramsar.

Besides the qualifying bird species, some habitats are also protected because they support the bird populations that are the interest features of the site (English Nature, 2004). The protected habitats are:

- intertidal sediments mudflats and sandflats, which provide feeding areas for overwintering birds;
- rocky shore and saltmarsh, which provide feeding and roosting areas for overwintering birds.

The Mersey estuary is a very dynamic system, with saltmarshes particularly vulnerable to erosion by the moving channel because of the hard structures on their landward margin. The main areas of saltmarsh in the Mersey estuary are Hale marsh on the right bank and Stanlow Bank, Ince Bank and Frodsham Score on the left bank (Phelan et al., 2011; Figure 5).

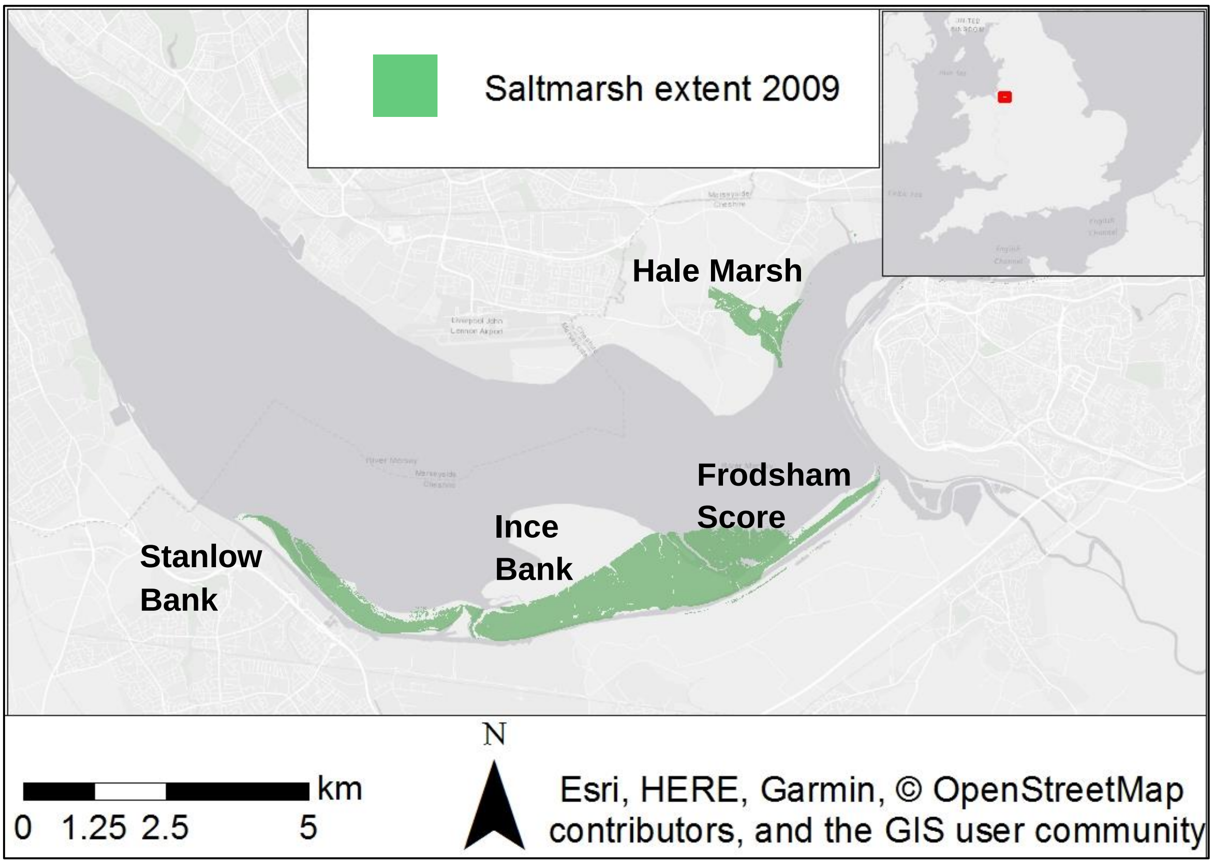

Figure 5. The Mersey Estuary SSSI/SPA/Ramsar with the main saltmarsh areas, which were determined by the Environment Agency in 2009.

3.3 Bird abundance and trends

In a recent site assessment, recent bird numbers (five-year mean from 2009/10 to 2013/14) were compared to the lowest bird count in the five years prior to SSSI designation (1980/81 to 1984/85), which represent the lowest threshold for the species to be considered in favourable condition (Table 1).

Table 1. Assessment of Mersey estuary SSSI population of protected bird species. For each species, the favourable condition threshold based on natural fluctuation (i.e the minimum count of the period 1980/81 to 1984/85), the most recent count (2013/14), the most recent five-year average (2009/10 to 2013/14) and an initial assessment are shown (Natural England, 2017).

Species	Favourable condition threshold (based on natural fluctuation – minimum count of the period 1980/81 to 1984/85)	Most recent count (2013/14)	Most recent 5-year average (2009/10 to 2013/14)	Initial assessment
Curlew	776	1,842	1,451	Pass
Dunlin	25,400	41,316	44,471	Pass
Golden plover	211	1,132	869	Pass
Pintail	8,240	85	52	Fail
Redshank	666	2,842	1,779	Pass
Shelduck	7,082	2,036	3,780	Fail
Teal	12,870	5,338	4,640	Fail
Wigeon	3,470	976	1,035	Fail

Four species (pintail, shelduck, teal and wigeon) fail this initial assessment. However, supplementary counts for shelduck in 2013/14 show that 12,000 birds used the estuary that winter. This suggests that the standard counts may not be representative of shelduck numbers in the estuary, and that shelduck is probably not declining in the area. The remaining three species seem to have decreased on the Mersey estuary more than it would be expected by looking at national and regional population trends.

3.4 Site suitability for the project

Decline in pintail, teal and wigeon overwintering populations in the Mersey estuary are larger than it would be expected looking at national and regional trends, strongly suggesting site-specific factors are playing a role (Holt et al., 2016). The Mersey estuary is a dynamic and complex system, which has greatly changed over the last 20 years. For example, changes in dredged sediment volumes have altered sediment fluxes in and out of the estuary, changing the saltmarshes' erosion and accretion dynamics (Ridgway et al., 2012). Increased human activity in the area has also changed the intensity of some pressures, such as recreational disturbance, on bird populations.

Habitat suitability models for the declining species could help disentangle the effects of several factors potentially affecting bird distribution and highlight high-quality habitat areas within the estuary which should be the focus of conservation measures. The Mersey estuary is suitable for testing such a model thanks to the abundance of available information. Large amounts of data have been collected in the area by several organisations over the years, and this will allow to test a large number of factors potentially affecting bird distribution at two different time points for which the most datasets are available (2002 and 2012). This could also inform data collection needs for any similar study in comparable systems.

4. Data

This study utilised data collected as part of existing monitoring programmes that cover most of the UK coasts. No datasets were collected specifically for this study, meaning that findings from this study could be easily replicated in other British saltmarshes because the datasets utilised already exist for most similar areas in the UK.

The datasets used in this project are summarised in Table 2 and further details are given in the following sections. The datasets used for this project were the only ones available for the study area for the chosen years. The aerial photography and LiDAR datasets had resolution and accuracy levels suitable to determine saltmarsh extent and zonation. Vegetation surveys in 2002 and 2016 were useful to validate saltmarsh zonation maps created from aerial photography and provided useful information on the distribution of Canada goose. However, the sward height information was only collected in the plant survey quadrats and grazing level information was only qualitative. More detailed information on sward height and grazing intensity would have improved the quality of the model.

More detailed information on where exactly wildfowling took place would also have been useful for the model, as well as more samples in the sandflat survey to determine the presence of *Hydrobia*. These last two datasets, however, were still suitable for model production because birds tend to avoid large areas around places where wildfowling takes place and they fly several kilometres a day to forage. It is thus unlikely that having more detailed information on wildfowling and *Hydrobia* distribution would have changed the model performance significantly.

Table 2. Summary of datasets used to assess habitat suitability for pintail, teal and wigeon.

Name	Format	Resolution	Accuracy	Collection date	Source	Variables derived from dataset
Aerial photography 2002	Raster	1 m	± 30 cm	December 2002	www.channelcoast.org	Saltmarsh extent, distribution of *Salicornia* and *Atriplex*, distribution of *Hydrobia*, presence of open water
Aerial photography 2012	Raster	10 cm	± 30 cm	May 2012	www.channelcoast.org	Saltmarsh extent, distribution of *Salicornia* and *Atriplex*, distribution of *Hydrobia*, presence of open water
LiDAR Digital Surface Model 2002	Raster	2 m	± 15 cm (vertical)	March 2002	Environment Agency	Saltmarsh extent, distribution of *Salicornia* and *Atriplex*, presence of open water, slope
LiDAR Digital Surface Model 2013	Raster	1 m	± 15 cm (vertical)	January 2013	Environment Agency	Saltmarsh extent, distribution of *Salicornia* and *Atriplex*, presence of open water, slope
Saltmarsh vegetation survey 2002	Polygon and point shapefiles	N/A	GPS accuracy	September - November 2002	Natural England (Skelcher, 2003)	Distribution of *Salicornia* and *Atriplex*, sward height, grazing levels, presence of Canada goose
Saltmarsh vegetation survey 2016	Polygon and point shapefiles	N/A	GPS accuracy	September 2016	Natural England (Neal, 2016)	Distribution of *Salicornia* and *Atriplex*, sward height, grazing levels, presence of Canada goose
Intertidal macroinvertebrate survey 2001	PDF	N/A	GPS accuracy	August - September 2001	Environment Agency (Scott, 2002)	Distribution of *Hydrobia*
Intertidal macroinvertebrate survey 2011	PDF	N/A	GPS accuracy	2011	Natural England (Centre for Marine and Coastal Studies Ltd, 2011)	Distribution of *Hydrobia*
Wildfowler's bag returns 2002-2016	Paper forms	N/A	Not reported	2002-2016	Natural England	Wildfowling intensity
Recreational disturbance questionnaires	PDF	N/A	Not reported	2015	Natural England (Still et al., 2015)	Recreational disturbance intensity
Bird feeding and roosting areas maps	Paper maps	N/A	Not reported	2000	Natural England	HSI threshold determination

Aerial photography and LiDAR Digital Surface Model:

Vertical orthorectified colour aerial photographs for December 2002 and May 2012 were obtained from the website of the National Network of Regional Coastal Monitoring Programmes of England (www.channelcoast.org; downloaded on 15 March 2017). Both datasets cover the whole Mersey estuary, with the 2002 images captured at a resolution of 1 m and those collected in 2012 having a 10 cm resolution.

Light Detection and Ranging (LiDAR) data from surveys carried out in March 2002 and January 2013 were obtained from the Environment Agency. LiDAR is an airborne mapping technique that accurately measures terrain elevation using a scanning laser that can provide tens to hundreds of thousands measurements per second. The data used in this study had a horizontal resolution of 2 m in 2002 and 1 m in 2013, while the guaranteed vertical accuracy was ± 15 cm for both datasets (Environment Agency, 2016). The 2002 LiDAR dataset covered the whole estuary, while 2013 data covered the saltmarsh, but not the river channel and intertidal mudflats.

Aerial imagery and LiDAR data were used to derive a number of variables for this project. Combining aerial photography and LiDAR data is especially useful in intertidal habitats, as some types of habitat look very similar on aerial photography (e.g. the different low-mid marsh communities), but elevation data gives additional information that allows to separate some of them (Adnitt et al., 2007).

Saltmarsh vegetation surveys:

Two saltmarsh vegetation surveys were available for the Mersey estuary, one carried out in the autumn of 2002 (Skelcher, 2003) and another in September 2016 (Neal, 2016). In 2002, the whole study site was surveyed and plant species cover was quantified in at least five 2x2 m quadrats for each vegetation type. The final products of this survey were a point shapefile with quadrats locations and results, a polygon shapefile representing plant communities' distribution across the study site and a report with a brief description of plant communities and management regime for each of the 11 monitoring units of the Mersey Estuary SSSI.

In 2016, 30 transects from the upper marsh to the lower marsh were surveyed. The surveyors stopped at regular intervals along each transect to record plant communities, sward height and management regime, as well as to determine plant species cover in 2x2 m quadrats. Canada goose presence was also recorded, both in 2002 and 2016.

Although the 2002 vegetation survey attempted to map saltmarsh zonation across the SSSI, no accuracy measurements were reported and comparison with aerial photography showed the polygon extents were not accurate, especially on the lower marsh. However, quadrat locations were accurate in both the 2002 and 2016 surveys as GPS trackers were used both times. GPS signals in space have a horizontal accuracy in of 7.8 m or less (95% confidence interval; US Department of Defence, 2008), however individual device error can be as high as several hundred meters in enclosed spaces. The 2016 survey results are not a map of the whole estuary, but only of the areas immediately surrounding the survey transects.

Both datasets were used to complement aerial imagery and LiDAR data to determine the distribution of *Salicornia* and *Atriplex*. *Salicornia* is especially difficult to distinguish from *Spartina* using aerial photographs (Hambridge and Phelan, 2014). The two surveys' results were also used to produce sward height, grazing levels and presence of Canada goose shapefiles.

Intertidal macroinvertebrate surveys:

Intertidal sediment cores were collected in 2001 (Scott, 2002) and 2011 (Centre for Marine and Coastal Studies Ltd, 2011) to determine macroinvertebrate community composition. The 2001 survey consisted of 45 sediment cores sampled across the study area following a 1 km grid sampling plan. The 2011 survey included less sediment cores (triplicate samples in four locations) complemented by Phase 1 biotope mapping following a 1 km grid sampling plan. Phase 1 surveys were carried out by visual inspection of the substrate and hand search for fauna. Both surveys were used to determine the distribution of *Hydrobia* snails across the Mersey estuary.

Wildfowler's bag returns:

Bag return forms should be returned every year to Natural England by wildfowling clubs operating in protected areas and include total number of birds shot by species, number of shootings and number of wildfowlers active during the year. Available wildfowlers bag returns paper forms for the period 2002-2016 from the four wildfowling clubs that operate in the study area (Frodsham & District Wildfowlers club on Ince and Frodsham bank, David Jones' syndicate on Hale marsh west, Halton Wildfowlers Association on Hale shore and Philip Lunt's syndicate on Hale marsh east) and used to build a shapefile of wildfowling disturbance for the study area.

Recreational disturbance questionnaires:

Bird counters who survey the Mersey estuary monthly as part of the Wetland Bird Surveys (WeBS) organised by the British Trust for Ornithology (BTO), staff from Natural England and other local organisations were asked to complete a questionnaire as part of a recent study (Still et al., 2015). The questionnaires dealt with perceived recreational disturbance levels across the Liverpool City Region Coast and how those had changed over the last 30 years. The three sectors relevant to this study (Ince Bank, Manisty Bay and Hale; Figure 6) had overall levels of recreational disturbance assigned based on questionnaire answers.

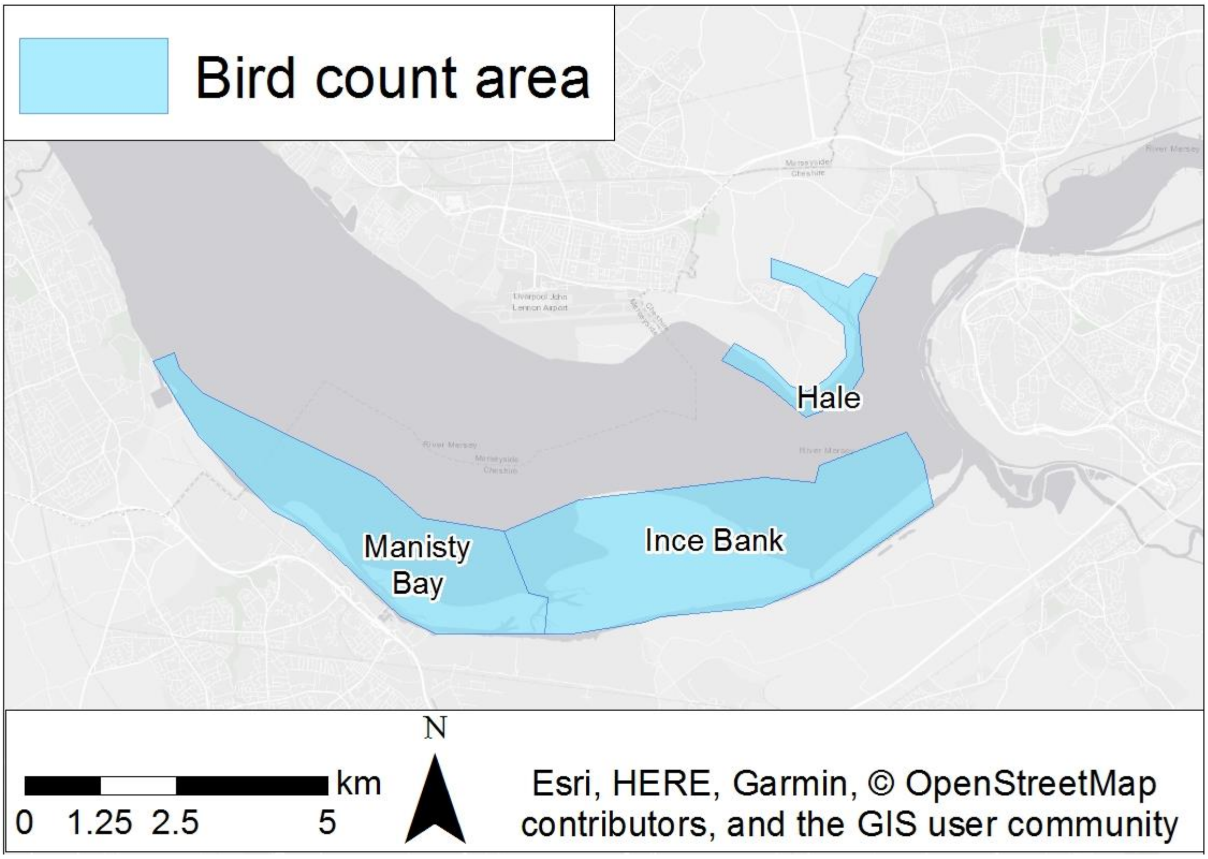

Figure 6. Location of each count sector in the Mersey Estuary SPA (Image from Still et al., 2015).

Bird roosting areas maps:

Paper maps of high tide roosting and feeding areas for the three species targeted by this project were produced in 2000 to inform the designation of the Mersey Estuary SPA. The maps did not have associated accuracy levels and were based on WeBS counters and Natural England staff observations.

5. Methods

Monthly bird distribution data from the British Trust for Ornithology (BTO) were available for the Mersey estuary, but their resolution was too coarse to correlate bird distribution and habitat characteristics. BTO counters aggregate recorded bird numbers by sectors, and the main saltmarsh areas on the estuary were covered by only three BTO sectors (Manisty Bay, Ince Bank and Hale; https://app.bto.org/websonline/public/index.jsp) and are published as total abundances for the whole Mersey Estuary. The lack of suitable bird abundance data meant it was not possible to produce an empirical habitat suitability model, so a model was constructed based on expert knowledge (Store and Jokimäki, 2003). Developing a habitat suitability model for the three target species generally involves several stages. In this project, the steps taken to produce the habitat suitability models are described in a subsection below:

1) Determine feasible area, i.e. the total available saltmarsh area;
2) Determine which factors affect habitat suitability for the target species and their relative importance;
3) Produce the data needed for the model;
4) Produce single-factor suitability maps;
5) Standardise and combine single-factor suitability maps into a weighted suitability map;
6) Quantify model uncertainty.

Subsection 1 describes the methods used to address the first objective of this project, i.e. to determine whether saltmarsh area changed during the study period. Subsections 2-4 illustrate how objectives 2-4 were addressed. Relevant factors to quantify habitat suitability with regards to food availability, habitat characteristics and disturbance were selected and mapped for all three target species in 2002 and 2012, making it possible to compare species-specific habitat suitability for all factors across time. Subsection 5 describes how objective 5 was addressed, as combining all single-factor suitability maps into overall habitat suitability maps made it possible to examine how habitat suitability changed for each species over the study period, and how it varied spatially across the site. Finally, subsection 6 does not relate specifically to a project objective, but it describes how model uncertainty was estimated and thus underpins all thesis objectives.

5.1 Determine feasible area (i.e. saltmarsh extent)

The method chosen to determine saltmarsh extent was the Environment Agency's standard methodology based on analyst's interpretation of aerial imagery combined with elevation data (Baylis et al., 2011). This method was chosen to make the data comparable to datasets produced by the Environment Agency in other sites and years and to ensure areas of pioneer saltmarsh were identified as accurately as possible. In fact, automatic saltmarsh extent methodologies do not normally identify pioneer saltmarsh accurately (Goodwin et al., 2018)

LiDAR data analysis

Data for LiDAR surveys in March 2002 and January 2013 were downloaded from the Environment Agency survey data store (http://environment.data.gov.uk/ds/survey/#/survey) for the whole Mersey estuary as Digital Terrain Model and Digital Surface Model ASCII tiles. The ASCII files were then converted into raster files using ArcGIS 10.2 and added to four separate mosaic datasets, two (DTM and DSM) per year. The datasets were then clipped to the Mersey Estuary SSSI area, and the 2013 datasets were resampled to 2 metres resolution using bilinear interpolation to make it comparable with the 2002 datasets. After visual inspection of the databases, it was clear that the DTM for both years had large gaps, whereas the DSM had a complete cover of the saltmarsh areas. The difference between the two datasets was calculated as DSM – DTM, and it was clear that where both models were available over 99% of the difference between datasets was < 30 cm, which is less than the sum of the 15 cm vertical accuracy for each dataset (Environment Agency, 2016). For this reason, the DSM datasets were used to extract saltmarsh extent for 2002 and 2013.

Three contour lines were extracted from each dataset. The first was the Mean High Water Neap (MHWN) tides height, which is the lower limit of saltmarsh. This was extracted from tide tables for the area (Admiralty Tide Tables, 2012) and its value was 2.90 m ODN (Ordnance Datum Newlyn). The second set of contour lines was the value of Mean Low Water Springs (MLWS), which are the lower limit of mudflats. Mudflats are important feeding areas for many bird species and those adjacent to saltmarsh represent areas not subject to erosion. The MLWS height was extracted from tide tables for the area (Admiralty Tide Tables, 2012) and its value was -3.83 m ODN. The resulting lines were very fragmented, so the mudflat extent could not be extracted using this method.

The third contour lines extracted were the upper limit of creeks, which are useful to examine changes in the creeks network. This value is highly site-specific and it was determined by visual inspection of the LiDAR datasets. For the study site, the chosen value was 4.2 m ODN. There was no need to produce contours for the higher saltmarsh limit as on the Mersey the landward saltmarsh limit is determined by man-made structures such as flood defences and the Manchester Ship Canal, which have not changed for over 50 years.

Aerial photography image analysis

LiDAR contour lines and manually digitised landward saltmarsh limit lines were converted to polygons (2 metres tolerance) and used as a base for saltmarsh extent polygons for 2002 and 2012. The polygons were then manually edited at a scale of 1:1000 to reflect the effective saltmarsh extent that could be seen from aerial photography for both years. Pans and mudflats in the study area were also manually captured, as in most cases the contours from the LiDAR data did not include them.

As none of the datasets had associated accuracy metadata, error in georeferencing was measured for all dates comparing fixed point in Ordnance Survey maps with their position in the aerial photography dataset. The horizontal Root Mean Square Error (RMSE) of 20 points per year was then calculated for latitude and longitude as:

$$RMSE_x = sqrt[\sum(x_{data,\,i} - x_{check,\,i})^2/n]$$
$$RMSE_y = sqrt[\sum(y_{data,\,i} - y_{check,\,i})^2/n]$$

where:

$x_{data, i}$, $y_{data, i}$ are the coordinates of the i^{th} check point in the dataset;

$x_{check, i}$, $y_{check, i}$ are the coordinates of the i^{th} check point in the Ordnance Survey map;

n is the number of check points tested;

i is an integer ranging from 1 to n.

Overall horizontal RMSE was calculated as:

$RMSE = sqrt(RMSE_x^2 + RMSE_y^2)$.

The resulting RMSE was used to produce buffers around the extent polygons for 2002 and 2013. The area of the buffer was then used to calculate confidence intervals for the saltmarsh extent polygons.

5.2 Selection of suitability factors and their relative weight

Following a review of scientific literature, a total of ten factors were selected to form the habitat suitability index. The selected factors were:

1) **Presence of *Salicornia*:** the genus *Salicornia* dominates pioneer saltmarsh areas in the United Kingdom (Hambidge and Phelan, 2014). Their seeds are an important source of food for all three target species (Kirby et al., 2000), with pintail and teal eating them preferentially to other species (Ferns, 1992).
2) **Presence of *Atriplex/Puccinellia*:** *Atriplex portulacoides* and *Puccinellia maritima* are dominant species in the mid-low area of British saltmarshes (Adnitt et al., 2007). Teal show a strong preference for *Atriplex* seeds and wigeon prefers eating *Puccinellia* rather than other grasses, and pintail feeds on *Atriplex* seeds as well (Ferns, 1992; Kirby et al., 2000; Owen, 1973).
3) **Presence of *Hydrobia*:** The gastropod *Hydrobia ulvae* is common in the estuarine mudflats of the study area (Scott, 2002) and is a source of food for all target species, although not as important as plant seeds and leaves (Kirby et al., 2000).
4) **Presence of open water:** all three target species select areas near open water to feed and roost (Tang et al., 2016). Pintail and teal need areas with shallow water (<25 cm) for feeding (Kirby et al., 2000) and teal often roost in or near shallow ponds and pans (Hsu et al., 2014).
5) **Sward height:** all species prefer short swards in order to be able to spot nearby predators. Wigeon prefer very short sward (<5 cm) in their feeding areas, while teal and pintail prefer vegetation to be shorter than 20 cm (Kirby et al., 2000).
6) **Slope:** All three target species prefer open flat areas where they can spot predators from a distance (Kirby et al., 2000). In addition, teal prefer areas with low slope for feeding and roosting (Genard & Lescourret, 1992; Hsu et al., 2014).

7) **Grazing intensity:** intermediate grazing levels have been shown to increase bird abundances in saltmarshes because of increased plant diversity. However, excessive grazing levels can negatively affect waterfowl by creating bare soil patches following excessive trampling (Davidson et al., 2017).
8) **Wildfowling intensity:** wildfowling affects all three target species directly through killing and indirectly through disturbance, unless shootings are several weeks apart (Fox & Madsen, 1997; Nichols, 1991). Wigeon and teal will avoid an area completely if wildfowlers operate there (Madsen, 1994; Bregnballe et al., 2004), while pintail may switch to nocturnal feeding during the hunting season (Casazza et al., 2012).
9) **Presence of Canada goose:** Canada goose (*Brenta canadensis*) has been shown to displace other aquatic birds (Giles, 1992) and compete with wigeon for grazing (Hughes & Watson, 1986).
10) **Recreational disturbance intensity:** recreational disturbance, defined as the collective impact of walkers, dog walkers and bird/wildlife watchers, is considered one of the main source of human disturbance to birds on saltmarshes (Liley et al., 2017).

Species-specific matrices to evaluate the relative importance of each factor to other factors were produced based on evidence from scientific literature. The ten habitat suitability factors were grouped into three criteria (food availability, habitat characteristics and disturbance) to produce a hierarchical habitat suitability model (Figure 7). Criteria and sub-criteria weights were produced using Expert Choice, a software that uses the Analytic Hierarchy Process (AHP; Saaty, 1977) to produce model weights based on pairwise comparisons between habitat suitability factors.

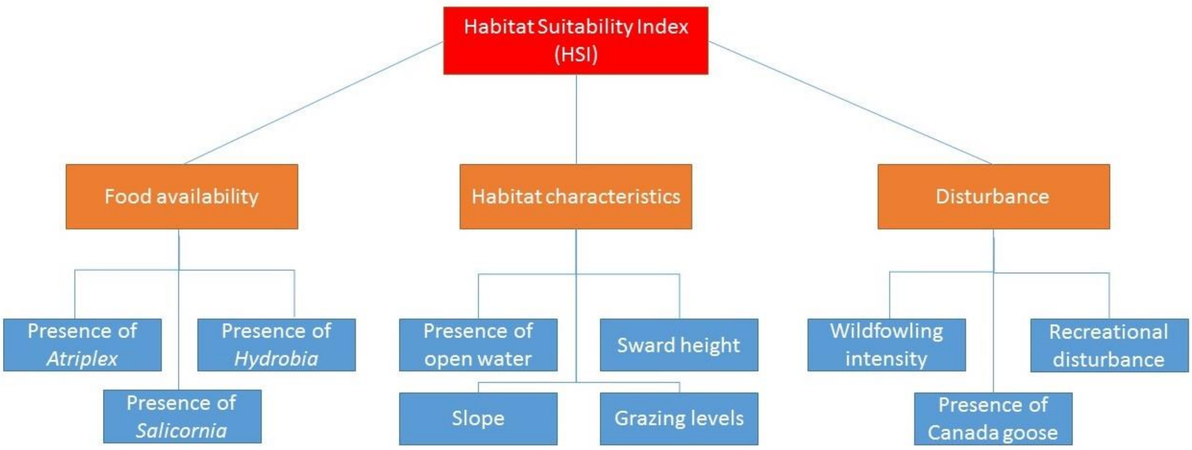

Figure 7. Structure of habitat suitability model for each of the target species, with sub-criteria (blue) and criteria (orange) forming an overall habitat suitability index (HSI, red).

AHP is a structured technique to compare and select different alternatives and criteria based on multiple attributes. AHP uses a tree-like decision model, where each category can be composed of several sub-categories, and every hierarchical level involves different types of criteria. The method determines criteria and sub-criteria weights between 0 and 1, with the values for each set of criteria summing up to 1. These weights are determined by comparing the importance of a factor to other factors through pairwise comparisons. Reducing complex decisions to a series of pairwise comparisons means it is possible to find the "best" solution and provide a clear rationale for the decision (Saaty, 1977). The criteria and sub-criteria weights thus produced were applied to the GIS model layers to produce an overall habitat suitability map.

5.3 Production of model data

Food availability – presence of Salicornia *and* Atriplex/Puccinellia

In order to determine presence of *Salicornia* and *Atriplex/Puccinellia*, saltmarsh zonation maps had to be produced first. The method selected was the Environment Agency's semi-automated method for determining saltmarsh zonation. After a preliminary selection of vegetated saltmarsh areas, a grid was superimposed to the aerial imagery in the selected area and each grid point was assigned to a saltmarsh zone. This method was chosen to make the data comparable to datasets produced by the Environment Agency in other sites and years and to ensure areas of pioneer saltmarsh were identified as accurately as possible. Predictive models can be used successfully to determine saltmarsh zonation, however pioneer zone points are often classified incorrectly (McGruer, 2017). On the other hand, the Environment Agency methodology consistently classified approximately 58% of pioneer data points in two areas of the Humber Estuary (Hambridge & Phelan, 2014).

For 2002 and 2012, saltmarsh zonation was determined by examining aerial photographs at a scale of 1:1000 superimposed upon a 10m x 10m grid and assigning a category to each point based on the area's appearance and data from the 2002 and 2016 surveys. The point layers were then manually digitised and converted to polygons. There are three years of difference between the latest survey (2016) and the most recent aerial photographs (2012), but this is not enough for substantial changes in saltmarsh zonation (Boorman, 2003). The only changes in such a short period of time would be due to erosion, but those changes would be evident from the survey data. For 2012, polygons were assigned to saltmarsh zones, whereas for 2002 polygons were assigned to saltmarsh zones and NVC communities (Table 3) where survey data were available.

Table 3. Environment Agency classification of saltmarsh zones, with principal and associated plant species and corresponding NVC communities (Hambidge and Phelan, 2014).

Zones	**Principal species**	**Other species**	**NVC**
Pioneer	*Salicornia*	*Suaeda, Puccinellia, Atriplex, Limonium, Aster, Arthrocnemum*	SM7, SM8, SM9
Spartina	*Spartina*	*Algae, Puccinellia*	SM4, SM5, SM6
Mid-low marsh			
- low	*Puccinellia*	*Salicornia, Suaeda, Aster, Spartina*	SM10, SM11, SM12, SM13
- mid mid	*Atriplex*	*Puccinellia, Juncus maritimus, Suaeda, Triglochin, Plantago, Glaux*	SM14, SM15
- upper mid	*Festuca*	*Plantago, Triglochin, Juncus gerardii, Agrostis, Glaux, Armeria, Limonium, Artemisia, Atriplex, Puccinellia, Juncus maritimus, Suaeda vera, Frankenia, Spergularia, Salicornia*	SM16, SM17, SM21, SM22, SM23
High marsh	*Elytrigia,* *Agrostis* without *Puccinellia,* *Festuca* without *Puccinellia,* *Juncus maritimus* without *Puccinellia,* *Bolboshoenus*	*Juncus geradii, Triglochin, Plantago, Oenanthe, Trifolium, Glaux, Blysmus, Inula, Atriplex, Suaeda vera, Elymus repens, Potentilla*, very small amounts of *Puccinellia*	SM18, SM19, SM20, SM24, SM25, SM26, SM27, SM28, S21
Phragmites	*Phragmites*	*Zostera noltii* at low levels; *Atriplex prostrata*; *Puccinellia* (V) in S4dii	S4d

Salicornia is the dominant macrophyte genus in the pioneer zone of a saltmarsh (Table 3), so pioneer polygons in the zonation layers for 2002 and 2012 were used to approximate *Salicornia* distribution. *Atriplex* and *Puccinellia* can be dominant in a saltmarsh in the mid-low marsh zone up to Mean High Water (Adnitt et al., 2007), which in the Mersey estuary has a value of 5.04 m ODN (Admiralty Tide Tables, 2012). The area of saltmarsh below 5.04 m ODN in 2002 and 2012 was determined using LiDAR data. The intersection of these layers and those showing mid-low marsh areas for the relevant years represented the total *Atriplex* and *Puccinellia* potential distribution in the study area for 2002 and 2012.

Food availability – presence of Hydrobia

Mudflat locations for 2002 and 2012 were manually digitised from aerial photographs and shapefiles were produced for each year. Macroinvertebrate abundances from sediment cores sampled in 2001 and 2011 were examined for presence of *Hydrobia ulvae* snails, which are an important food source for pintail and teal (Kirby et al., 2000). For each year, *H. ulvae* presence/absence data for each mudflat were added to the corresponding mudflat polygons.

Habitat characteristics – presence of open water

All three target species require vicinity to shallow open water, whether for feeding (teal and pintail) or roosting (wigeon). The ideal water depth they need is < 25 cm during low tide (Kirby et al., 2000). At the study site, all three species are known to congregate around large creeks at high tides (Rehfisch et al., 1991). Therefore, areas where creeks were wider than 20 m were manually digitised and shapefiles for 2002 and 2012 representing suitable open water areas were produced.

Habitat characteristics – sward height

The 2002 polygons from the NVC survey of the estuary (Skelcher, 2003) also had sward height assigned to them. Vegetation height was supplied as 3 categories: <5 cm, 5-20 cm and > 20 cm. The 2016 vegetation survey also provided sward height in cm for the surveyed quadrats rather than for polygons like the 2002 survey. The 2016 sward heights were converted from centimetres to height ranges to compare them with 2002 data. Sward height shapefiles for 2002 and 2012 were produced manually examining aerial photographs and combining them with 2002 and 2016 survey data and reports, as well as conversations with Natural England employees responsible for the site.

Habitat characteristics – slope

Slope was calculated in degrees from the 2002 and 2013 LiDAR saltmarsh rasters using the slope tool in the Spatial Analyst extension of ArcGIS 10. Both rasters had a resolution of 2 m. The slope tool calculates slope of a cell based on the nine cells surrounding it, and the formula for slope measured in degrees is:

$$slope\_degrees = \mathrm{ATAN}\left(\sqrt{([dz/dx]^2 + [dz/dy]^2)} \right) * 57.29578$$

At the edge of a raster, not all nine surrounding cells will be present. In this case, the missing cells were assigned a z value equal to the centre cell, which resulted in a reduction of the slope value (http://desktop.arcgis.com/en/arcmap/10.3/tools/spatial-analyst-toolbox/how-slope-works.htm). The edge cells were kept in the resulting slope raster because at 2 m scale, the error introduced by these cells at the site scale was very small.

Habitat characteristics – grazing levels

Grazing levels were quantified using maximum livestock units per hectare (LU/Ha) specified in the agri-environment agreement for the area. This information was combined with observation in the 2002 and 2016 reports to produce shapefiles with grazing levels for different areas of the saltmarsh. Grazing categories were:

- *Low*: saltmarsh is not grazed or grazing rates are very low, sward height is usually > 20 cm and saltmarsh may be rank.
- *Medium*: there is some evidence of grazing, vegetation forms a mosaic of patches with different sward heights and saltmarsh is not rank.
- *High*: there is evidence of intense grazing, sward height is mostly < 5 cm and bare ground patches from livestock trampling may be present.

Disturbance – wildfowling intensity

Available bag returns from 2000 to 2015 for wildfowlers' club that hunt on the Mersey estuary were collated and added to a polygon feature class, which was then analysed to detect changes in wildfowlers' visits and number of killed pintail, teal and wigeon. Bag returns data were patchy, meaning that every year in the period 2000-2015 at least one wildfowling club did not submit any data. Consequently, it was not possible to derive meaningful statistics for number of wildfowler visits and number of birds killed.

The dataset was therefore used to determine which sections of the saltmarsh wildfowling clubs used in 2002 and 2012. In addition, over the last five years clay pigeon shooting has been regularly observed just outside Stanlow Bank (Alice Kimpton, personal communication). This information was used to produce a shapefile with three categories, "wildfowling", "clay pigeon shooting" and "no shooting disturbance".

Disturbance – presence of Canada goose

Areas of the estuary where Canada geese was present in 2002 were digitised into shapefiles, while data from the 2016 survey were already provided as shapefiles.

Disturbance – recreational disturbance

Results from a questionnaire on perceived change in recreational disturbance on the estuary over time (Still et al., 2015) and conversations with landowners were combined to produce a feature class associating each part of the saltmarsh in 2002 and 2012 with a specific level of recreational disturbance (low, medium, high).

5.4 Single-factor suitability maps production

All data layers previously produced were converted to rasters with resolution of 2 metres. Given that suitability levels for most factors involved expert judgment rather than analysis of empirical data, categorical suitability values were considered more appropriate than suitability functions (Hirzel et al., 2006). The single-factor datasets were therefore standardised to values between 0 and 1 to represent three different suitability levels:

- High suitability: 1
- Medium suitability: 0.6
- Low suitability: 0.3

For two food availability criteria representing food sources normally exploited at low tide (i.e presence of *Salicornia* and presence of *Hydrobia*), highly suitable area could be relatively far from high tide roosting and feeding areas, as long as they were situated within a distance an individual bird could be expected to travel daily (Johnson et al., 2014). Therefore, two buffers were added to the distribution of the food sources or habitat of interest. The two buffers were different for each species and corresponded to the mean foraging flight distance (FFD) and FFD/2 (Table 4). Flight foraging distance is the distance a bird species will fly from its roosting area in order to feed. FFD values for overwintering pintail, teal and wigeon were taken from Johnson et al. (2014). When more than one value was available for overwintering birds in Europe, an average distance was calculated.

Table 4. Mean foraging flight distance (FFD) and mean FFD/2 expressed in kilometres for overwintering pintail, teal and wigeon. Data from Johnson et al. (2014).

Species	Mean FFD	Mean FFD/2
Pintail	1.30	0.65
Teal	2.65	1.33
Wigeon	3.13	1.62

A summary of suitability categories for presence of *Salicornia* and presence of *Atriplex/Puccinellia* are shown in Table 5.

Table 5. Suitability categories for presence of *Salicornia*, presence of *Atriplex*, presence of *Hydrobia* and presence of open water.

Suitability	Distance from attribute	Standardised value
High	0 - FFD/2	1
Medium	FFD/2 - FFD	0.6
Low	> FFD	0.3

The criteria representing food resources most valuable during high tide (i.e presence of *Atriplex/Puccinellia* and presence of open water) would need to be sensibly closer than low tide feeding areas to affect the suitability of high tide roosting or feeding areas. For these factors, two buffers were added to the highly suitable areas: 200m (value assigned: 1, highly suitable) and 500m (0.6, medium suitability). Areas further than 500m were assigned a value of 0.3 (low suitability) for the relevant criteria.

Sward height categories were assigned different suitability levels depending on the species. Wigeon prefers a very short sward, while a medium sward height is more suitable for the other two species (Kirby et al., 2000). Suitability categories for the three species are summarised in Table 6.

Table 6. Suitability categories for pintail, teal and wigeon based on sward height categories.

Species	High suitability (1)	Medium suitability (0.6)	Low suitability (0.3)
Pintail	5-20 cm	< 5 cm	> 20 cm
Teal	5-20 cm	< 5 cm	> 20 cm
Wigeon	< 5 cm	5-20 cm	> 20 cm

Slope was deemed highly suitable (1) if its value in a cell was below 0.80 degrees (Hsu et al., 2014). Cells with slope between 0.80 and 1.60 degrees were classified as medium suitability (0.6) and cells with slope larger than 1.60 degrees were classified as low suitability (0.3).

For the grazing intensity layer, cells with high grazing levels were converted to the low suitability category (0.3) as heavily grazed areas would be poached, with very little vegetation left and thus unsuitable for birds feeding or roosting. Medium grazing levels had a high suitability value (1), while low grazing levels were converted to the medium suitability value (0.6).

Areas of the study site where wildfowling took place had a low suitability value (0.3) assigned to them, while cells near the clay shooting area had a medium suitability value (0.6) assigned. The different values were chosen because wildfowlers entered and shot in the saltmarsh, aiming at birds, while clay pigeon shooting took place outside of the saltmarsh and birds were not directly targeted. Areas where no shooting took place were highly suitable as bird habitat and were assigned a value of 1.

Cells where Canada goose presence had been recorded had a low suitability value (0.3), while areas without Canada goose were highly suitable for that criterion and therefore were converted to a value of 1. As for recreational disturbance, high levels meant the area suitability was low (0.3), while medium recreational disturbance was assigned a value of 0.6 (medium suitability) and low recreational disturbance areas were assigned a value of 1 (high suitability).

5.5 Weighed suitability maps

All single factor suitability maps for each species were combined using the weighing factors obtained with Expert Choice. This was done by multiplying each single factor suitability map by its weight coefficient. The resulting factor scores were summed to produce an overall habitat suitability index for each 2 m x 2 m cell. A total of six maps were obtained, one per target species and study year (2002 and 2012).

5.6 Quantification of model uncertainty

Habitat suitability models are prone to several error categories, which can be divided into five main types: measurement error, systematic error (e.g. bias in the measuring equipment), natural variability, subjective judgement and model uncertainty (Regan et al., 2002). Habitat suitability models based on expert judgement are particularly affected by subjective judgement, such as relative importance of factors and model uncertainty (Ray and Burgman, 2006). The subjective judgment element in deciding the relative importance of factors was minimised in this study using the AHP process to assign criteria weights (see section 5.2). Model uncertainty can be defined as the set of decisions taken by the modeller to translate qualitative expert judgment into a quantitative suitability measure with a defined spatial representation. Model uncertainty can often affect habitat suitability models based on expert judgment much more than other error sources (Elith and Burgman, 2002). Model uncertainty magnitude can be assessed by generating "bounding maps" representing the most extreme plausible scenarios for each factor (Ray and Burgman, 2006). For this project, bounding maps were produced for all factors contributing more than 10% to the HSI value. These factors were presence of *Salicornia*, wildfowling intensity and recreational disturbance for pintail, presence of open water, sward height, slope and wildfowling intensity for teal, presence of open water, sward height, wildfowling intensity and presence of Canada goose for wigeon. For more details, see section 6.

All possible combination of factors and bounding maps for the 2002 models were compared against the main high tide roosting and feeding areas for pintail, teal and wigeon in 2000 which had been mapped by English Nature prior to the Mersey Estuary SPA designation. A model that assigned equal weight to all factors was also examined to determine whether assigning weights to factors based on expert opinion had improved the model compared to a simple weighted sum of all factors, and therefore evaluate the effect of subjective judgement on model performance (Ray and Burgman, 2006). A total of 28 models were tested for pintail (bounding maps were used for three criteria; Figure 8) and 82 for teal and wigeon (bounding maps were used for four criteria).

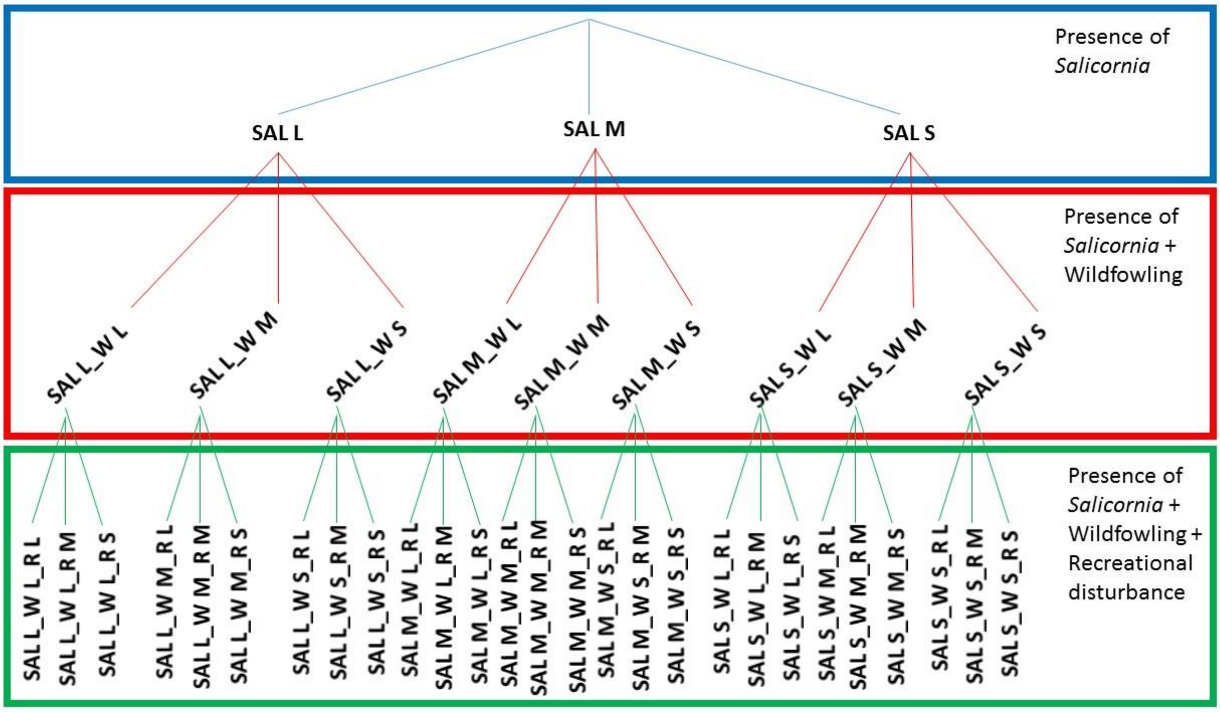

Figure 8. Diagram of criteria combinations tested to evaluate model uncertainty for pintail. Bounding maps were used for the three criteria individually contributing to more than 10% of the HSI value for this species: presence of *Salicornia* (SAL), wildfowling intensity (W) and recreational disturbance (R). Each criterion had three versions: the version used in the model (M), the loose suitability bounding map (L) and the strict suitability bounding map (S). The 28 models representing all possible version combinations for the three criteria (green box) were used to estimate model uncertainty.

Given the uncertainties involved, using a full continuous habitat suitability scale ranging from 0 to 1 would have been likely to artificially inflate the level of detail (Hirzel et al., 2006). Therefore, suitability index values were converted into two categories, “suitable” and “unsuitable”. The best threshold between suitable and unsuitable areas for every one of the factor combinations described above was determined for 2002, as a dataset locating the main roosting areas for all three target species was available for 2000 (Natural England, 2000). The best threshold between suitable and unsuitable index values was defined as the HSI value corresponding to its maximum true skill statistic (TSS; Allouche et al., 2006). TSS is a model evaluation index calculated using the following formula:

$a/(a+c) + d/(b+d) - 1$

where:

a = number of suitable area pixels correctly classified

a = number of suitable area pixels incorrectly classified

c = number of unsuitable area pixels correctly classified

d = number of unsuitable area pixels incorrectly classified

TSS is a measure of model performance that compensates for extreme prevalence values when applied to model training (Mouton et al., 2010) and was therefore considered appropriate for use in this project given the areas where birds have been known to roost or feed at high tides is only a small proportion of the total saltmarsh area (Rehfisch et al., 1991).

After a threshold was selected for each model combination, all 2002 model performances were compared to determine whether the chosen model had been significantly outperformed by the equal weight model or by any of the models including one or more bounding maps. A 100 m buffer around the bird distribution polygon edges was excluded from this process because the bird distribution datasets had been digitised from paper maps with unknown accuracy. Thus, the 100m area around the digitised polygons were not considered in the model performance assessment.

The threshold values between suitable and unsuitable HSI values determined for 2002 for all models were then applied to the corresponding 2012 models. In addition to the HSI maps for the three species in 2002 and 2012, the model testing and evaluation allowed the production of suitability maps based on species-specific thresholds and standard deviation maps summarising the spatial patterns of model uncertainty.

5.7 Statistical data analyses

All statistical analyses were performed using R (R Core Team, 2017). Changes in overall suitable habitat area and in standard deviation across scenarios by species and year were tested using aligned rank transformation ANOVA, a non-parametric method for analysis of variance that can be used when data do not have normal distribution or homogeneous variances (Wobbrock et al., 2011). The main analyses and following post-hoc comparisons were performed using the R packages ARTools and emmeans (Wobbrock et al., 2018).

6. Results

Sections 1-5 report the results relevant to each of the thesis objectives, while section 6 reports the results of the model uncertainty estimation.

6.1 Saltmarsh extent

The contour lines extracted from LiDAR data for 2002 and 2012 at 2.90 m ODN (MHWN) represented potential saltmarsh area. Potential saltmarsh area on Stanlow Bank and Frodsham Score reduced between 2002 and 2012 due to erosion, while some accretion was evident on the western end of Stanlow Bank. However, the lower saltmarsh limit was not accurately captured by the 2.90 m contour, as vegetation was not present on the whole potential saltmarsh area. These areas had to be manually edited to accurately estimate saltmarsh extent. The LiDAR 4.2 m contours very accurately reflected the creek structure and the upper marsh limit on the eroding edge and could therefore be used as a base to map the extent of some parts of the marsh. Saltmarsh extent changed between 2002 and 2012 as areas of lower marsh, especially on Stanlow Bank, underwent significant erosion in that period. The creek system remained stable between 2002 and 2012, with no large shifts in channel position or any sign of human intervention.

The georeferencing accuracy for both years expressed as RMSE varied from 2.34 m in 2012 to 3.58 m in 2012 (Table 7), although the error is likely to be larger on the seaward limit of the saltmarsh, where the lack of reference points makes both georeferencing and accuracy checking more difficult. The estimated saltmarsh area on the Mersey estuary was 8.38 km^2 in 2002 and decreased to 6.81 km^2 in 2012 (Table 8). The estimated loss in saltmarsh area, mostly pioneer zone, was 1.57 km^2. Taking into account the 95% confidence intervals, saltmarsh loss between 2002 and 2012 could range between 1.06 and 2.08 km^2. Therefore, saltmarsh area decreased by 12-20% in the study period, significantly decreasing the space available to sustain bird populations.

Table 7. Root mean square error (RMSE) in meters for 2002 and 2012 for aerial photographs of the study site and number of check points used to calculate it. Aerial photographs were used with LiDAR data to produce the saltmarsh extent polygons.

Year	RMSE (m)	Number of check points
2002	3.58	20
2012	2.34	20

Table 8. Saltmarsh area estimate (km^2) for 2002 and 2012 and area estimates (km^2) at the upper and lower limit of the 95% confidence interval (CI).

Year	Area estimate (km^2)	Low 95% CI limit (km^2)	High 95% CI limit (km^2)
2002	8.38	8.09	8.68
2012	6.81	6.60	7.03

6.2 Change in food availability between 2002 and 2012

Highly suitable areas for presence of *Salicornia* decreased for all species between 2002 and 2012. The main reason of this decrease was the erosion of Frodsham Score. This meant the eastern part of the study site no longer had suitable areas for this criterion in 2012 (Figure 9). The overall erosion of pioneer zone during the study period caused a large decrease in *Salicornia* extent, negatively affecting habitat suitability for all species. Habitat suitability for pintail was particularly affected by *Salicornia* extent decrease, as *Salicornia* presence contributed 23.2% to the total HSI score, while it only contributed to 3.8 and 1.5% to the HSI score for teal and wigeon, respectively.

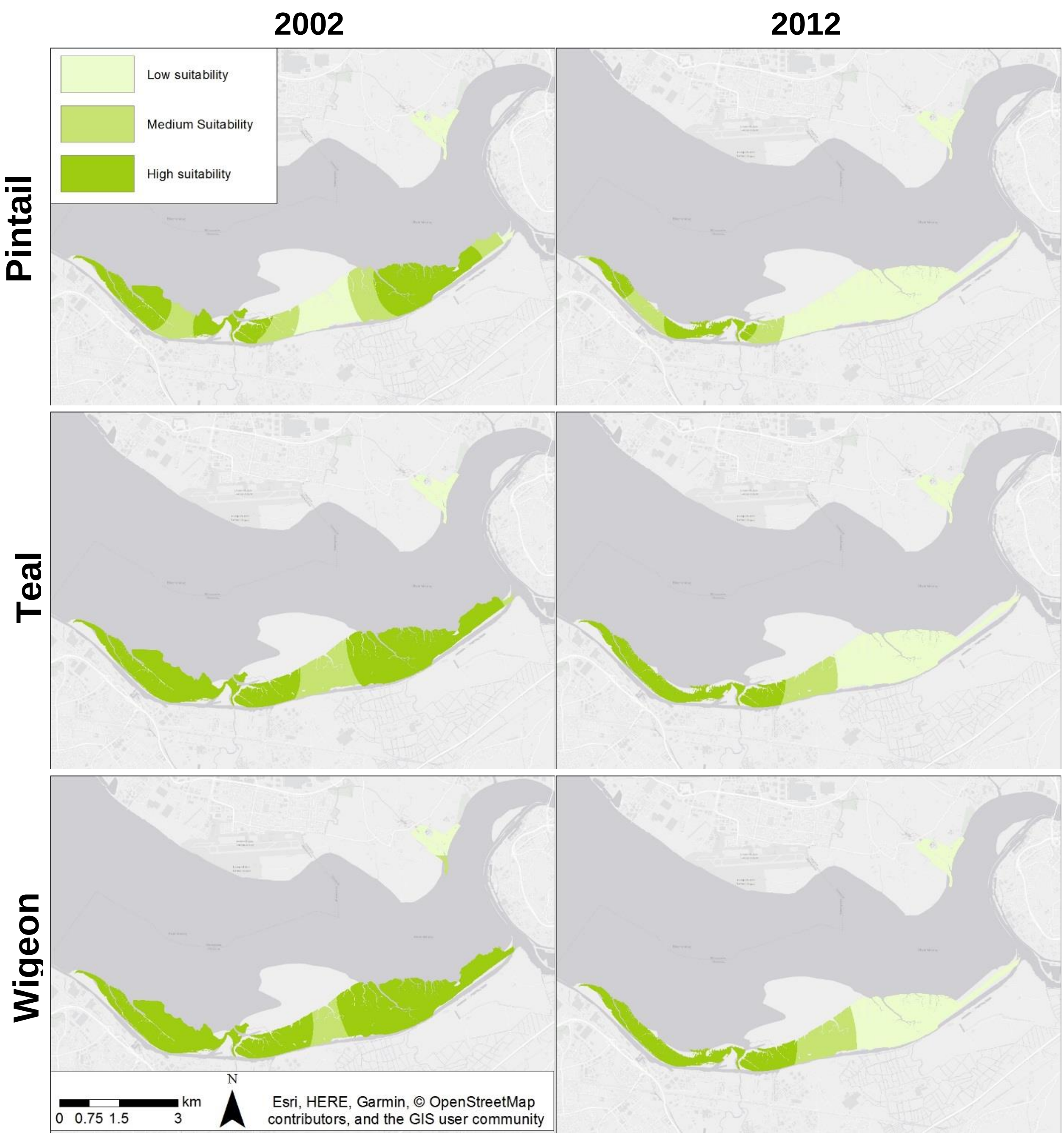

Figure 9. Suitability categories for presence of *Salicornia* for all species in 2002 and 2012. Highly suitable areas decreased for all species between 2002 and 2012, mostly because of the erosion of Frodsham Score.

On the other hand, *Atriplex* and *Puccinellia* were less affected by saltmarsh erosion and remained widespread in the study site. As a result, most of the study site was highly suitable for presence of *Atriplex* and *Puccinellia* both in 2002 and in 2012. This factor contributed to reduce changes in HSI values between 2002 and 2012. However, this factor had low importance for all species, as it contributed 2.6-3.8% to total HSI scores.

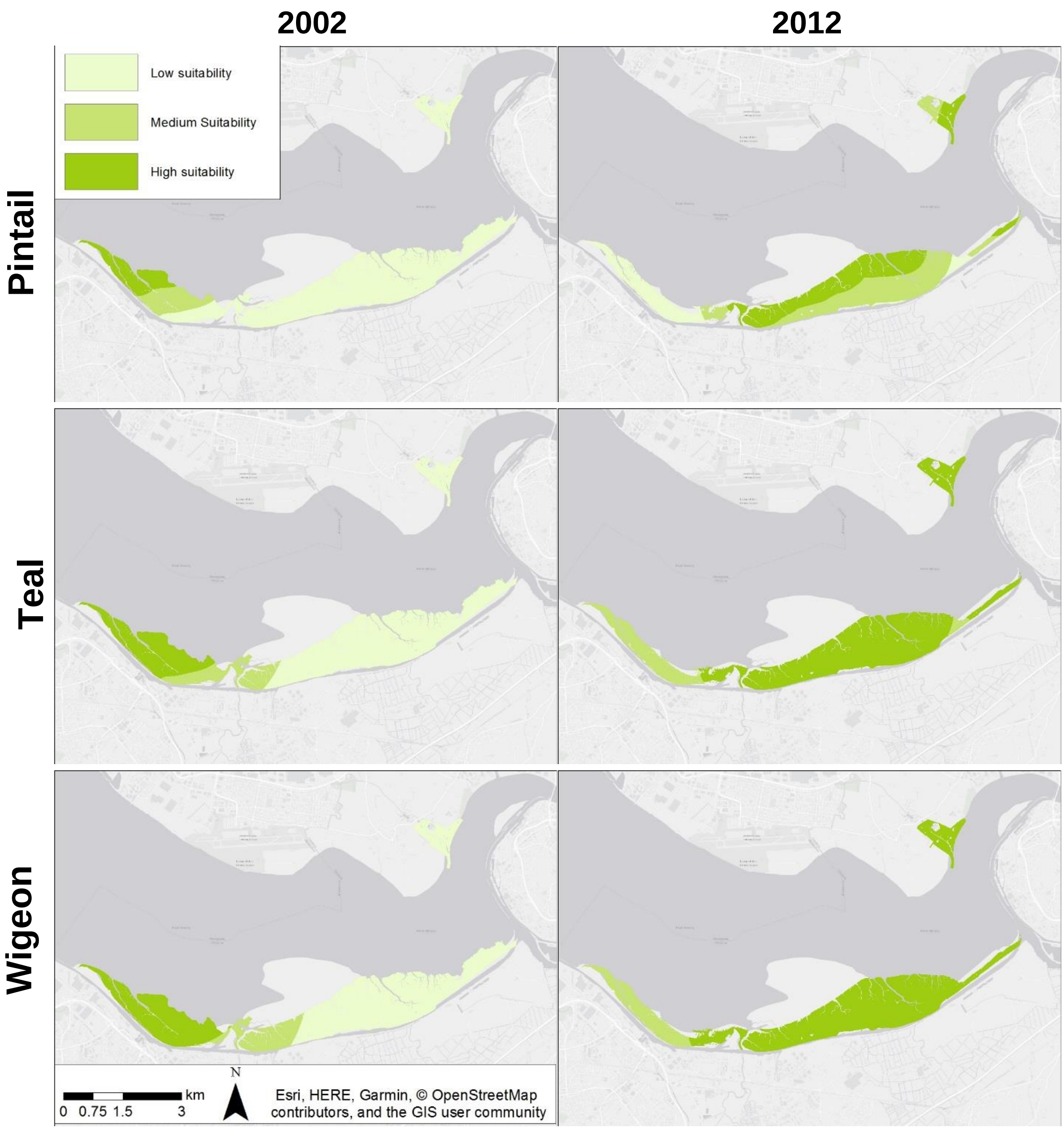

Figure 10. Suitability categories for presence of *Hydrobia* for all species in 2002 and 2012. The highly suitable area increased between 2002 and 2012 for all species because *Hydrobia* was recorded in mudflats close to a large area of saltmarsh.

The area highly suitable for presence of *Hydrobia* increased markedly between 2002 and 2012 for all species, especially for teal and wigeon (Figure 10). *Hydrobia* was recorded in the sandflats in the western part of the study site in 2002 and in the eastern part of the site in 2012, and that was reflected in the distribution of suitable areas in 2002 and 2012. The difference in suitable area between species was due to the longer foraging distances of teal and wigeon compared to pintail. The increase in highly suitable area for this factor, however, only had a small effect on total HSI scores, to which it contributed between 6.0% (pintail) and 0.4-0.8% (teal and wigeon). Overall, changes in food availability between 2002 and 2012 had a dramatic effect on HSI scores for pintail, which was strongly affected by the reduction in *Salicornia* extent. For the other two species, the cumulative effect of the three food availability criteria only contributed 8.4% (teal) and 5.4% (wigeon) to total HSI values.

6.3 Changes in habitat characteristics between 2002 and 2012

All main creeks in the saltmarsh remained in the same position between 2002 and 2012. Therefore, the change in suitable area for presence of open water was likely due exclusively to the reduction in saltmarsh area between 2002 and 2012. Lack of change for this criterion stabilised HSI scores between 2002 and 2012 for teal and wigeon, for which presence of open water contributed 34.6% and 22.3% of total HSI values, respectively. On the other hand, habitat suitability for pintail was not greatly affected by presence of open water, which contributed less than 6% to total HSI scores for this species.

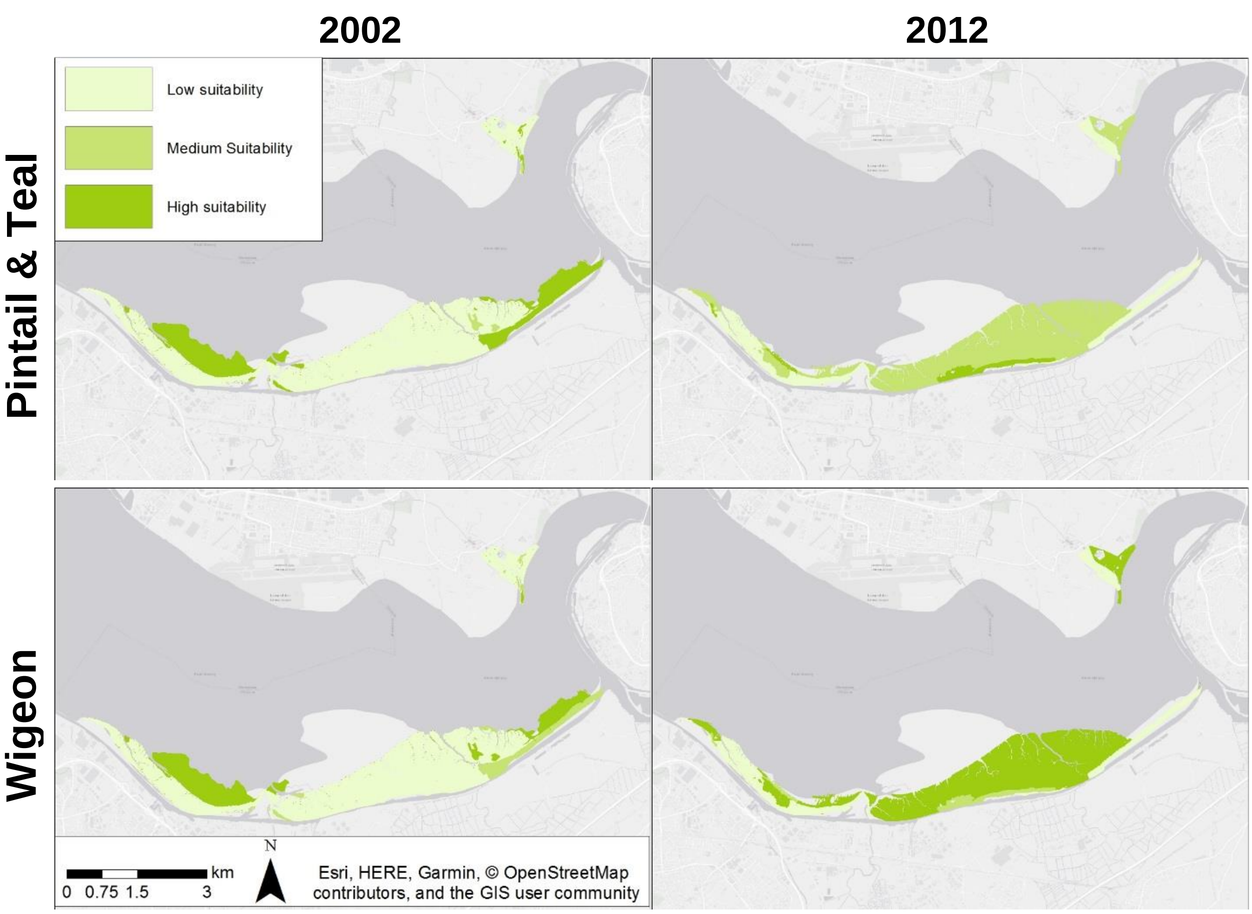

Figure 11. Suitability categories for sward height for all species in 2002 and 2012. Overall, suitability for this criterion improved between 2002 and 2012 for all species, but especially for wigeon. This was due to the shorter sward on Ince Bank in 2012, which is more suitable than the high sward (>20 cm) recorded there in 2002.

In 2002, most of the study area had low suitability for sward height for all species. In 2012, sward height had medium suitability in most of the study area for pintail and teal and high suitability for wigeon. The main change between 2002 and 2012 was in Ince Bank and Frodsham Score, where sward height in 2002 was mostly over 20 cm (Figure 11). This is the least suitable height for all species. In 2012, the dominant sward height in the same area was less than 5 cm, which is highly suitable for wigeon and of medium suitability for teal and pintail. Therefore, these changes improved HSI scores between 2002 and 2012 for wigeon more than for teal and pintail. However, sward height only contributed to less than 3% of the overall HSI values for pintail, so the improvement in HSI scores between 2002 and 2012 for this species was actually negligible. Sward height was more important (between 11 and 15%) for teal and wigeon, so higher suitability values for this criterion probably increased habitat suitability of large parts of the study area between 2002 and 2012. Slope in the study area remained very similar between 2002 and 2012. Therefore, the area reduction observed for all suitability categories between 2002 and 2012 were due to the reduction in saltmarsh area over time due to erosion. Slope only contributed less than 2% to overall HSI scores for pintail and wigeon, but approximately 15% for teal.

The study area had mostly medium suitability for grazing intensity in 2002, while in 2012 all three categories were similar in extent. This was due to an increase in overall grazing pressure, which caused Frodsham Score to change its suitability category from high to low between 2002 and 2012, as high density of cattle led to poaching (Figure 12). At the same time, Ince Bank was not grazed in 2002, which corresponded to a medium suitability category. This same area was subject to intermediate grazing levels in 2012, which made it highly suitable for all species. However, grazing levels only had a small weight, contributing less than 5% to the overall HSI score for all species.

2002 **2012**

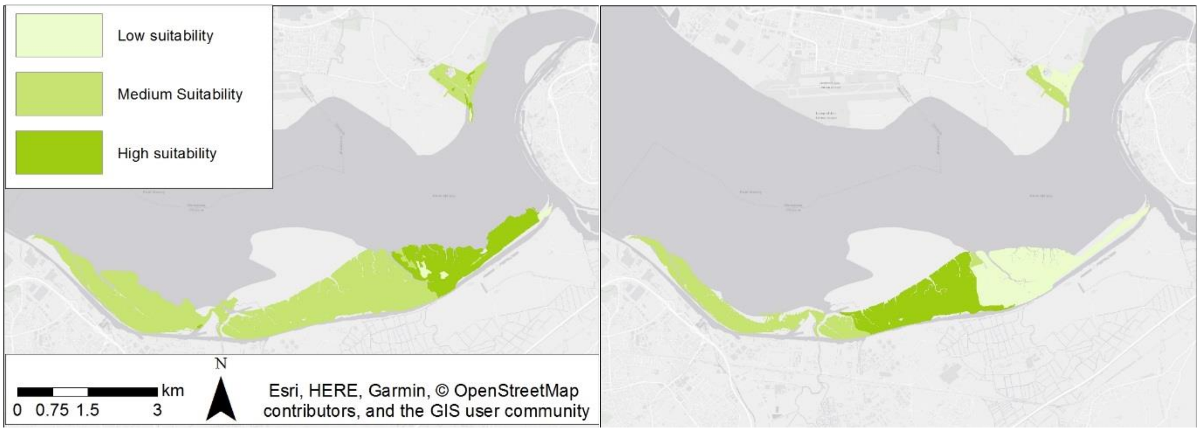

Figure 12. Suitability categories for grazing intensity for all species in 2002 and 2012. The study area had mostly medium suitability for grazing intensity in 2002, while in 2012 all three categories were similar in extent. This was due to an increase in overall grazing pressure, which caused Frodsham Score to change its suitability category from high to low, as high density of cattle led to poaching. At the same time, Ince Bank was not grazed in 2002 (medium suitability) and was subject to intermediate grazing levels in 2012 (high suitability).

Overall, habitat characteristics either remained stable or improved for all species between 2002 and 2012, with the exception of grazing levels. Habitat characteristics strongly influenced teal HSI scores (68.3% of total scores) and wigeon (38.9%), while they were less important for pintail (10.4%).

6.4 Changes in disturbance between 2002 and 2012

The main change in wildfowling intensity between 2002 and 2012 was the transformation of highly suitable areas into areas of medium suitability. This change happened on Stanlow Bank, where clay-pigeon shooting exposed the previously undisturbed area to a medium level of disturbance. The rest of the study site, where wildfowlers regularly hunt, remained of low suitability across the study period (Figure 13). Wildfowling intensity was the single most important factor in determining HSI scores for pintail and wigeon, for which this criterion contributed more than 35% of the total value. The negative effects of changes in wildfowling intensity between 2002 and 2012 had a lower influence on habitat suitability for teal, for which wildfowling intensity contributed about 15% of the total HSI score.

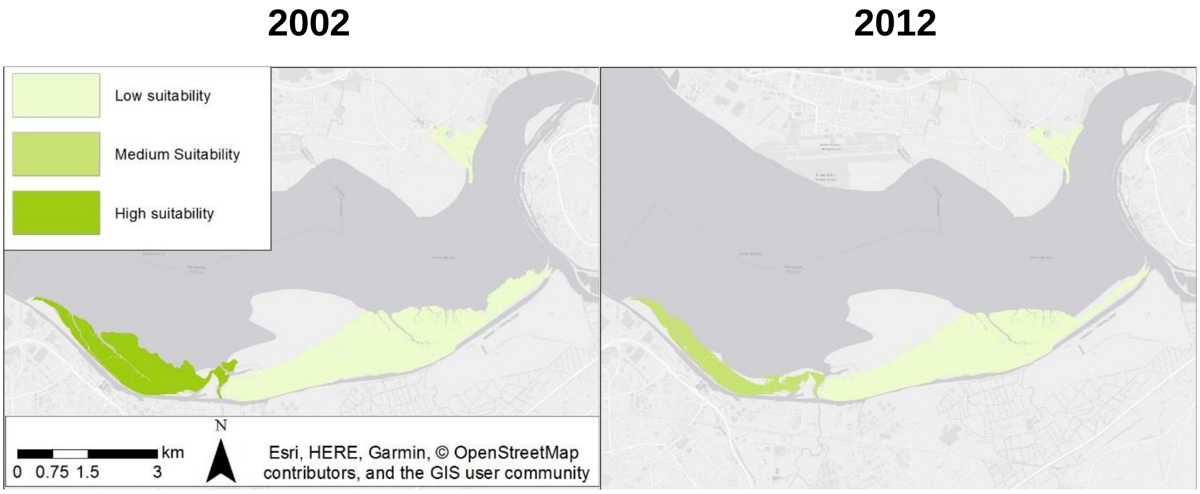

Figure 13. Suitability categories for wildfowling for all species in 2002 and 2012. On Stanlow Bank, clay-pigeon shooting transformed highly suitable areas into areas of medium suitability. The rest of the study site remained of low suitability across the study period.

The large expansion in Canada goose territory between 2002 and 2012 transformed approximately half of the study area from highly suitable for all species to low suitability for all species in 2012. Most of this change was caused by the colonisation of Frodsham Score by Canada goose (Figure 14). Presence of Canada goose, however, only had a strong influence on wigeon (14.4% of total HSI score), but not on pintail and teal (6.1 and 2.4% of total HSI score, respectively).

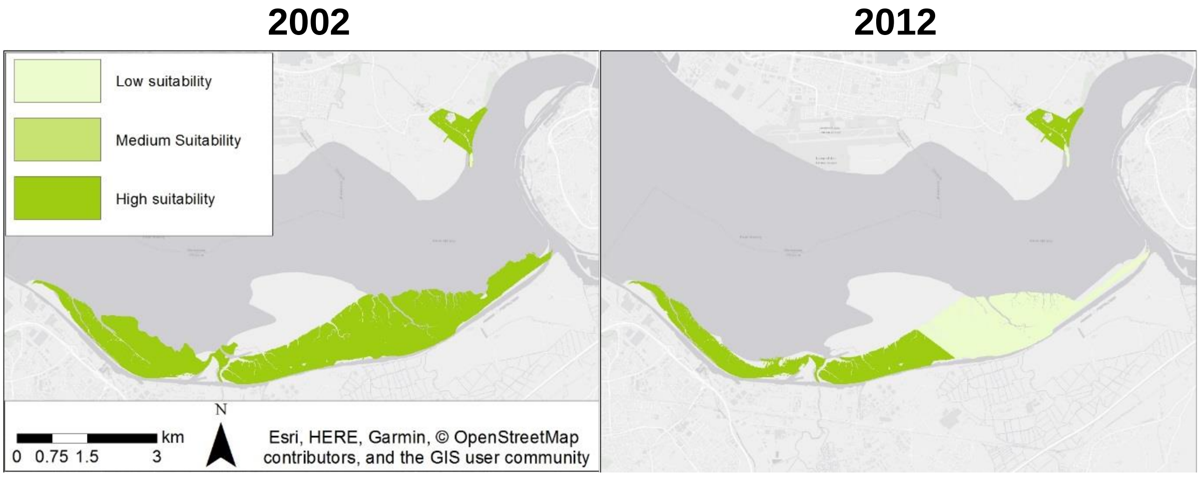

Figure 14. Suitability categories for presence of Canada goose for all species in 2002 and 2012. The colonisation of Frodsham Score by Canada goose between 2002 and 2012 transformed approximately half of the study area from highly suitable for all species to low suitability for all species in 2012.

Recreational disturbance levels did not change between 2002 and 2012. Areas on the southern bank, which are not accessible to the public, remained highly suitable for all species, while the accessible areas on the north bank had medium suitability levels both in 2002 and 2012. This criterion likely had a significant role in stabilising HSI scores for pintail between 2002 and 2012, as it contributed to approximately 15% of the total HSI values for this species. On the other hand, the effect of this factor on the teal and wigeon models was fairly small, with recreational disturbance only contributing less than 6% to the total HSI score for these two species. Overall, disturbance lowered HSI scores for all species between 2002 and 2012. Pintail and wigeon were particularly sensitive to changes in disturbance, as it contributed 57.9% and 55.7% to total HSI scores, respectively. Disturbance was less important, but still significant, for teal, contributing 23.3% to total HSI scores.

6.5 Changes and spatial patterns in overall habitat suitability

Relative importances of model criteria were calculated using Expert Choice. Global model weights (Table 9) can range from 0 to 1 and represent the percentage each criterion contributes to the overall HSI. The most significant factors contributing to HSI were presence of *Salicornia*, wildfowling intensity and recreational disturbance for pintail. For teal, the factors contributing more than 10% to the total HSI were presence of open water, sward height, slope and wildfowling intensity, while presence of open water, sward height, wildfowling intensity and presence of Canada goose were the most important for wigeon.

Table 9. Global weight on HSI for each model factor for pintail, teal and wigeon. Factors contributing over 10% to the HSI value are shown in orange cells.

Variable	Pintail	Teal	Wigeon
Presence of open water	0.059	0.346	0.223
Sward height	0.027	0.148	0.110
Slope	0.006	0.148	0.020
Grazing levels	0.012	0.041	0.036
Presence of *Atriplex/Puccinellia*	0.026	0.038	0.035
Presence of *Salicornia*	0.232	0.038	0.015
Presence of *Hydrobia*	0.060	0.008	0.004
Wildfowling intensity	0.369	0.149	0.355
Presence of Canada goose	0.061	0.024	0.144
Recreational disturbance	0.149	0.060	0.058

Total suitable habitat area significantly decreased for all species between 2002 and 2012, with no significant interaction between species and year. Total suitable area for pintail was 1.22 (± 0.01 S.E.) km^2 in 2002 and significantly decreased to 0 (± 0.004 S.E.) km^2. Suitable area was significantly higher for teal and wigeon in both years, but decreased for both species between 2002 and 2012 (Figure 15). The decrease was more marked for teal (3.35 ± 0.07 S.E. km^2 to 1.86 ± 0.20 S.E. km^2) than for wigeon (4.26 ± 0.10 S.E. km^2 to 3.67 ± 0.29 S.E. km^2). Decrease in suitable area for teal was about half the saltmarsh area lost to erosion, while suitable area for widgeon decreased less than the eroded saltmarsh area.

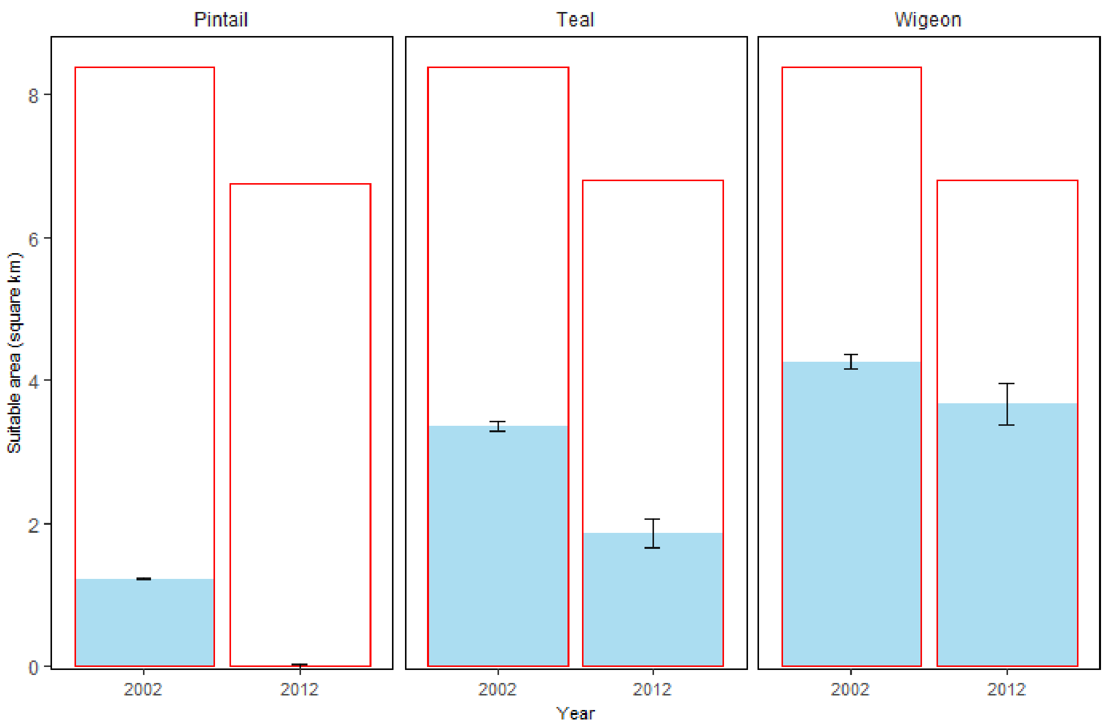

Figure 15. Suitable habitat in km^2 (± SE; blue bars) for the main scenario and total saltmarsh area in km^2 (red outline bars) for all species in 2002 and 2012. Total habitat suitability decreased for all species between 2002 and 2012, especially for pintail. Decrease in suitable area for teal was about half the saltmarsh area lost to erosion, and suitable area for widgeon decreased less than the eroded saltmarsh area.

Suitable habitat for pintail in 2002 was in the western part of Stanlow Bank and on Manisty Point, while no suitable area remained in 2012 (Figure 16). Suitable area on Stanlow Bank decreased between 2002 and 2012 for teal as well. On the other hand, other areas on Ince Bank, Frodsham Score and Hale Marsh near the main creeks remained suitable or increased slightly in suitability between 2002 and 2012. Stanlow Bank remained suitable for wigeon between 2002 and 2012, while suitable area decreased on Frodsham Score and increased on Ince Bank. Therefore, the slight decrease in suitable area observed for wigeon between 2002 and 2012 was probably due for the most part to saltmarsh erosion on Stanlow Bank. Most alternative scenarios identified similar suitable areas as the main model, although there was more variation for the teal and wigeon models than for the pintail ones.

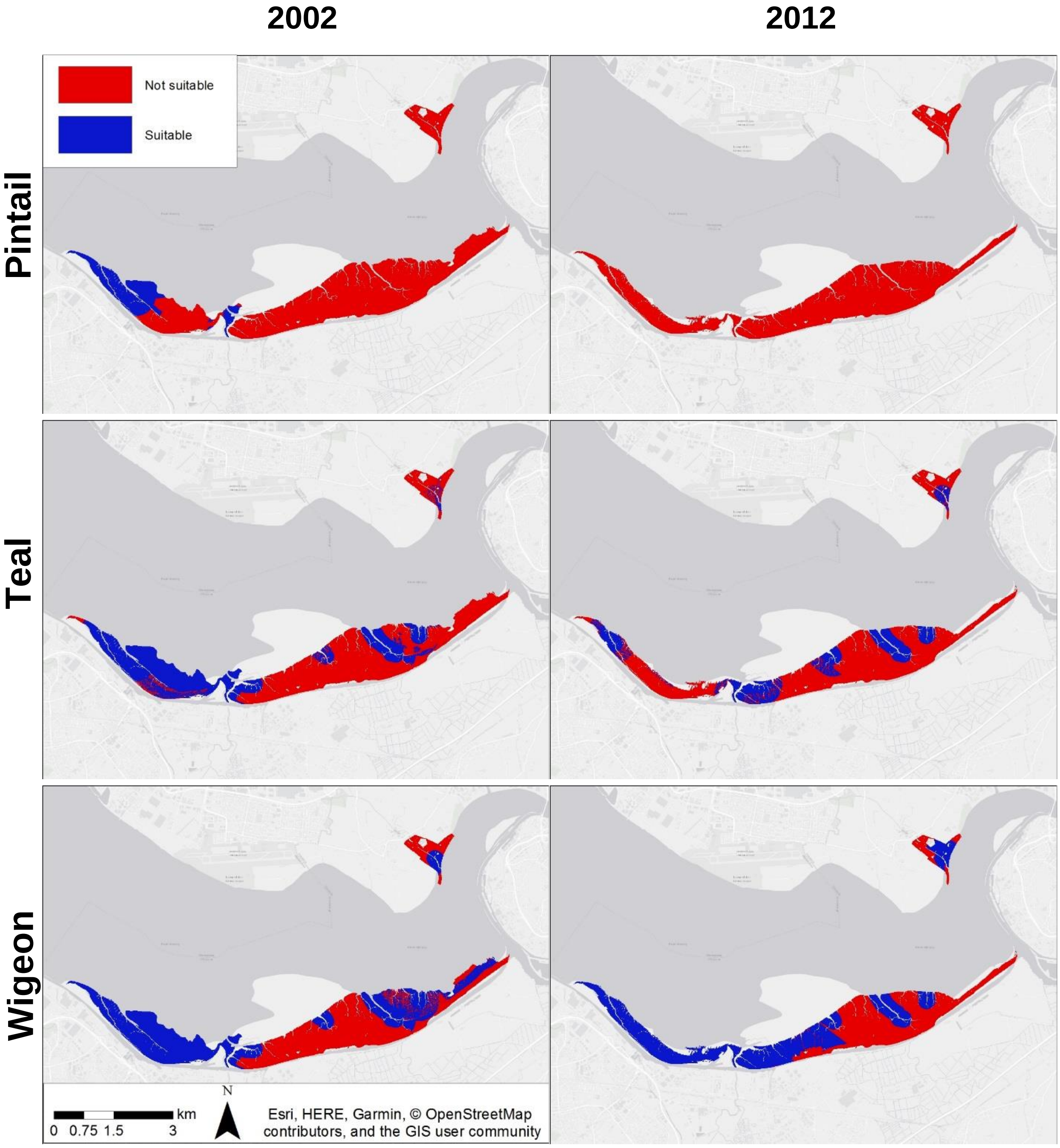

Figure 16. Habitat suitability for the main scenario for all species in 2002 and 2012.

6.6 Uncertainty estimation

The main model for all three species performed better than all or most alternative scenarios according to True Skill Statistics (TSS) scores (Figure 17). The main model for pintail had a TSS value of 0.93, which was the highest across all species and equal to or higher than all other scenarios for pintail. The main scenario for teal had a TSS value of 0.45, which was lower than that for pintail and slightly lower than the value of 0.46 of some alternative scenarios for teal. For wigeon, the TSS value for the main scenario was even lower (0.38), and slightly lower than a number of alternative scenarios, which had a TSS value of 0.40.

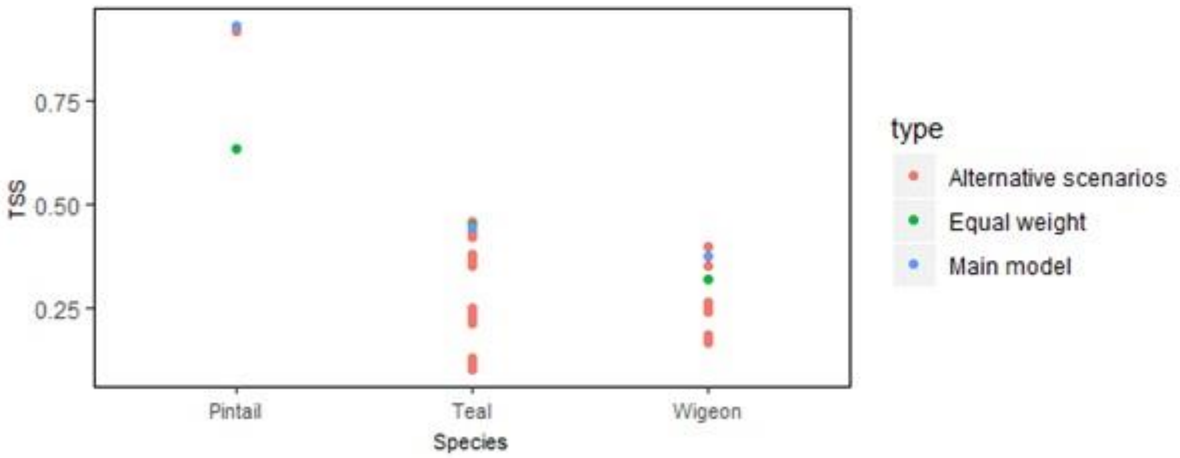

Figure 17. True Skill Statistics (TSS; unitless, range 0-1) across all scenarios for pintail, teal and wigeon in 2002. The higher the TSS value for a model is, the better the model predicts the 2002 habitat suitability for a species against the birds' presence/absence as shown by the 2000 bird roosting areas dataset. Main models for each species had TSS values higher or very similar to all alternative scenarios and equal weight models. Pintail models had the higher TSS scores than teal and wigeon.

Standard deviation across models was significantly different between all species and years. Standard deviation markedly increased between 2002 and 2012 for pintail and wigeon, while it remained similar between years for teal (Figure 18). Standard deviation across models was higher for teal than for wigeon and pintail. This means that models for teal had higher uncertainty levels than those for wigeon and pintail, and that the 2012 models for these two species had higher uncertainty levels than the corresponding 2002 models. The highest standard deviation values for pintail were recorded on Frodsham Score in 2002 and Stanlow Bank in 2012 (Figure 18). For teal, high standard deviation values were evenly distributed across the study site and did not change markedly between 2002 and 2012. Similarly, standard deviation across models for wigeon was uniformly distributed in 2002, but with levels lower than teal, while in 2012 the highest standard deviation values were recorded on Stanlow Bank.

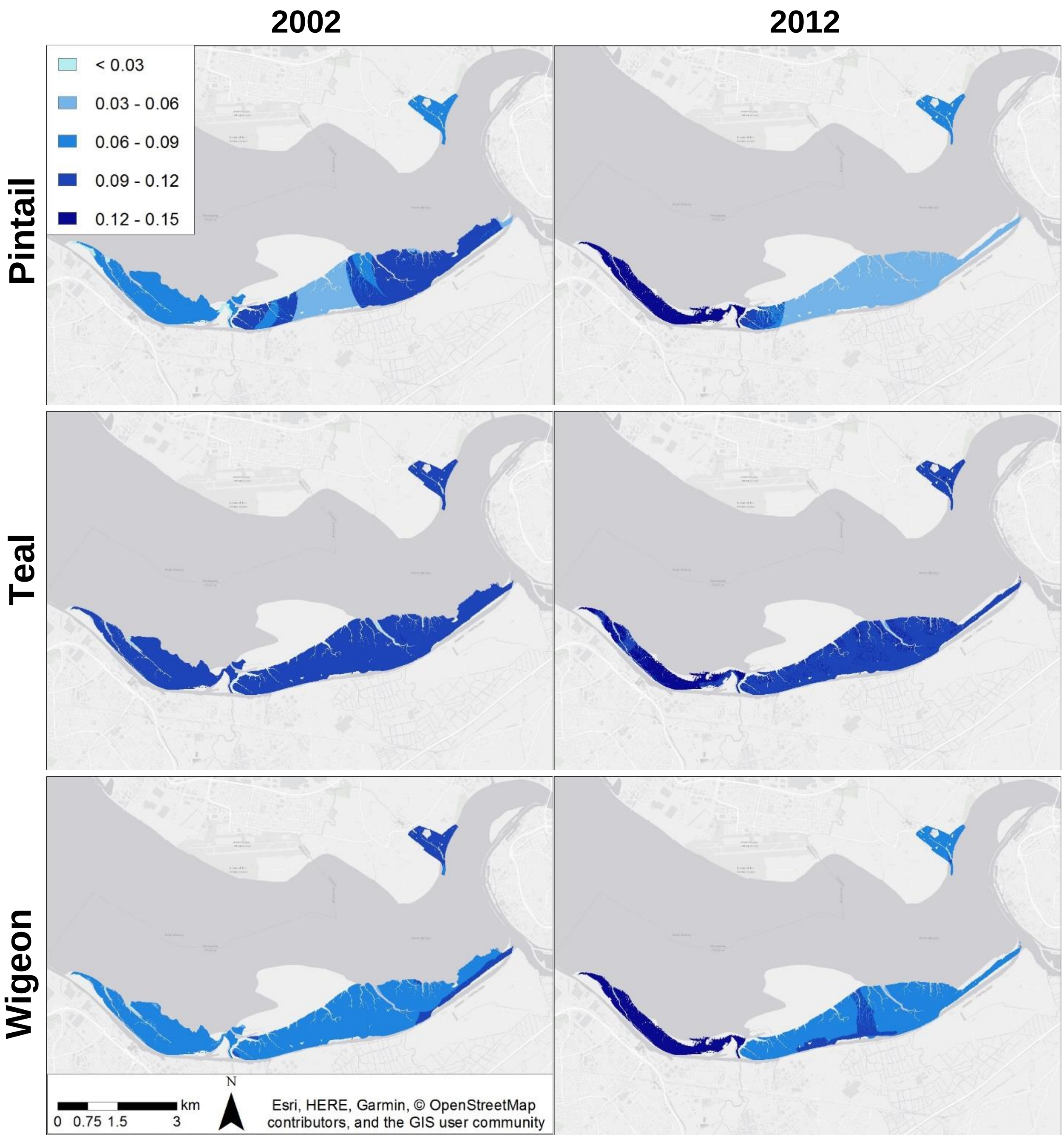

Figure 18. Standard deviation of Habitat Suitability Index (unitless, range 0-1) across all scenarios for all species in 2002 and 2012. Standard deviation increased between 2002 and 2012 for pintail and wigeon, while it remained similar between years for teal. Overall, standard deviation was higher for teal than for wigeon and pintail.

7. Discussion

7.1 Saltmarsh extent

Saltmarsh area decreased between 2002 and 2012 in the Mersey Estuary, therefore reducing available habitat for all three target species. This confirms the initial hypothesis of this project and is consistent with a declining trend in saltmarsh extent across the UK (Baylis et al., 2011). The 95% confidence interval for the saltmarsh area estimate was approximately 3.4% of the total area estimate. The performance of the method used to estimate saltmarsh extent was consistent its previous applications, with an accuracy > 96% (Baylis et al., 2011).

Although saltmarsh habitats are dynamic and change rapidly over the years (Boorman, 2003), in this case it is likely that changes in sediment balance in the estuary are reducing the sediment available for saltmarsh accretion. A reduced rate of sediment supply to the inner estuary since 1977, combined with continued dredging, are likely to have caused a slight net loss of sediment in the area (Blott et al., 2006). As a result, saltmarsh erosion between 2002 and 2012 was not compensated by accretion of different parts of the saltmarsh. Bioturbation and herbivory by *Nereis* could also cause the loss of pioneer zone plants and increase sediment instability (Hughes & Paramor, 2004).

In the Mersey estuary, erosion mostly affected the pioneer zone, while creeks remained constant over the study period. In the UK, most saltmarsh erosion is in the pioneer zone and by expansion of internal creeks (Burd 1992). The latter type of erosion was not observed in this study, but in many UK saltmarshes it constitutes most of the observed saltmarsh erosion. Bioturbation and herbivory by *Nereis* are likely to also affect creek erosion, which may lead to faster tidal currents and further erosion until creeks have widened to their new equilibrium morphology (Paramor & Hughes, 2004).

7.2 Changes and spatial patterns in food availability

Vast areas of pioneer zone disappeared during the study period, confirming the initial hypothesis that saltmarsh erosion would negatively affect food availability for the target species. Species like pintail, which preferentially feed on pioneer zone species such as *Salicornia* (Ferns, 1992), were negatively affected by reduced food availability, but all species suffered a reduction in habitat availability. All three species have been shown to undergo displacement and local population declines in response to reduced habitat availability (Laursen et al., 1983).

On the other hand, saltmarsh erosion did not affect the extent of mid marsh and thus *Atriplex* and *Puccinellia* extent remained similar between 2002 and 2012. Mid marsh is currently decreasing due to erosion in a number of British saltmarshes, where large scale lateral erosion of salt marshes can start when the marsh edge becomes disturbed from, for example, a storm surge or stronger currents and waves due to dredging or shipping traffic (Allen, 2000). This phenomenon is often referred to as cliff erosion. At the disturbed edge of the saltmarsh, sediment is more vulnerable to wave action and currents, so once a cliff starts eroding, this process is not easy to reverse until the area is protected by new marsh vegetation emerging in front of the cliff (van de Koppel et al., 2005). This process was not observed in this study; however, should pioneer zone erosion continue, it is possible large areas of mid marsh will start disappearing as well once all pioneer saltmarsh has been eroded. This would affect food availability for all bird species in the estuary.

The hypothesis that *Hydrobia* densities would increase in mudflats in the Mersey estuary between 2002 and 2012 was also confirmed, as a much larger area of saltmarsh was suitable for this factor in 2012 than in 2002. Diversity and biomass of benthic macroinvertebrate populations in the estuary is likely to have increased thanks to the general improvement of river water quality in England during the study period (Environment Agency, 2018). Nutrient inputs and pollutant loads in British rivers have steadily decreased since the adoption of the EU Water Framework Directive, and the Mersey estuary has been the object of targeted anti-pollution campaigns to reduce inputs from local industries and sewage plants (Jones, 2006). However, all three target species feed mostly on plants rather than macroinvertebrates during the winter (Dessborn et al., 2011). The overall effect of increase in *Hydrobia* abundances is therefore likely to be small.

7.3 Changes and spatial patterns in habitat characteristics

With regards to the open water and slope criteria, the hypothesis of this project was that saltmarsh erosion would reduce the area suitable for these two criteria. In fact, the observed saltmarsh erosion did not affect the distribution and width of main creeks. Distance from open water and slope therefore remained stable during the study period, except for the erosion of part of a creek on Stanlow Bank. This is different from other British saltmarshes, where creeks underwent notable changes as a consequence of erosion (Paramor & Hughes, 2004).

The hypothesis that habitat suitability for the target species would change as a result of difference in management practices between 2002 and 2012 was confirmed. Increased cattle densities, and possibly increased grazing from Canada goose, lowered sward height across most of the study site. Short sward is beneficial for all three target species, as they all prefer feeding and roosting in areas where they can easily spot predators (Kirby et al., 2000). Although some areas became less suitable for birds because of poaching, a much larger part of the site were subject to moderate grazing levels, and thus became more suitable for all species in 2012. Intermediate grazing levels are beneficial for wintering birds in saltmarshes (Davidson et al., 2017), although even low densities of cattle can be detrimental for wading birds during breeding season and timing of grazing should be carefully planned (Sharps et al., 2015).

Habitat characteristics were especially important in determining habitat suitability for teal and wigeon. In particular, teal needs areas with low slope for feeding and roosting (Genard & Lescourret, 1992; Hsu et al., 2014) and both teal and wigeon prefer roosting near open water, especially on large creeks (Rehfisch et al., 1991). Relative stability of these two factors explains why HSI values for these two species did not decrease as dramatically between 2002 and 2012 as they did for pintail.

7.4 Changes and spatial patterns in disturbance intensity

Disturbance is widely considered one of the main threats to habitat suitability for European wildfowl populations, given the ever increasing urbanisation of coastal areas (Davidson & Rothwell, 1993). The increase in human population in the Liverpool area during the study period lead to the hypothesis that recreation disturbance would be higher in 2012 than in 2002. However, evidence suggested that although recreational disturbance is likely to be an issue at Hale (Liley et al., 2017), its intensity did not change notably during the study period (Still et al., 2015). Recreational disturbance, especially from dog walkers, is a serious issue in large parts of north-western England (Liley et al., 2017), and reducing it at Hale may improve the area's suitability for all wintering birds.

Wildfowling, however, significantly affected the suitability of the study site for all species. While wildfowling intensity did not change between 2002 and 2012 in most of the site, Stanlow Bank was an area with no shooting disturbance in 2002 but by 2012 a clay-pigeon shooting club had opened nearby. Although this activity does not cause direct damage to birds, the shooting noise is likely to make birds avoid an area (Madsen, 1994; Bregnballe et al., 2004). In fact, shootings can disturb birds and alter their feeding patterns unless they are several weeks apart (Fox & Madsen, 1997; Casazza et al., 2012) and losing a sanctuary area (like Stanlow Bank was in 2002) can lead to a decrease in the overall number of birds utilising an estuary (Hirons & Thomas, 1993).

In addition, wigeon was also negatively affected by the increase in Canada goose presence in the eastern part of the study site. This species can compete with wigeon for grazing and cause displacement of their population (Hughes & Watson, 1986), however there is little quantitative research on the effect of this invasive species on native species (McLaughan et al., 2014). Overall, pintail and wigeon were especially affected by the changes in disturbance between 2002 and 2012, as these three criteria accounted for more than 55% of the total HSI scores.

7.5 Changes and spatial patterns in overall habitat suitability

The models produced in this project allowed to measure the changes in overall habitat suitability for the three target species between 2002 and 2012. Suitable habitat decreased for all three species, and mapping HSI also made it possible to examine in what parts of the study site this index increased and where it decreased. Suitable habitat for pintail drastically decreased between 2002 and 2012 in the study area. Reduced presence of *Salicornia* was the main driver of change in habitat suitability for pintail. Grazing intensity, presence of *Hydrobia* and wildfowling intensity were also significant. Grazing intensity and presence of *Hydrobia* improved habitat suitability for pintail on Ince Bank and Frodsham Score between 2002 and 2012, however it did not increase the overall HSI enough to make the area suitable for roosting. On the other hand, the decrease in habitat quality driven from changes in wildfowling intensity between 2002 and 2012, combined with the decreased presence of *Salicornia*, lowered the HSI values on Stanlow Bank enough for the habitat in the area to no longer be suitable for roosting pintail.

For the other two species, more factors were at play. The main cause of habitat change for teal between 2002 and 2012 was sward height, which slightly improved habitat quality on Ince Bank and Frodsham Score. This was probably the reason for the larger areas of suitable teal habitat around large creeks observed on Ince Bank and Frodsham Score in 2012. The other main factors affecting habitat suitability change for teal were wildfowling intensity, which decreased habitat quality on Stanlow Bank, presence of open water and slope. These two last factors did not show a clear overall change between 2002 and 2012, meaning that their contribution to habitat suitability change were likely due the combination of their high weight in the HSI formula and small random changes in the case of slope, as well as the erosion of one main creek on Stanlow Bank for presence of open water.

There was not a single factor clearly influencing change in habitat suitability for wigeon between 2002 and 2012. Wildfowling decreased habitat suitability on Stanlow Bank, but not enough to affect the overall habitat suitability in that part of the site. On Ince Bank, the increased suitability values due to shorter sward and increased presence of *Hydrobia* caused the HSI to become suitable for wigeon in 2012. On the other hand, suitable habitat on Frodsham Score decreased because of the expansion in Canada goose distribution during the study period.

7.6 Uncertainty estimation

Habitat suitability models based on expert judgement are infrequently validated, probably because they are used when presence data for the target species are unavailable or inadequate (Johnson and Gillingham, 2004). This was also the case in this study, with annual bird presence data only available as totals for the whole of the Mersey Estuary. The only information at the appropriate spatial scale was a map of indicative roosting areas in 2000, which did not have any associated abundance data, which made carrying out a full model validation problematic. Assuming that the main roosting areas of a species would be in areas with highly suitable habitat, the latter dataset could be used to determine which HSI value was the most suitable threshold to separate suitable and unsuitable HSI values, i.e. the HSI value that, used as a threshold, would maximise the model's TSS score.

Model performance according to TSS scores was much better for pintail than for teal and wigeon. Pintail has more specific habitat requirements than the other two species, with fewer factors being crucial in determining its distribution. In fact, just three factors in the model for pintail contributed to over 10% of the total HSI value, while in the teal and wigeon models four factors contributed to more than 10% of the total HSI value. The pintail habitat suitability model represented very closely the 2000 distribution of roosting areas for this species. The large difference in TSS values between the main model and the equal weight model (0.93 vs 0.63) also suggests that assigning different weights to each criterion sensibly improved the model's performance. In contrast, teal and wigeon's models represented the 2000 roosting areas less accurately. The effect of assigning weights to the criteria was also small for these two species, although it still improved TSS scores for wigeon. However, it must be remembered that the 2000 roosting areas dataset used to calculate TSS scores only represented the main roosting areas, meaning that areas not marked in the dataset may still have been suitable and/or hosted low density of the target species. TSS scores are therefore only indicative because bird distribution does not fully represent habitat suitability, unless we can assume all suitable areas in the site are fully utilised by the target species.

In particular, wigeon is a very adaptable species, as it has been shown to change its feeding preferences depending on which plant species are available (Owen & Williams, 1976). Generalist species are often more difficult to predict than specialist species, as generalist species are able to persist in a wide range of environmental conditions that are not easily defined by the data, independent variables or model design (Evangelista et al., 2008). On the other hand, habitat requirements for pintail, which has specific and unchanging feeding preferences, were represented well in the model developed in this study, which accurately reflected pintail distribution when compared with 2000 bird distribution.

Since full model validation could not be carried out with the available bird distribution data, understanding the variability due to uncertainty was important to determine the quality of model predictions. Standard deviation across scenarios was higher in 2012 than in 2002 for all species, especially on Stanlow Bank. This is probably due to the start of a clay-pigeon shooting club near Stanlow Bank between 2003 and 2012. Clay-pigeon shooting was classified as moderate suitability category for wildfowling intensity, but no clear information was found in the scientific literature regarding its effects on bird populations compared to wildfowling. As a result, variability for this category was very high in the bounding maps for this factor.

For teal, standard deviation was higher than for the other two species across the whole study area for both years. This was probably due to the strong influence of presence of open water, which accounted for approximately 35% of HSI values for this species. Similar to wildfowling intensity, variability between scenarios was very high for this factor, with highly suitable areas ranging from 200 metres from a major creek to half of the foraging flight distance (FDD) for the species. Regardless of standard deviation values, most model scenarios consistently agreed on which parts of the study area were suitable for the target species.

In general, model uncertainty magnitude estimated by bounding maps high for all factors considered and was the main source of error for the models. For example, presence of *Salicornia* was an important factor in determining pintail distribution (global weight 0.232) and the suitability map for this factor assigned the maximum value (1) to those areas within FFD/2 of *Salicornia* patches, a medium value (0.6) to areas at a distance of between FFD/2 and FFD from *Salicornia* and a low value (0.3) to areas further than FFD from *Salicornia* patches. The bounding maps for this factor varied from one in which the high suitability area was limited to parts of the saltmarsh where *Salicornia* was present and the rest of the study area was deemed to have low suitability for this factor ("strict suitability" map) to one in which all parts of the study sites with distance lower than pintail FFD were classified as highly suitable with respect to this factor ("loose suitability" map). The measurement error associated to *Salicornia* distribution assessment was the same as that of the saltmarsh zonation process (> 90% accuracy at a 10m resolution), while changes in the modelling criteria could lead to up to 85% of points being classified incorrectly (Figure 19). This is in accord with results of previous studies, where model uncertainty was the main source of error in habitat suitability models based on expert judgement (Elith and Burgman, 2002; Ray and Burgman, 2006).

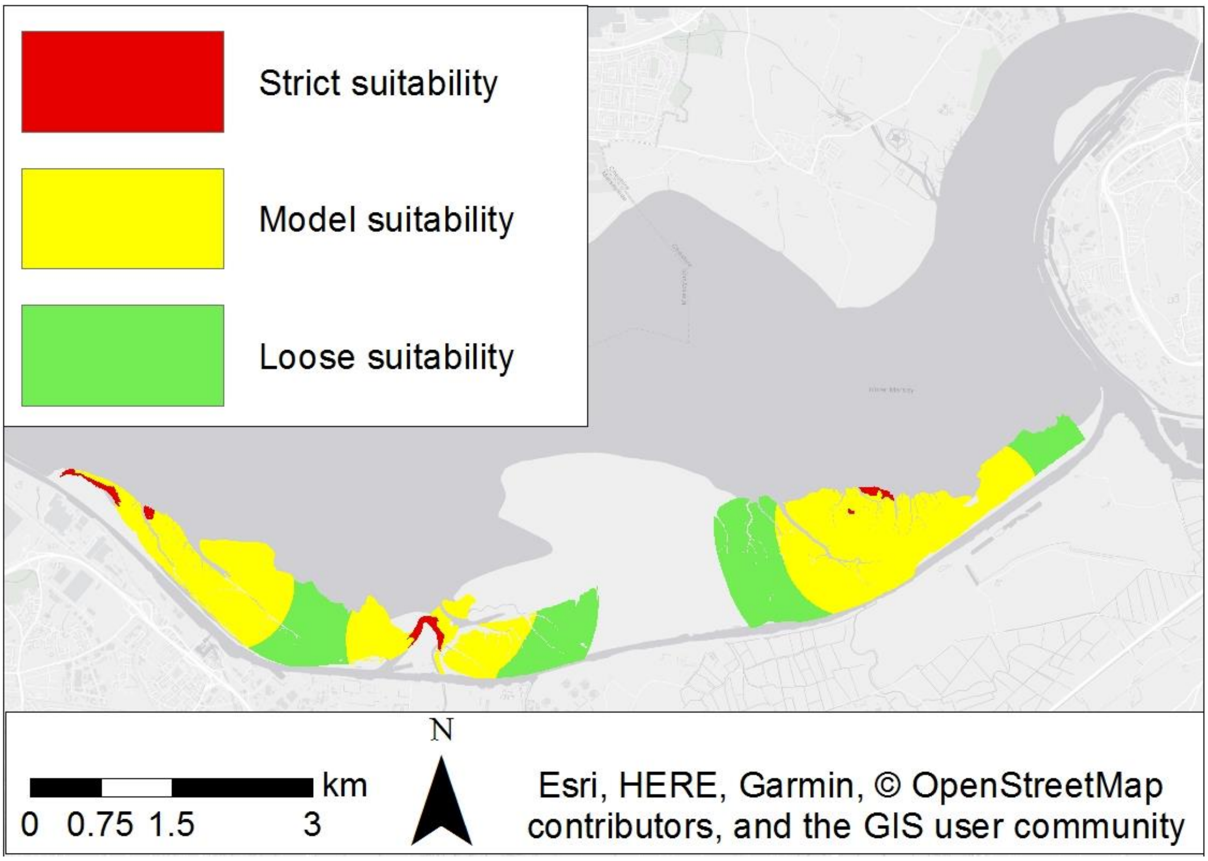

Figure 19. High suitability areas for pintail in 2002 with regards to presence of *Salicornia* according to the modelling criteria used in the HSI model, in the loose suitability bounding map and in the strict suitability bounding map.

7.7 Conclusions

The observed decline in pintail, teal and wigeon numbers overwintering in the Mersey estuary saltmarshes between 2002 and 2012 could only partly be explained by habitat changes. While all three species numbers decreased in the Mersey Estuary more than they did at national level, the decline in suitable habitat was not always consistent with percent change in bird numbers on the Mersey Estuary (Figure 20). Suitable habitat for pintail drastically decreased and could fully explain this species' decline between 2002 and 2012, but the decrease in suitable area for teal and wigeon was not as marked as the decline in bird numbers, especially in the case of wigeon. In fact, wigeon numbers in the Mersey Estuary decreased by approximately 88% but suitable saltmarsh habitat only decreased by about 14% in the same period.

For teal and wigeon, factors other than changes in habitat may be involved. For example, saltmarshes on the River Dee estuary accreted significantly over the last few decades (Flint, 2007), providing an alternative to eroding saltmarshes on the River Mersey. In addition, approximately 10% of the Dee estuary is kept as a reserve where wildfowling is not allowed, providing a sanctuary area now lacking in the Mersey estuary. The Dee estuary is less than 20 km away from the Mersey estuary, and since all three species have low site fidelity (Wright et al., 2014), birds could easily decide to overwinter in either of these areas depending on which one has the most suitable habitat available. In addition, overwintering birds do not only exploit saltmarsh area, but use surrounding functionally linked land such as surrounding arable fields, grassland or wetlands (Holt et al., 2015). Analysis of functionally linked land was outside of the scope of this project, but changes in land use in the wider area may explain part of the observed decrease in bird numbers that are not explained by changes in habitat suitability in the study area or regional and national population trends (Parejo et al., 2019). As bird abundances were only available as totals for the whole estuary, wigeon abundances may have reacted to changes in other parts of the area that were not considered in this study.

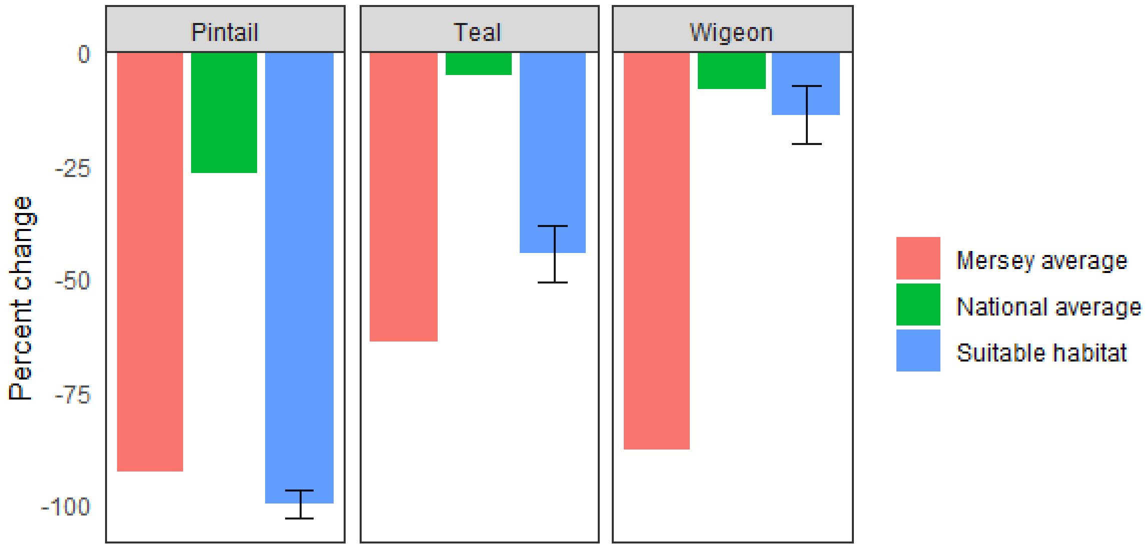

Figure 20. Percent change between 2002 and 2012 in pintail, teal and wigeon abundances on the Mersey Estuary (red) and in the UK (green), as well as changes in suitable habitat in the study area (±SE, blue). Percent changes in bird abundances were calculated based on the change in the previous 5-year average.

It must also be remembered that habitat suitability models do not necessarily predict actual species distribution, because the target species may not fully exploit all suitable habitat (Hsu et al., 2014). Deductive models, based on expert judgement, represent total suitable habitat, or a species' fundamental niche (Hutchinson, 1957). On the other hand, empirical models, based on distribution data, represent the species' actual distribution, or their realised niche (Brown and Lomolino, 1998). The models developed in this study, therefore, predict which areas are likely to be suitable for the target species although currently unexploited.

The approach to modelling habitat suitability used in this project is widely applicable. However, the specific models developed in this project determined habitat requirements based on a review of scientific literature, mostly from the United Kindgom, and are probably only applicable to other sites in the country. The thresholds between suitable and unsuitable HSI values were chosen using bird distribution data from 2000 and are therefore highly site-specific. If these models were to be used at other location, the threshold determination process should be repeated using local bird distribution data or avoided altogether.

The possible management measures that could help reverse or limit the decline in overwintering numbers of the three target species in the Mersey estuary include:

1) Determine how much sediment would be needed to reverse the net saltmarsh erosion observed in this study and adjust the dredging regime accordingly. This would create new areas of pioneer saltmarsh where *Salicornia* could grow and provide an abundant food source for pintail, as well as increased habitat availability for all species.
2) Address the lack of a wildfowling sanctuary area in the study site. Even infrequent shooting noises have been shown to cause birds to entirely avoid an area (Fox & Madsen, 1997). This measure is likely to improve habitat suitability for all three species.

The models produced in this study could easily be used to forecast the effects of these measures on habitat suitability for pintail, teal and wigeon.

Appendices

Appendix 1. Statistical analyses

Table S1. ANOVA and post-hoc test results for the analysis of variance of standard deviation across scenarios between species and years.

Factor	Degrees of freedom	Degrees of freedom residuals	F value	P value
Species	2	11363510	4742984	**< 0.001**
Year	1	11363510	72552	**< 0.001**
Species x Year	2	11363510	835480	**< 0.001**
Contrasts				
Contrast	**Estimate**	**Degrees of freedom**	**T ratio**	**P value**
Pintail,2002 - Teal,2002	1905586	11363500	640.673	**< 0.001**
Pintail,2002 - Wigeon,2002	2646365	1136350	889.729	**< 0.001**
Pintail,2002 - Pintail,2012	3890279	1136350	1235.830	**< 0.001**
Pintail,2002 - Teal,2012	1031817	1136350	328.355	**< 0.001**
Pintail,2002 - Wigeon,2012	1364424	1136350	434.201	**< 0.001**
Teal,2002 - Wigeon,2002	740779	1136350	249.064	**< 0.001**
Teal,2002 - Pintail,2012	1984694	1136350	630.498	**< 0.001**
Teal,2002 - Teal,2012	-873769	1136350	-278.068	**< 0.001**
Teal,2002 - Wigeon,2012	-541162	1136350	-172.219	**< 0.001**
Wigeon,2002 - Pintail,2012	1243914	1136350	395.167	**< 0.001**
Wigeon,2002 - Teal,2012	-1614549	1136350	-513.813	**< 0.001**
Wigeon,2002 - Wigeon,2012	-1281942	1136350	-407.964	**< 0.001**
Pintail,2012 - Teal,2012	-2858463	1136350	-864.355	**< 0.001**
Pintail,2012 - Wigeon,2012	-2525856	1136350	-763.780	**< 0.001**
Teal,2012 - Wigeon,2012	332607	1136350	100.736	**< 0.001**
P value adjustment: Tukey’s method for comparing a family of 6 estimates				

Table S2. ANOVA and post-hoc test results for the analysis of variance of total suitable area between species and years.

Factor	**Degrees of freedom**	**Degrees of freedom residuals**	**F value**	**P value**
Species	2	375	131.0910	**< 0.001**
Year	1	375	52.3367	**< 0.001**
Species x Year	2	375	1.7712	0.172
		Contrasts		
Contrast	**Estimate**	**Degrees of freedom**	**T ratio**	**P value**
Pintail - Teal	-136.6	375	-10.324	**< 0.001**
Pintail,2002 - Wigeon,2002	-211.7	375	-16.002	**< 0.001**
Pintail,2002 - Pintail,2012	-75.1	375	-7.995	**< 0.001**
P value adjustment: Tukey’s method for comparing a family of 6 estimates				
Results are averaged over the levels of: year				

Appendix 2. Additional figures

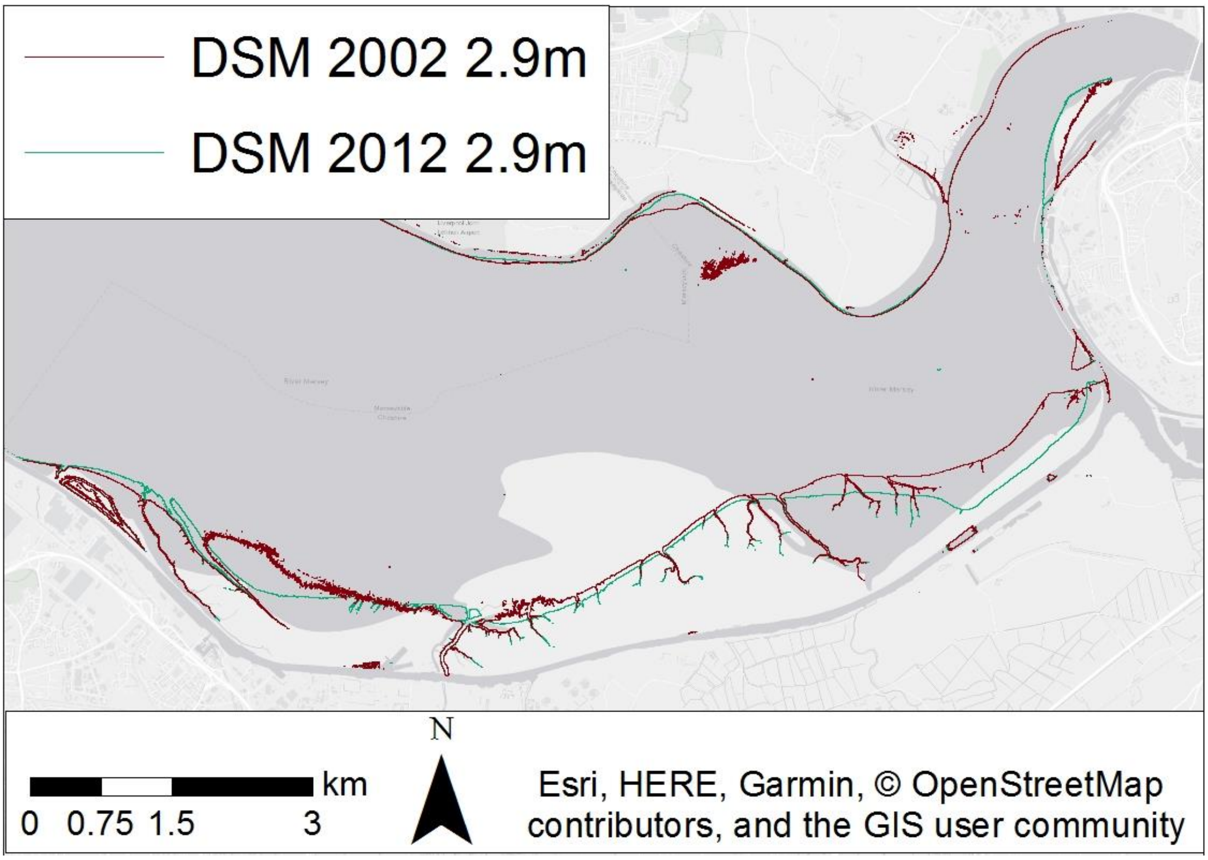

Figure S1. Potential saltmarsh extent in 2002 (red lines) and 2012 (green lines) on the Mersey estuary identified by contour lines at 2.90 m ODN. Potential saltmarsh area on Stanlow Bank and Frodsham Score has reduced due to erosion, while some accretion is evident on the western end of Stanlow Bank.

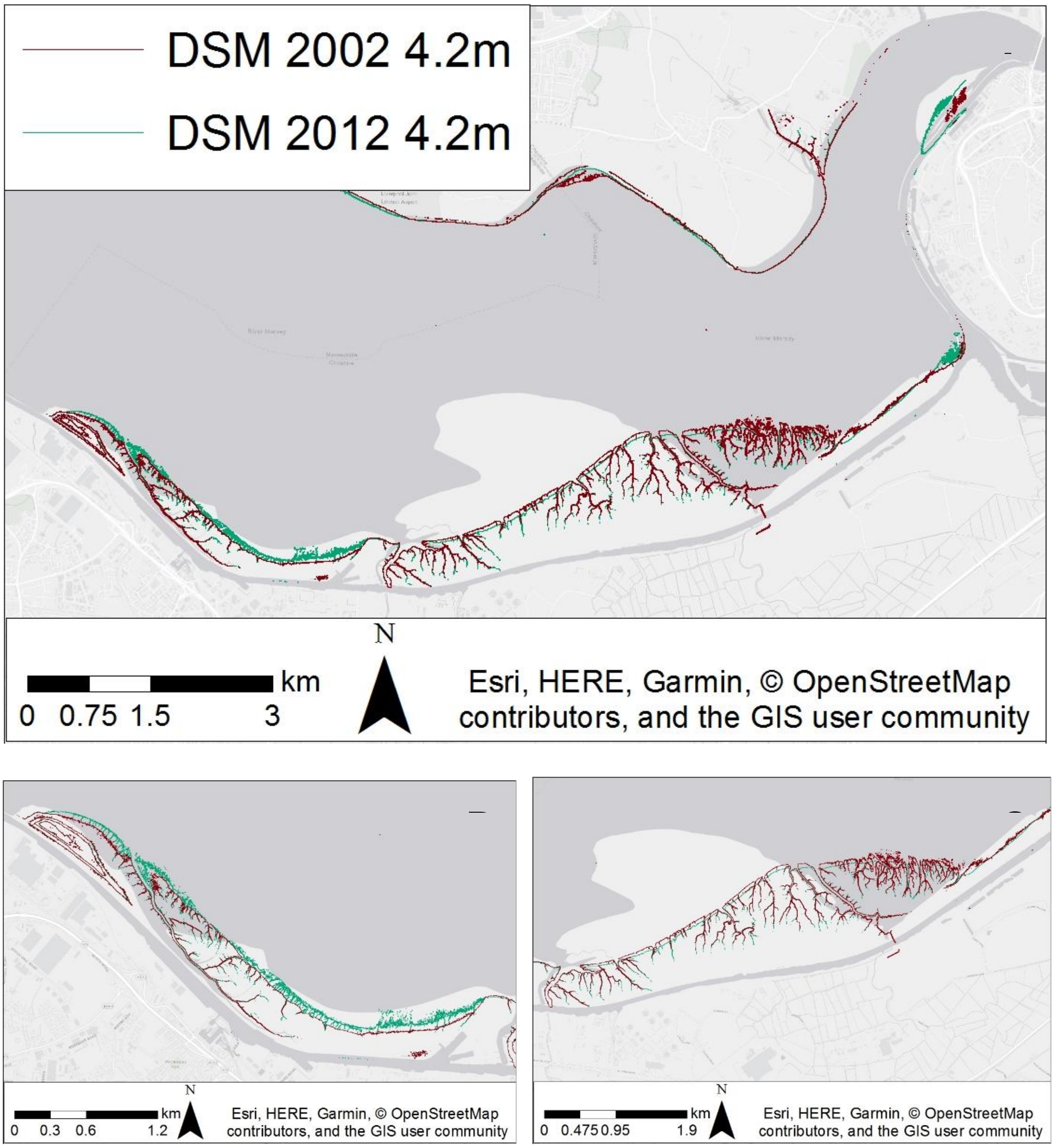

Figure S2. Top of creeks in 2002 (red lines) and 2012 (green lines) identified by contour lines at 4.20 m ODN on (A) on the Mersey estuary; (B) Stanlow Bank and (C) Ince Bank. These contours identify the high marsh area, which accreted on Stanlow Bank and eroded on Ince Bank between 2002 and 2012.

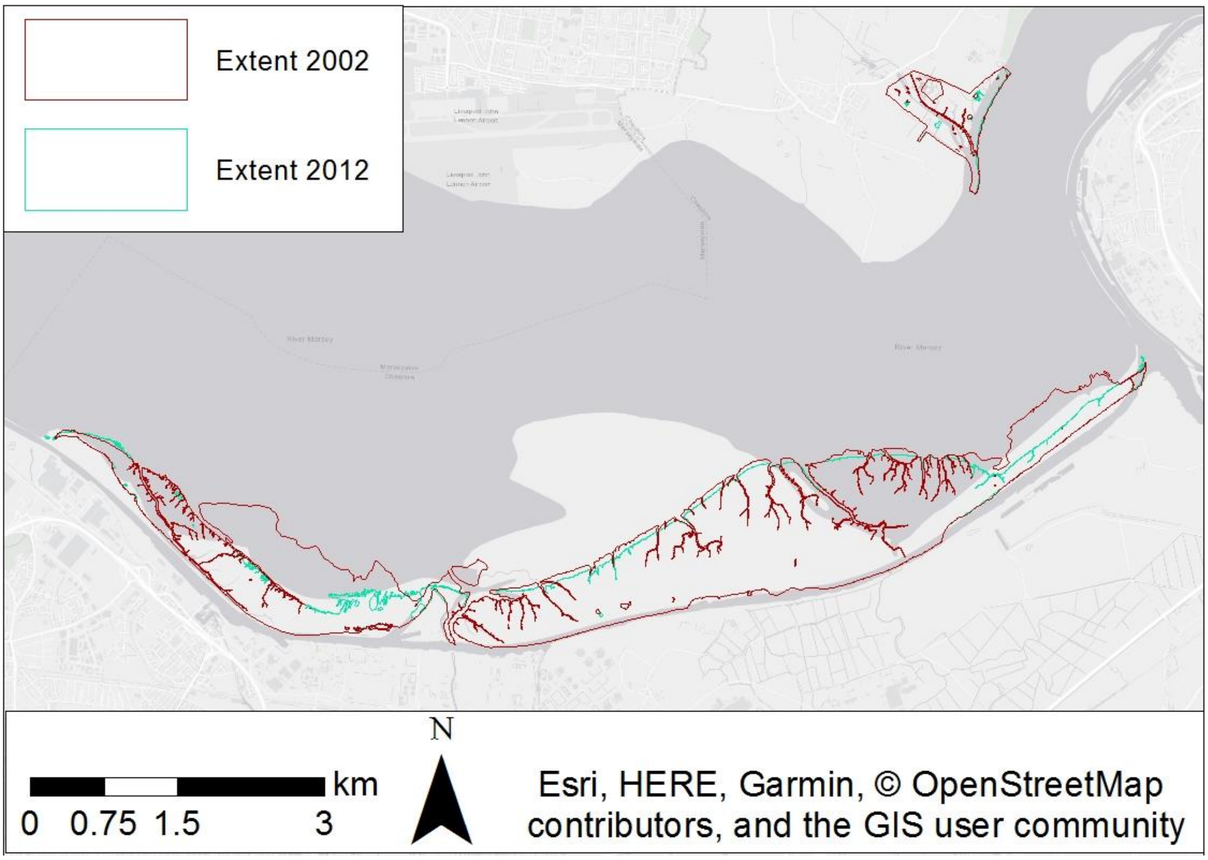

Figure S3. Saltmarsh extent on the Mersey estuary modified from LiDAR contour lines for in 2002 (red lines) and 2012 (green lines). Between 2002 and 2012, areas of lower marsh on the southern river bank underwent significant erosion.

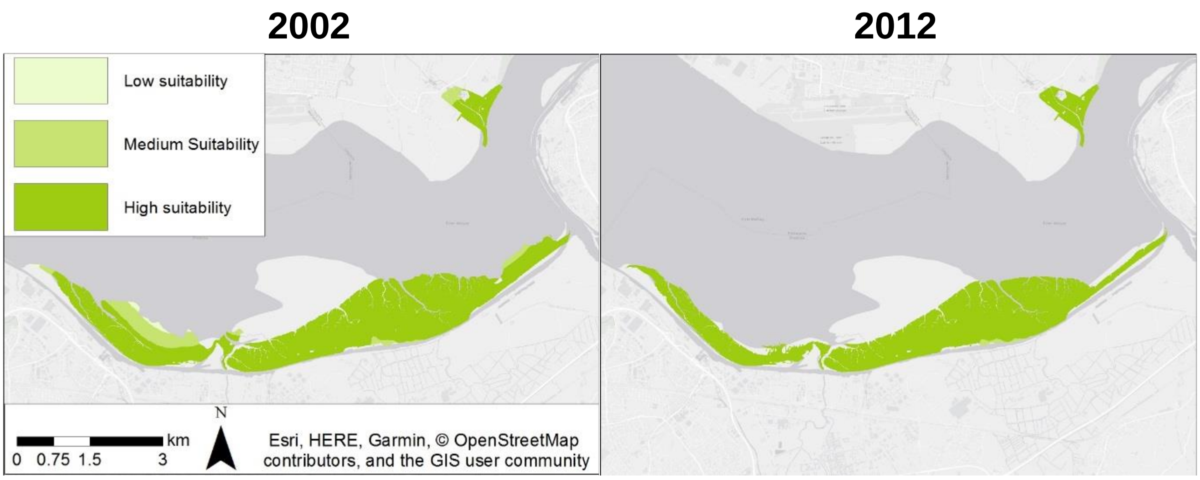

Figure S4. Suitability categories for presence of *Atriplex/Puccinellia* for all species in 2002 and 2012. Most of the study site was highly suitable, both in 2002 and in 2012.

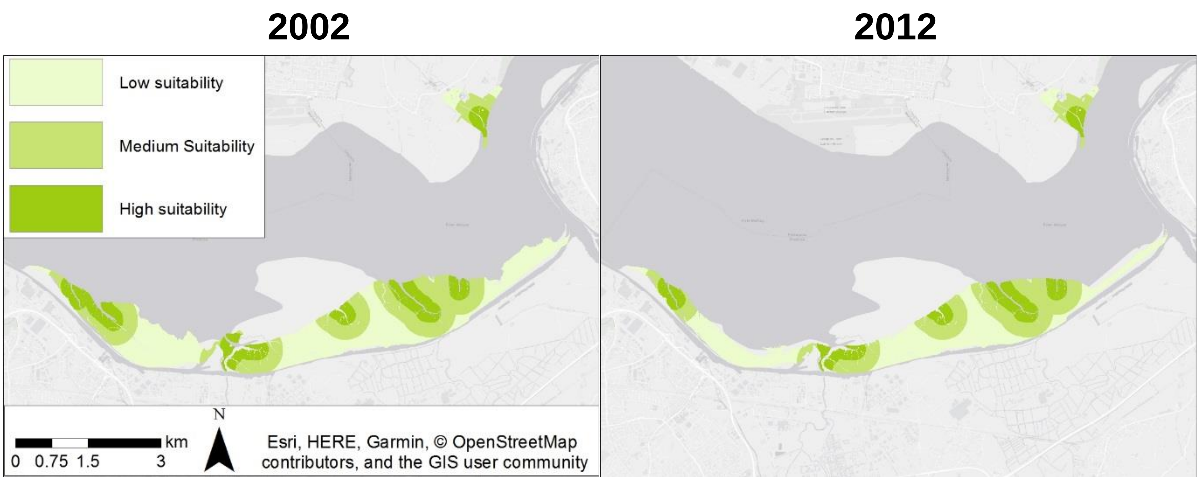

Figure S5. Suitability categories for presence of open water for all species in 2002 and 2012. All main creeks in the saltmarsh remained in the same position between 2002 and 2012. However, the suitable area decreased in this period, probably due to saltmarsh erosion.

Figure S6. Suitability categories for slope for all species in 2002 and 2012. Slope in the study area remained very similar between 2002 and 2012.

2002 2012

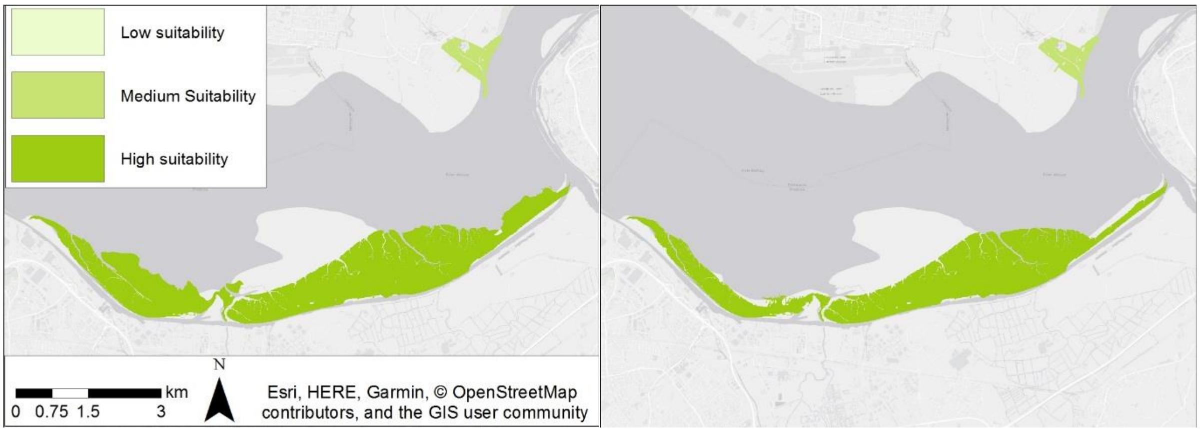

Figure S7. Suitability categories for recreational disturbance for all species in 2002 and 2012. Recreational disturbance levels did not change between 2002 and 2012. Areas on the southern bank, not accessible to the public, were highly suitable for all species, while the accessible areas on the north bank had medium suitability levels.

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