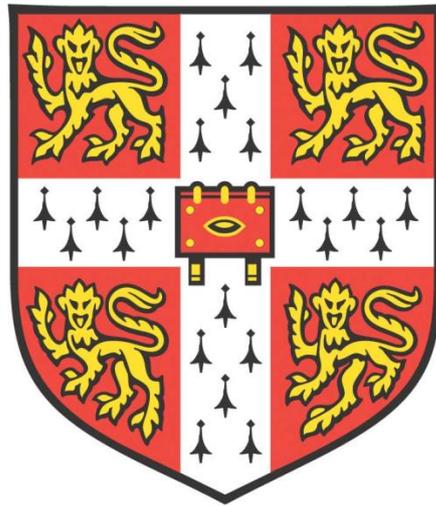


*IMPACTS OF FLOOD-MEDIATED
DISTURBANCE ON SPECIES OF HIGH
NATURE VALUE FARMLAND*



Timothy Aneal Kasoar

King's College

Conservation Science Group

Department of Zoology

University of Cambridge

This dissertation is submitted for the degree of Doctor of Philosophy

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DECLARATION

This dissertation is the result of my own work and includes nothing, which is the outcome of work done in collaboration except where specifically indicated in the text. It has not been previously submitted, in part or whole, to any university or institution for any degree, diploma, or other qualification.

In accordance with the Degree Committee for the Faculty of Biology guidelines, this thesis does not exceed 60,000 words, and it contains less than 150 figures.

Signed:  _____

Date: 20 December 2018 _____

Timothy Aneal Kasoar, MA (Cantab)

Cambridge

IMPACTS OF FLOOD-MEDIATED DISTURBANCE ON SPECIES OF HIGH NATURE VALUE FARMLAND

SUMMARY

High Nature Value farmland (HNVf) refers to traditional agricultural landscapes which support high levels of biodiversity. HNVf is declining across Europe, through both intensification and abandonment, raising concerns about the conservation of species associated with it. One argument is that such HNV species are better described as being dependent on disturbance, and that management practices on HNVf mimics the effects of natural disturbance processes such as herbivory, fire, severe weather and flooding, which are often suppressed across much of Europe.

If true, one innovative approach for conserving HNV species would be to restore natural disturbance processes, as advocated by the “rewilding” conservation movement. I set out to explore the feasibility of this approach, focusing on flooding. Restoration of flood regimes is receiving growing attention, not only for its biodiversity benefits but also to reduce the risk of flooding in downstream urban areas, improve water quality, and increase the amenity value of rivers.

I carried out four linked studies. Each followed a broadly similar approach: I selected sampling locations both in floodplain areas and comparable surrounding farmland, I surveyed birds and butterflies as indicator taxa of biodiversity, I carried out habitat mapping, and I estimated disturbance through both field measurements and remotely sensed data.

My first study was around the Pripyat river in Ukraine, which has a large floodplain that has had minimal human intervention. I found that several, but not all, HNV species had higher population densities in the floodplain than in the surrounding HNV farmland, and several more had approximately equal population densities in the two habitats. This suggested intact flood regimes can retain some species that are elsewhere restricted to HNVf.

My second study was around the river Rhône, France, where a restoration project has increased flow in floodplain channels and improved their connectivity with the main channel. I compared restored and non-restored segments of floodplain channel, as well as farmland and other habitats. While I found significant differences in population densities

between habitat types, few species showed significant differences between restored and non-restored segments, suggesting that restoration had only limited ecological impacts on the wider landscape.

My third study investigated a more ambitious restoration project which has reconnected a large area of floodplain to the river Peene in Germany. I found many HNV species had equal or higher population densities in the restored floodplain than in the surrounding unrestored farmland. This demonstrates that it is possible to restore the effect of natural flood disturbance on habitats and species. However, not all HNV species benefitted from flood-disturbed habitats, so clearly other conservation interventions need to be considered.

For the final study, pooling data from all three sites I looked for associations between species' traits and environmental variables. My aim was to identify traits which predict species' responses to the environment, and hence which species are most likely to benefit from restoration. However, I did not find any significant associations in my data.

In conclusion, I demonstrated that flood-disturbed habitats are suitable for many species traditionally associated with HNV farmland, and further that restoring flood disturbance processes can recreate those habitats. As such, reconnecting rivers and restoring floodplains would be a useful conservation intervention for species threatened by the abandonment or intensification of HNV farmland in Europe. However, other species did not benefit, and require other conservation interventions, perhaps other forms of rewilding, or continued incentivisation of favourable farming practices.

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LIST OF ABBREVIATIONS AND ACRONYMS

AES	Agri-Environment Schemes
AIC _c	Akaike Information Criterion (corrected for small sample sizes)
CA	Correspondence Analysis
CAP	Common Agricultural Policy
CCA	Canonical Correspondence Analysis
EC	European Commission
EEA	European Environment Agency
ETM+	Enhanced Thematic Mapper Plus (satellite imagery)
EU	European Union
GLM	Generalised Linear Model
GPS	Global Positioning System
GSW OL	Global Surface Water Occurrence Layer
HLS	Higher Level Stewardship (agri-environment scheme)
HNV	High Nature Value
HNV species	Species associated with High Nature Value farmland
HNVf	High Nature Value farmland
LHP	Larval Host Plant
LYF	Low-yielding farmland
MIR	Middle Infrared (spectral band)
PCA	Principal Components Analysis
PSNNP	Pripyat-Stokhid National Nature Park
TM	Thematic Mapper (satellite imagery)
Tukey HSD	Tukey Honest Significant Difference (statistical test)

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1 INTRODUCTION

1.1 Agriculture and biodiversity in Europe

Europe has a long history of human land use and management. Agriculture first arrived in Europe from the east around 9,000 years ago, and spread to cover most of the continent over the next 3,000 years (Price, 2000). Along with the spread of agriculture came a wide range of other changes to the natural habitats previously present, in particular the clearance of forests and woodland both to make space for agriculture and to supply wood for fuel and construction (Kaplan, Krumhardt & Zimmermann, 2009).

Whilst such wholesale changes in landcover would have led to dramatic changes in biodiversity, throughout most of Europe the level of biodiversity remained high (Strohbach *et al.*, 2015). Natural habitats were replaced with “semi-natural habitats”, habitats created by human actions, but still heavily influenced by natural processes and supporting a wide range of species (Rackham, 2000; Fuller *et al.*, 2017). Examples include meadows, extensively grazed pastures and coppiced woodland. In addition, the long history of human land use may have given species a chance to adapt to anthropogenic landscapes and even evolve to thrive in them (Wright, Lake & Dolman, 2012).

In recent years, this high biodiversity in anthropogenic landscapes has given rise to the concept of “High Nature Value farmland” (HNVf): areas of farmland which retain high levels of biodiversity due to the way in which they are managed. HNVf landscapes are typically mosaics of semi-natural habitats, with patches of natural habitats (Andersen *et al.*, 2003). Many species are strongly associated with HNVf, meaning that they are rarely found in other habitats; such species can be referred to as “HNV species” (Andersen *et*

al., 2003). Some HNV species are charismatic and culturally important, such as the Black grouse, Crane and Great bustard (EEA, 2004). Areas of HNVf may even have higher levels of biodiversity than natural habitats on a local scale, as they can be highly heterogeneous (Figure 1.1; EEA, 2004).

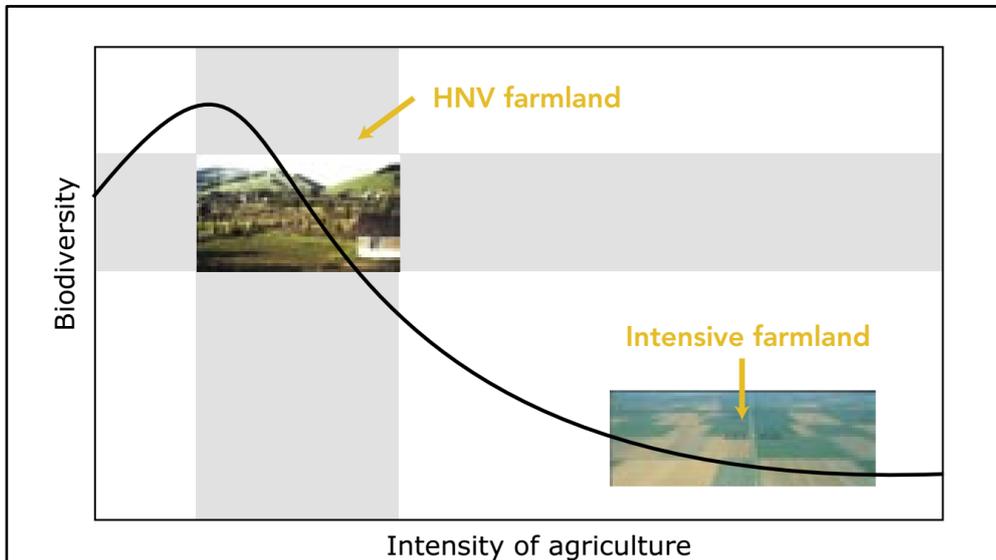


Figure 1.1 – It has been suggested that, on a local scale, HNV farmland supports higher biodiversity than natural habitats. Figure from EEA (2004)

However, the extent of HNVf has been declining across Europe. Historically, this decline has been driven by agricultural intensification (EEA, 2004). Intensification, through larger field sizes with fewer habitat features such as ponds and hedges, greater use of pesticides and fertilisers, increasing mechanisation and so on, leads to declines in biodiversity (Donald, Green & Heath, 2001; Stoate *et al.*, 2001). In parts of Europe, this trend continues, especially in countries such as Poland which have relatively recently joined the European Union and, with membership, gained access to large amounts of funding for agricultural and rural development (Wigier, 2014).

More recently, the opposite trend, land abandonment, has also become a threat to HNVf, particularly on marginal land where intensification is not an option (Keenleyside & Tucker, 2010). Traditional agricultural practices are often economically inviable compared to modern alternatives, and often the work is physically demanding. Many people are choosing to move to more urban areas, seeking a better quality of life and more lucrative employment opportunities (MacDonald *et al.*, 2000; Navarro & Pereira, 2012). This abandonment typically leads to a loss of heterogeneity as vegetation succession takes place, leading to a loss of open habitats and habitat edges. This can result in the habitat becoming unsuitable for HNV species (EEA, 2004), although other species may benefit

(Regos *et al.*, 2016). For both abandonment and intensification, the common theme is that traditional management is socially and economically unattractive.

1.2 The history and ecology of HNV species

HNV species currently depend on human land management to maintain suitable habitat in Europe, yet such management has only started in the past 9,000 years, whereas most species had evolved far longer ago (Lawton & May, 1995). Where did these species live prior to humans altering the landscape?

Until relatively recently, most ecologists operated on the assumption that, in the absence of human intervention, most of Europe would be covered with closed canopy forest (Clements, 1916; Tansley, 1939; Evans, 1971; Tilman, 1985; Rackham, 2000). It was acknowledged that catastrophic events, such as floods, or certain animals, such as beavers *Castor fiber*, could create gaps in the woodland (Watt, 1947; Coles & Orme, 1983) but it was generally assumed that such processes were relatively insignificant and that trees quickly regenerated after such events.

However, this paradigm was challenged by Frans Vera, who argued that large, wild herbivores such as aurochs *Bos primigenius* and tarpan *Equus ferus* would have been important regulators of vegetation, and that Europe would have been covered with a park-like mosaic of woodland, open areas and scrubby areas (Vera, 2000). This was supported by ongoing advances in the field of palynology (the study of ancient pollen deposits), which revealed non-arboreal, open-habitat plant species were present widely across the landscape (Vera, 2000). This was further supported by analysis of sub-fossil snails and beetles, which also found species which require open habitats to be abundant (Svenning, 2002; Allen & Gardiner, 2009; Sandom *et al.*, 2014b).

While Vera focused on large grazing herbivores, over the following decade, numerous scientists suggested that natural disturbance processes more generally would have played a major role in shaping habitats across Europe. While herbivory is one type of disturbance, so too are fire, flooding, storms, diseases, ice damage and other processes. All of these processes, according to the local conditions, would have influenced the vegetation and prevented closed canopy forest from continuously dominating the landscape. Instead, there would have been a dynamic mosaic consisting of patches in various stages from freshly disturbed bare ground through grasslands and shrublands to mature forests (Hodder *et al.*, 2009; Navarro *et al.*, 2015).

Most ecologists now acknowledge that natural disturbance processes were important influences on the pre-agricultural European landscape, but there remains significant debate and uncertainty about the magnitude of their role. Was the landscape, as Vera claimed, “park-like” and mostly open with isolated copses of trees and few areas of more continuous woodland? Or was it mostly forested, with relatively small patches of open habitats? The evidence can be hard to interpret. The palynological record is complicated by the fact that different plants produce different amounts of pollen, have different dispersal mechanisms and distances, and the pollen grains themselves may be more or less prone to preservation. Therefore, the abundance of pollen in sediment cannot be treated as a direct proxy for the vegetation community in the surrounding area (Svenning, 2002; Allen & Gardiner, 2009). Similar problems arise when using other forms of evidence, such as snail shells or beetle carapaces from sediment records (Allen & Gardiner, 2009; Müller, Jarzabek-Müller & Bussler, 2013). The issue is further complicated by the suggestions that species may have survived in small refugia not reflective of the wider landscape, may have changed their habitat preferences in response to changing landcover, or may have migrated into and across Europe as suitable habitat became more widespread (Thomas, 2009).

Humans have suppressed most, if not all, of these disturbance processes to some extent. Wild herbivore populations have been reduced, in many cases to local or global extinction (Dirzo *et al.*, 2014; Sandom *et al.*, 2014a). This has particularly affected megafauna, which are also (by virtue of their size) thought to have had large impacts on ecosystems (Bakker *et al.*, 2016; Malhi *et al.*, 2016). Rivers are controlled through dams and dykes to prevent flooding, and over 90% of floodplains in Europe are thought to be functionally extinct, in many cases having been converted to agricultural use (Tockner & Stanford, 2002). Fire regimes are managed by creation of firebreaks, fire fighting and removal of dead wood (Kulakowski *et al.*, 2017). Anthropogenic climate change is already thought to have impacted the disturbance regime, although overall the effect of climate change may be to increase disturbance by increasing fire frequency and extreme weather patterns (Dale *et al.*, 2001; Seidl, Schelhaas & Lexer, 2011; Kulakowski *et al.*, 2017). Continued climate change is expected to further alter disturbance regimes (Kulakowski *et al.*, 2017).

Human activities, such as farming and forestry, can be considered as anthropogenic disturbance (Attiwill, 1994; Fuller *et al.*, 2017). There can be direct parallels with natural disturbance: anthropogenic disturbance often creates patches of open habitat, is spatially

and temporally heterogeneous, and some of the mechanisms are even the same, for example fire is frequently used as a management tool, and domestic livestock can substitute for wild herbivores (Navarro *et al.*, 2015). In HNVf landscapes, this anthropogenic disturbance creates small patches and a diverse landscape; in contrast to intensive farming which could be considered as a much larger, more homogenous form of disturbance (Fuller *et al.*, 2017). It could therefore be argued that HNV species are, in fact, better described as species of moderately-disturbed habitats, and that the spread of human land management substituted natural disturbance processes for anthropogenic ones (Merckx & Pereira, 2015; Navarro *et al.*, 2015).

Land abandonment means that anthropogenic disturbance will cease in those areas. With natural disturbance processes also greatly reduced across much of Europe, the result is that large areas of land may end up with very low levels of disturbance, allowing a homogeneous landscape of closed canopy forest to develop. While undisturbed forests do support high biodiversity, they have a very different community to that of disturbed landscapes, and few HNV species are able to thrive (Regos *et al.*, 2016; Brambilla *et al.*, 2017). Intensively farmed landscapes represent the other extreme: high levels of disturbance and homogeneously open landscapes, equally unsuitable for HNV species.

1.2.1 Disturbance Defined

“Disturbance” in an ecological context has no agreed formal definition, although many authors have attempted to do so (Attiwill, 1994 and refs. therein). For the purposes of this thesis, I use a broad working definition of “processes which retard or reverse succession”. This definition is broader than many others, such as that given in the textbook of Begon, Townsend & Harper (2006) of “a relatively discrete event that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment”. Other definitions may also require the disturbance to be exogenous to the ecosystem (i.e. created by some outside event; Bormann & Likens, 1979). However, as discussed at length in Attiwill (1994), such narrower definitions invariably face the challenge that they require an arbitrary distinction between discrete, exogenous disturbance “events” and ongoing, endogenous ecological processes, when the reality of the situation is that there is a continuous spectrum between those extremes. There are no clear limits on how infrequent, how unpredictable or how catastrophic an event has to be to be considered disturbance, nor where to draw the boundaries of an ecosystem to determine exogenous events, and the impact of a

disturbance event will always be mediated by endogenous factors (for example, the damage caused by a storm will be influenced by the size and age of trees). My broad definition avoids these complications by setting no requirements on the nature of a disturbance process beyond the impact it has on the ecosystem. Furthermore, my definition is the most relevant one for this thesis. It is clear from the literature that openness and heterogeneity in natural landscapes is thought to be influenced by a wide range of ecological processes acting over a spectrum of duration and intensity and, in the absence of a more precise general term, I consider it to make more sense to call all of them “disturbance processes” than to arbitrarily dichotomise them (Svenning, 2002; Merckx & Pereira, 2015; Navarro *et al.*, 2015).

1.3 Rewilding as a solution

The conservation of HNV species may therefore depend on maintaining disturbance processes, either natural or anthropogenic. In Europe, there has historically been an emphasis on the latter and on conserving biodiversity by incentivising maintenance of traditional land management, particularly via agri-environment schemes (AES) which offer financial incentives to farmers to carry out farming in a more wildlife friendly manner. In the European Union (EU) AES are primarily delivered through the Common Agricultural Policy (CAP). In 2012, the total CAP budget was around €53 billion (42% of the total EU budget), of which around 10% was spent on AES or preventing land abandonment (Merckx & Pereira, 2015). AES can be expensive and have limited benefits for biodiversity, especially if poorly targeted (Princé, Moussus & Jiguet, 2012; Princé & Jiguet, 2013; Pe'er *et al.*, 2014; Batáry *et al.*, 2015). Another option would be to focus on restoring natural disturbance processes (Navarro *et al.*, 2015), which falls within the concept of “rewilding”.

In contrast to AES, which require ongoing payments to people to manage the land, natural processes are free and self-sustaining. While there may be a large initial cost in carrying out restoration as part of a rewilding project, once this restoration has been carried out there should be minimal need for ongoing management and the associated costs. Rewilding could therefore be a much more economically viable option, especially over long time scales.

1.3.1 Rewilding defined

“Rewilding” has become a contentious term, with different people using it to mean different things (Jørgensen, 2015; Lorimer *et al.*, 2015; Corlett, 2016; Pettorelli *et al.*, 2018). For the purposes of this thesis, I use rewilding in the broadest sense, defined as “to return (land) to a wilder and more natural state” (OED Online, 2018). This definition encompasses many types of rewilding, such as “trophic rewilding” (species introductions to restore top-down trophic interactions) and “ecological rewilding” (allowing natural processes to regain dominance) (Corlett, 2016), although even those definitions overlap (predation and herbivory are ecological processes). Such a definition avoids much of the controversy associated with, for example, “Pleistocene rewilding” which advocates restoring megafaunal diversity to levels comparable to those in the Pleistocene, through taxon substitution and de-extinction if necessary (Zimov, 2005; Donlan *et al.*, 2006; Caro, 2007; Svenning *et al.*, 2015).

There is also significant overlap with the term “restoration”, which can be defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Society for Ecological Restoration International Science & Policy Working Group, 2004). The definitions of both rewilding and restoration are quite broad and open to some interpretation, and further confusion arises from inconsistent usage of both terms. In my view, the key distinction is ideological rather than practical: restoration aims to recreate and maintain a specified ecosystem while rewilding aims to make “wild” spaces where natural processes, not human intervention, control the ecosystem.

As such, an area can be rewilded but not restored (such as through the abandonment of farmland, which has been termed “passive rewilding”) or restored but not rewilded (such as Lakenheath Fen RSPB reserve, wherein the water levels are controlled by pumps, sluices and dykes; Sills & Hirons, 2011). In general, however, most rewilding projects could be described as restoration projects with a focus on trophic interactions or other ecosystem processes.

1.3.2 Benefits and disbenefits of rewilding for people

In addition to affecting biodiversity, rewilding will have impacts on people, both those living locally and further afield. These impacts may be positive, resulting from ecosystem services and economic opportunities, but they may also be negative.

Rewilded landscapes may provide a range of valuable ecosystem services, such as carbon storage (Barral *et al.*, 2015; Cerqueira *et al.*, 2015) and flood alleviation (Iacob *et al.*, 2014). However, natural processes are temporally and spatially heterogeneous, and therefore the maximum benefits are only felt on a landscape or regional scale. Certain habitats, such as ancient woodland, may take centuries to develop. Therefore, rewilding is only a viable option if carried out on a large scale and considering long timeframes (Navarro & Pereira, 2012).

Rewilding can also bring economic opportunities. Nature-based tourism is the fastest growing element within the tourism sector (Kuenzi & McNeely, 2008) and rewilded landscapes offer opportunities to attract tourists for wildlife watching, photography or hunting (Navarro & Pereira, 2012). Charismatic megafauna are a particular attraction, and have been associated with dramatic boosts to local economies (Enserink & Vogel, 2006; Molloy, 2011; Deinet *et al.*, 2013).

However, rewilding does also have risks and costs. There has been vocal opposition to the return of large predators such as wolves, primarily due to the risk of depredation of livestock but also the risk to humans and pets and the potential for negative impacts on recreational hunting (Kleiven, Bjerke & Kaltenborn, 2004; Boitani, Ciucci & Raganella-Pelliccioni, 2010; Chapron *et al.*, 2014; Kovařík, Kutal & Machar, 2014). Herbivores can also come into conflict with people by eating or trampling crops, or damaging trees (Goulding & Roper, 2002; Decker *et al.*, 2010). Beavers in particular have the potential to damage large areas through building dams which create large ponds or raise the level of the water table across large areas (Macdonald *et al.*, 1995; Law, McLean & Willby, 2016; Law *et al.*, 2017). Wildlife can harbour diseases and transmit these to humans or domestic animals (Fritzemeier *et al.*, 2000; Sandom & MacDonald, 2015). The open-ended nature of rewilding projects and the (deliberate) lack of a defined target state increase the uncertainty about the costs and benefits that will result from a project, which makes it hard to carry out cost/benefit analyses or risk assessments (Pettorelli *et al.*, 2018).

Given both rising human population and rising *per capita* demand for food, global crop production is expected to approximately double between 2005 and 2050 (Tilman *et al.*, 2011). Rewilding requires, or is driven by, taking large areas of land out of production. Therefore, the loss of production associated with rewilding must be compensated for, either through increased yields or agricultural expansion in other regions. The net impact of rewilding on both biodiversity and ecosystem services will therefore depend on how

and where this demand for food is met (Green *et al.*, 2005; Foley *et al.*, 2011; Tilman *et al.*, 2011; Balmford, Green & Phalan, 2012).

Furthermore, while rewilding has been much discussed in opinion pieces within the academic community, there has been relatively little evidence produced, leading to calls for caution and the need to enhance our scientific understanding before advocating rewilding (Svenning *et al.*, 2015; Nogués-Bravo *et al.*, 2016; Rubenstein & Rubenstein, 2016; Sandom *et al.*, 2016).

1.4 Focus on flooding

Rewilding is a broad and complex topic, so I have chosen to focus on one natural disturbance process: flooding. Water is an essential element of all ecosystems. Plants differ in how much or how little water they can tolerate (Ellenberg *et al.*, 1991) and thus water is important in determining the dominant vegetation (Begon *et al.*, 2006). It is also a powerful physical force: extreme flood events can dramatically reshape the landscape in a matter of hours (Richards, Brasington & Hughes, 2002) and even without extreme events, rivers can shape landscapes through gradual erosion and deposition (Makaske, 2001). However, rivers and wetlands are also subject to strong human influences.

Rivers across Europe have been heavily modified for centuries, and vast areas of former floodplain drained (primarily for agriculture) (Brinson & Malvárez, 2002; Tockner & Stanford, 2002; Davidson, 2014; Davidson, Fluet-Chouinard & Finlayson, 2018). Many rivers, especially larger ones, have been used for transport, and this has driven flow regulation to keep rivers navigable all year round (Berga *et al.*, 2006). More recently, power generation has become another driver of river regulation, to maximise energy generation potential and spread it across the year (Berga *et al.*, 2006; Lehner *et al.*, 2011; Olden *et al.*, 2014). There are around 7,000 large dams in Europe, and many smaller ones (EEA, 2007), and almost all of Europe's major rivers are regulated to some extent (Nilsson *et al.*, 2005; Birnie-Gauvin *et al.*, 2017), mirroring the global trend (Berga *et al.*, 2006; Lehner *et al.*, 2011). As well as discharge regulation, both navigation and energy generation often require modification to the river channel (Čížková *et al.*, 2013). Overall, >90% of riverine floodplains in Europe are thought to be functionally extinct, cut off from the river and often cultivated (Tockner & Stanford, 2002).

Recently, however, there has been a reversal in the approach to managing rivers and the number of dams is reducing in both Europe and North America (Poff & Hart, 2002; EEA,

2007; Lovett, 2014). EU projects such as REFORM (*REFORM Policy brief*, 2015) and a range of national or local projects aim to restore rivers or floodplains (for example Bernhardt *et al.*, 2005; Pearce, 2013; Room for the River, 2014; Lamouroux *et al.*, 2015; Hein *et al.*, 2016; Angelopoulos, Cowx & Buijse, 2017; Golfieri *et al.*, 2017; RESTORE, 2017; Zingraff-Hamed *et al.*, 2017). Most of these projects do recognise the potential for improving biodiversity, although often either with a very narrow focus on improving connectivity for migratory fish or a very vague stated motivation about improving ecological health (Golfieri *et al.*, 2017; RESTORE, 2017; Zingraff-Hamed *et al.*, 2017). Even when improving biodiversity is among the stated aims, often a far stronger driver is recognition of the range of ecosystem services local residents gain from healthy rivers and floodplains (Bernhardt *et al.*, 2005; Golfieri *et al.*, 2017). Of these, reducing the risk of flooding in downstream urban areas can be the most pressing, and damaging floods are often the catalyst for restoration upstream (POST, 2011; Pilkington *et al.*, 2015; Zingraff-Hamed *et al.*, 2017). Floodplains act as temporary storage areas for excess water, so peak discharge can be reduced, lowering the likelihood of flooding downstream (Acreman & Holden, 2013; Alfieri, Feyen & Di Baldassarre, 2016). There are also benefits for amenity value and recreation, carbon storage, and water quality (Sutfin, Wohl & Dwire, 2015; Bridgewater & Aricò, 2016; Hein *et al.*, 2016; Zingraff-Hamed *et al.*, 2017).

River and floodplain restoration does have costs: within the continental United States, over \$1 billion is spent every year on restoration of streams and rivers (Bernhardt *et al.*, 2005). Most obviously, there will be a cost involved in carrying out the restoration work in terms of labour, equipment and materials (Bernhardt *et al.*, 2005). There will also be an opportunity cost: many floodplains have been drained and used for agriculture so restoring them to functioning floodplains would require taking that land completely out of production, or switching to lower yielding and less profitable forms of agriculture such as wet grazing (Pedersen *et al.*, 2007; Schrautzer *et al.*, 2016). In other cases, floodplains will have houses, roads or other infrastructure on them, and there may be a significant cost in relocating these (EEA, 2017a). One example is the Nijmegen project within the Dutch Room For The River programme, which cost €359m and involved relocating 50 houses (ClimateWire, 2012). Where dams are removed or flow regimes altered, this could lead to less energy being produced and the associated opportunity cost (Olden *et al.*, 2014; Barthélémy & Armani, 2015). From an ecological point of view, there is some evidence that river restoration may benefit invasive species (Roni, Hanson & Beechie, 2008; Paillex *et al.*, 2015; Toth, 2017).

1.5 This study

Given the potential link between natural disturbance processes and HNV species, and the current political interest in floodplain restoration for both biodiversity and ecosystem services, I felt it was an ideal opportunity to test the hypothesis that HNV species can also be considered as species dependent on disturbed habitats, and therefore that restoring natural disturbance processes can benefit those species.

I first considered a naturally flood-disturbed area, to investigate the potential of natural flood regimes to provide the kind of disturbance-reliant habitats that HNV species require. I then considered two areas where projects have been undertaken to restore flood regimes and floodplains. These two projects differed significantly in their scope and methods. This enabled me to investigate whether restoration projects can successfully recreate disturbance-reliant habitats, and whether the success is influenced by the restoration interventions carried out.

To investigate these things, I focused on two taxa as indicators of biodiversity: birds and butterflies. I carried out fieldwork in three regions as described above. In each region, I surveyed birds and butterflies throughout the bird breeding season, in order to estimate population densities of each species in different land cover types. I also mapped habitats and aspects of the disturbance regime, including attempting to understand the frequency of flood events.

These data enabled me to compare species' population densities between land cover types and to begin to look for patterns which may link species' population densities to certain habitat features, and for patterns linking disturbance regimes with creating those habitats.

Finally, I carried out a trait-environment analysis to look for patterns linking species' traits to environmental features. It may be expected that certain traits are associated with certain environmental features. For example, early-successional habitats may be associated with highly mobile species capable of dispersing and finding these ephemeral habitat patches.

2 GENERAL METHODS

2.1 Introduction

The bulk of the data used in this thesis were collected during three field seasons. While there were some variations between seasons (which are described in detail in the respective chapters) many of the protocols for both data collection and analysis were common throughout, or only slightly modified from the general protocol. To minimise repetition, I have detailed the general methods here.

In choosing study regions, I aimed to test three key hypotheses. Firstly, that naturally flood disturbed habitats support high levels of biodiversity, including HNV species. Secondly, that restoring floodplains recreates the conditions of a natural floodplain. Finally, that the nature of the restoration carried out changes the effectiveness of the restoration project. To this end, my first study region was in a large, nearly natural floodplain in Ukraine. My second and third regions, in France and Germany respectively, were both locations where restoration projects had been carried out, and the two projects differed significantly in their situation and implementation. Fieldwork was carried out in Ukraine, France and Germany in 2015, 2016 and 2017, respectively. I have briefly introduced the study sites in this chapter, but each is given a more detailed introduction in the subsequent chapters.

2.2 Study systems

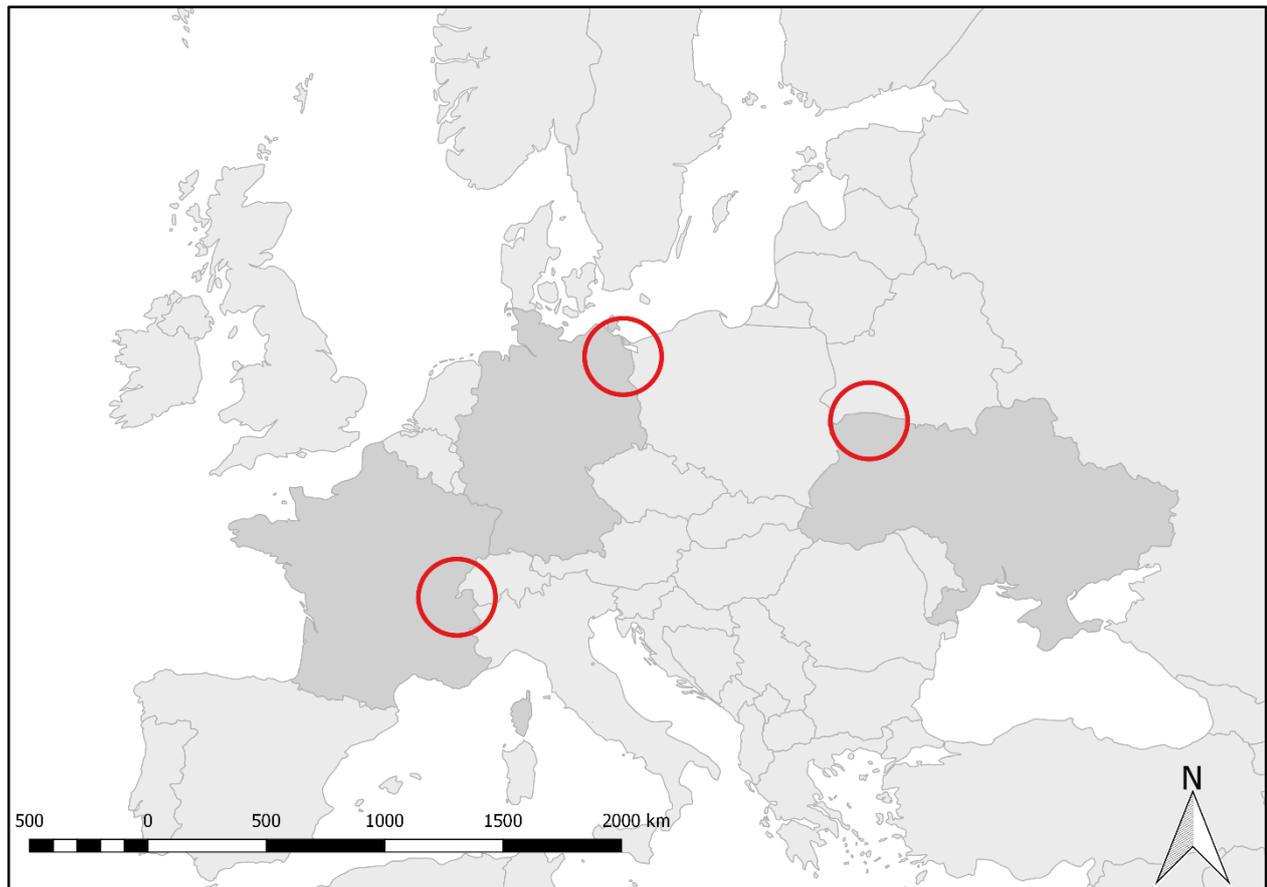


Figure 2.1 – Map showing approximate locations of three study regions (red circles) and highlighting the countries in which each was located: Ukraine, France and Germany (dark shading). More detailed maps are included in subsequent chapters.

2.2.1 Ukraine – Pripjat-Stokhid National Nature Park and surroundings

Pripjat-Stokhid National Nature Park (PSNPP) is in Volyns'ka oblast, Ukraine. The park itself is on the northern edge of Ukraine (directly bordering Belarus), and close (~100km) to the western border of Ukraine with Poland. PSNPP is one of the best examples of a natural floodplain in Europe, having never been subjected to flow regulation or channel management (Čížková *et al.*, 2013). The rivers Pripjat and Stokhid (which have their confluence in the park) both display dynamics and morphologies typical of lowland meandering rivers (Richards *et al.*, 2002).

The land surrounding the park is used for a mixture of agriculture and forestry. Following the collapse of the Soviet Union, agriculture in the surrounding countryside reverted to smallholder farming with very low chemical inputs and low yields (Hostert *et al.*, 2011). Land was returned to the people, with the result that most households own a small plot of

land on which they grow a variety of crops. Many households also own livestock. Pigs are fed on swill, while cattle and horses are grazed on communal land. Hay is used to feed cattle and horses over winter. There is little mechanisation; a lot of the work is done manually or using horses, although tractors or other machinery may be hired for specific tasks (pers. obs.). These characteristics are typical of High Nature Value farmland (HNVf) (Andersen *et al.*, 2003).

PSNPP and its surroundings therefore offered an ideal location to test my first hypothesis, that naturally flood disturbed habitats support high levels of biodiversity, including HNV species. The park itself is a naturally flood disturbed ecosystem, while the surrounding agricultural land is HNVf. If the hypothesis is correct, then I would expect several HNV species to have population densities in the park that are equal to or higher than the population densities in the surrounding HNVf. This location has the added benefit of being geographically close and ecologically and climatically similar to the Lubelskie region of Poland studied previously (Feniuk, 2015), which I used as a reference to contextualise the population density estimates I observed (see below).

2.2.2 France – The Rhône

My second study region was a section of the Rhône between Lyon and Geneva. The Rhône is one of the major rivers in Europe, flowing from the Swiss Alps through France to the Mediterranean Sea. It has a long history of human use, dating back to ancient times (Koch, 2006). Over time, but particularly in the mid-20th Century, the river was modified and regulated, including the construction of several dams and diversionary canals, and canalisation of the natural river. These modifications were carried out to improve navigability, provide a reliable water source for agricultural irrigation, reduce flood risk, and generate hydro-electric power (Olivier *et al.*, 2009).

However, in 1990 damaging floods in Lyon prompted a re-evaluation of the management (Lamouroux *et al.*, 2015). It was decided to implement a restoration project, which commenced in 1999. The restoration can be broken down into two key components. One component was to increase the minimum discharge through the natural channel and the other was to carry out engineering works to reconnect or rehabilitate floodplain channels (small erosional channels within the floodplain) (Lamouroux *et al.*, 2015). Not all floodplain channels were subject to restoration, giving the opportunity to directly compare restored and non-restored channels.

There is diverse land use within the study region: some areas within the floodplain are protected as nature reserves, others are used for forestry or agriculture (Olivier *et al.*, 2009). Both agriculture and forestry in the region are typical of modern, intensive systems with high chemical inputs and mechanisation. Study sites were selected to represent different land cover categories, enabling comparisons across them. This addresses the question of how species' population densities are related to habitat type over a wider range of potential habitats.

2.2.3 Germany – The Peenetal

My third study region was the Peene river valley, or Peenetal, in the north-east of Germany. Although not a major river like the Rhône, the Peene has still been important for local people for centuries, for example being used for transport, irrigation and industry (*Museum im Steintor*, 2009). The natural floodplain was also disconnected from the river using dykes, and drained using ditches and pumps. This “reclaimed” land was then used for agriculture.

As with the Rhône, recent decades have seen a re-evaluation of the management strategy and a restoration project has been implemented (Zweckverband Peenetal-Landschaft, 2018). However, the restoration carried out in the Peene valley was significantly different from that carried out in the Rhône. The focus of the Peene project was reconnecting and rewetting the natural floodplain, by removing or setting back dykes and decommissioning pumping stations. The result was that several large areas have been re-exposed to a natural flooding and inundation regime. Unlike the Rhône, which focused on water channels within the floodplain, this project has rewetted large areas of terrestrialised floodplain.

My study points were chosen to sample both these areas of restored habitat, and the surrounding agriculture, which represents the non-restored land cover. The surrounding agriculture is intensive, with large fields and widespread use of chemicals and machinery. This comparison of restored versus unrestored allowed me to investigate the hypothesis that restoring flood disturbance recreates disturbance-reliant habitats and supports the associated species.

2.3 Field survey methods

2.3.1 Introduction

Within each study region (Ukraine, France and Germany), a number of study sites were chosen. The exact protocol for each region is described in their respective chapters, but broadly sites were chosen to capture both floodplain habitats, and agricultural landscapes representative of the type of agriculture that could be, or used to be, carried out on drained floodplain within the region. The “study point” is the exact location at which bird point counts were carried out; the “study site” consists of a 100m radius circle around each study point. Butterfly and disturbance transects were contained entirely within the study site, and the entire study site was covered by habitat mapping.

All fieldwork was carried out between the start of April and the end of June, corresponding to the bulk of the breeding season for birds. Each site was visited at least twice, normally three or four times, spread regularly over the course of the field season.

2.3.2 Selection of focal taxa

Given the constraints of field data collection, it was necessary to select focal taxa to represent biodiversity. Birds and butterflies were chosen due to a number of characteristics which made them particularly suitable. Firstly, both have been studied closely in relation to agriculture and the effects of changing agricultural practices (for example Donald *et al.*, 2001; Thomas, 2005; Rundlöf, Bengtsson & Smith, 2008; Kleijn *et al.*, 2011). Both taxa can be considered useful as ecological indicators, representative of wider biodiversity (Kremen, 1992; Buckland *et al.*, 2005; Gregory & Strien, 2010). However, it has also been suggested that birds are a relatively insensitive indicator group, declining less than other taxa in response to anthropogenic changes (Thomas *et al.*, 2004; Gregory, 2006). Perhaps this is because birds are highly mobile, relatively long lived and large bodied compared to most taxa, or because they are relatively intelligent and adaptable (May, 1988; Gregory, 2006; Balanoff *et al.*, 2013). Finally, both birds and butterflies are relatively easy to survey in the field, a key consideration given the limited time and resources available.

2.3.3 Bird survey methods

I surveyed birds using point counts. Point counts were chosen instead of transects as the nature of the landscape made carrying out suitable transects infeasible in many of my

study sites. Impenetrable vegetation or deep water made it impossible to traverse a fixed transect route for any significant distance, and even where possible to move through the vegetation it would have been impossible to do so while simultaneously carrying out an effective survey.

Most surveys were carried out between sunrise and three hours after sunrise, as this is the period of greatest activity and therefore highest detection probability (Bibby *et al.*, 2000). For logistical reasons, in some cases this was extended by up to 30 minutes on either side. Surveys were not carried out in strong wind or rain, as these could both suppress bird activity and reduce detection probabilities (Sutherland, 1996).

As mentioned previously, the sampling period was chosen to align with the bird breeding season. This maximises detectability, as bird song is primarily associated with establishing territories and attracting mates (Bibby *et al.*, 2000). Repeat surveys over the field season maximised the number of species detected, as individual species' breeding seasons are often subsets of the complete season.

Surveys were for a fixed duration of 10 minutes. I recorded all birds detected, along with the detection method (visual, calling, singing or drumming) and distance from the observer, which I estimated with the help of a laser rangefinder. As some species are aerial feeders and rarely detected when stationary, I included an instantaneous "snapshot" of birds in flight at the end of the survey period; I discarded all other records of birds in flight prior to analysis. The unit of detection was the "cluster"; in practice most detections were of solitary birds (cluster size = 1) but occasionally groups or flocks were detected, in which case the number of birds in the cluster was counted or (for large flocks) estimated visually (Sutherland, 1996).

Most detections were by song. Where I could not identify a song in the field, whenever possible I made a sound recording for later identification by comparison with known samples (xeno-canto.org, 2018). Where a species' identification remained uncertain, I discarded those records.

Given that detection of birds was imperfect, and that the probability of detection at a given distance is likely to vary between species and habitats, it was necessary to account for probability of detection in order to estimate absolute abundances or even compare relative abundances between species or sites. "Distance sampling" is one way to do this (Buckland *et al.*, 2001, 2007). I estimated detection distance-decay functions using the *mrds* package

(Laake *et al.*, 2015) in R (R Core Team, 2017). Species with ≥ 30 detections were modelled individually; species with < 30 detections were grouped based on detectability characteristics (for example species that could be reliably acoustically identified at long distances such as cuckoo and bittern were grouped together) such that each group had ≥ 30 detections, and detection functions were fitted to the group as a whole. Records were right-truncated at 100m, and left-truncated at 20m due to evidence of reduced detection near the survey point (birds may freeze, hide or fall silent if they feel threatened by a nearby presence; Buckland *et al.*, 2001). Both the detection method and the proportion of closed habitats could influence the probability of detection; therefore detection functions were fitted with no covariates, detection method as a covariate, proportion of closed habitats as a covariate, and both detection method and proportion of closed habitats as covariates (Buckland *et al.*, 2007). With no *a priori* reason to favour a particular shape of detection function, I fitted functions using combinations of Key Function, Adjustment Term and Number of Terms, as outlined in Table 2.1. Some species showed no decline in detection probability (for example cuckoo, whose song can be easily heard over 100s of metres) so a uniform detection function was used for these species. Models which failed to fit, showed severe non-linearity on a quantile-quantile plot, or produced detection probability curves which violated the assumptions of distance sampling were excluded. The estimated density and estimated effective detection radius were then calculated using model averaging of the remaining models, weighted by AIC_c (Burnham & Anderson, 2002).

Table 2.1 – Key Functions, Adjustment Terms and Number of Terms used in fitting detection models to bird survey data.

Key Function	Adjustment Term	Number of terms in series expansion
Hazard Rate	Cosine	0, 2, 3
	Simple polynomial	0, 2, 4
Half-normal	Simple polynomial	0, 2, 4
	Cosine	0, 2, 3

2.3.4 Butterfly survey methods

I surveyed butterflies using “Pollard Walks” (Pollard, 1977): strip transects 5m wide (2.5 m to either side of the observer) and 5m high, in which the observer counts all butterflies within 5m in front of them. Transects were typically 200m long (100m in my French study region) although some were truncated due to practical constraints. In most cases transects were a straight line passing through the study point, although in some cases a turn of $<90^\circ$ was introduced at the study point due to practical considerations.

I calculated density estimates assuming perfect detection; however, all the conclusions presented herein apply equally if detection was not perfect but still a constant probability across sites and species. As detection is unlikely to have been perfect, densities quoted in results should not be treated as absolute but only reflect relative abundance per unit area. Nevertheless, it has been shown that detection probabilities using Pollard walks are high across different species and sites, and that results with and without distance sampling are highly correlated (Isaac *et al.*, 2011). The results and conclusions drawn from them are therefore unlikely to be significantly influenced by this assumption.

Butterfly surveys were only carried out in suitable conditions (van Swaay *et al.*, 2012). This meant between 3.5 hours before and 3.5 hours after solar noon, extended by up to an hour either side under exceptionally hot ($>25^\circ\text{C}$) conditions; air temperature of at least 18°C , or at least 13°C if there was $<50\%$ cloud cover; and wind level ≤ 5 (“fresh breeze”) on the Beaufort scale.

When a butterfly could not be identified in the field, if possible photographs were used for later identification. When a butterfly could not be reliably identified to species level, it was identified to the finest possible taxonomic level. Identification and taxonomy were primarily based on the Collins Butterfly Guide (Tolman & Lewington, 2009).

Butterfly species often have relatively short flight periods, and species differ in their flight period and voltinism (number of generations per year). Repeat surveys therefore increase the number of different species detected. Butterfly monitoring schemes often run throughout the summer months (van Swaay *et al.*, 2012), but it was not feasible to extend my fieldwork to span the entire period of butterfly flight activity. My results are therefore not comparable with surveys which cover the entire summer and certain species may be over- or under-represented in my surveys. However, as each of my field seasons was carried out at the same time of year they can be compared to each other, and there is no

reason to believe that this period of surveying prejudices the results to favour a particular conclusion with regards to the hypotheses posed.

2.3.5 Biotic disturbance survey methods

In both Ukraine and Germany, I estimated the level of biotic disturbance in my study sites by recording any signs of biotic disturbance observed from a transect. The transect line used was the same as for butterfly surveys in all cases, and all signs of disturbance observed were recorded, with no limit on distance from the transect line. I assumed that, for each type of disturbance, detection probabilities remained constant across sites. Examples of signs recorded include tree stumps felled by beavers, deer droppings, and animal trails in the vegetation. I classified signs of disturbance into a small number of categories (seven and four in my Ukrainian and German studies, respectively). I have included a complete list of disturbance types and their respective categories in Appendix 1. Scores were standardised to 0-1 within each disturbance category.

In addition, I checked shrubs for signs of browsing by large mammals. All shrubs within 2.5m of the line of the transect and at least 5m from the previous recorded shrub were checked and recorded as a binary (browsing present/absent). I excluded sites with <5 shrubs in total because of the small sample size. For the remaining sites, I calculated the proportion of browsed shrubs, which was then added to my disturbance data as a separate category.

I carried out each transect twice, and used mean values from the two transects. Within each study region, I then used category scores to carry out a Principal Components Analysis (PCA). After considering the PCA outputs, in both cases I used the first two components of the resulting matrices as metrics of disturbance in each site. Further details and interpretation of the components used are given in the relevant chapters.

2.3.6 Habitat and vegetation structure survey methods

I mapped habitats and vegetation structures for each study site. Each study site was divided into habitat patches, where each patch was an approximately homogeneous area of habitat. An initial sketch of habitat patches was made from satellite imagery of each site, although this was modified in the field where the imagery was out of date, or failed to distinguish between patches of different habitat. For each habitat patch, the following data were recorded:

- Habitat type
- Dominant vegetation height (the height at which ground cover equals 50%), in metres
- Water depth, in centimetres
- % vegetation cover at 1m height
- % vegetation cover at 2m height
- % vegetation cover at 5m height
- % vegetation cover at 10m height

An example is shown in Figure 2.2.



Figure 2.2 – Example of a habitat patch, showing estimated vegetation cover and dominant vegetation height. The “patch” is the area of scrub in the middle ground of the photo – the open vegetation in the foreground is a separate patch. Blue lines indicate approximate cover in height classes: ~85% at 1m, ~60% at 2m, ~55% at 5m and 0% at 10m (no line visible). The orange line shows the dominant vegetation height of ~5.5m. Note that in the field vegetation height and cover were estimated across the whole of each patch, not based on a single viewpoint. This photo is therefore best considered as a rough illustration of the method used rather than a complete example.

I digitised habitat maps using QGIS, and used a built-in function to extract the area of each patch. For analysis purposes, permanent water bodies that were too deep to measure in the field were assigned a depth of 100cm.

From the above data, I calculated the following for each study site (with my shorthand term for that variable in brackets):

- Area of each habitat, in m² (area)
- Area-weighted mean dominant vegetation height, in metres (mean.height)
- Area-weighted mean % vegetation cover at 1m (mean.1m)
- Area-weighted mean % vegetation cover at 2m (mean.2m)
- Area-weighted mean % vegetation cover at 5m (mean.5m)
- Area-weighted mean % vegetation cover at 10m (mean.10m)
- Area-weighted standard deviation in % vegetation cover at 1m (sd.1m)
- Area-weighted standard deviation in % vegetation cover at 2m (sd.2m)
- Area-weighted standard deviation in % vegetation cover at 5m (sd.5m)
- Area-weighted standard deviation in % vegetation cover at 10m (sd.10m)
- Area-weighted mean water depth, in centimetres (water depth).

Those variables, except for area-weighted mean water depth, were then used in a PCA for each region, with full details given in the relevant chapters. Based on the results of these PCAs, in all cases I decided to use PC1 as the primary metric of vegetation structure for analysis. This corresponded well with a gradient between open and closed habitats. Water depth was not used in the habitat PCA as water depth was hypothesised to be an independent disturbance factor that influences vegetation structure and so was analysed separately.

2.3.6.1 Principal Components Analysis

PCAs have been much discussed in the literature, both in comparison to other ordination techniques and with regards to the virtues (or lack thereof) of carrying out any kind of ordination (e.g. Kessell & Whittaker, 1976; Nichols, 1977; Austin, 1985; Kent & Ballard, 1988; Vaughan I. P. & Ormerod S. J., 2005). For both my disturbance data and habitat data, and for the purposes of this study, I felt that the PCA approach was the most appropriate.

The primary objective of a PCA is to reduce dimensionality by transforming the data such that the greatest variance is contained within the fewest dimensions (Crawley, 2013). Both my habitat data and disturbance data have high dimensionality in the raw data; I took many different measurements related to the habitat and recorded many different types of disturbance. In both cases, reducing the dimensionality allows the strongest patterns to be extracted and therefore allows greater discrimination between sites. Reducing the dimensionality also allows more powerful statistical testing of the impact of habitat or disturbance on other variables, such as the density of birds and butterflies.

No single raw variable fully describes the habitat or the disturbance regime of a site, and fitting models with many explanatory variables reduces the explanatory power of the models and can lead to overfitting. Using a PCA to reduce the dimensionality overcomes this, by combining raw variables to create a single or small number of explanatory variables that more fully describe the variation in habitats or in disturbance regimes.

A common criticism of ordination approaches is that they are a “black box” and the output can be hard to interpret. While in some cases this can be true, it is not an inherent problem with the PCA approach but rather a reflection of frequent poor communication. If explained carefully, as I believe I have done in this thesis, then the results of a PCA can be satisfactorily understood.

2.3.7 Flood Risk Score

In addition to water depth measured in the field, I wanted a metric that gave an indication of long-term flood disturbance. I therefore used time series of remotely sensed data to calculate a “Flood Risk Score” for each of my study regions. This score is intended to reflect what proportion of time a particular parcel of land is inundated with water. At one extreme, permanent water bodies should have a score of one and, at the other, areas which are never inundated should have a score of zero. Most of the floodplain should have intermediate values, representing a gradient between wetlands which are inundated most of the time, to the edges of the floodplain which might only be inundated in severe flood events.

I decided Landsat data were appropriate for this task. Landsat data have high spatial resolution, with a 30x30m pixel size. This enables Flood Risk Score to be calculated at a scale which is relevant to the size of my study sites and can capture fine patterns. Landsat data also have high temporal resolution, with repeat cover of each scene every 8 days.

While this may be insufficient for some purposes (such as real-time monitoring of water levels; Ticehurst, Guerschman & Chen, 2014) it is sufficient for estimating flood frequency over many years. Landsat data are freely available from USGS EarthExplorer (<https://earthexplorer.usgs.gov/>) in the form of “scenes” which cover a defined parcel of land at a single moment in time.

First, data were downloaded according to the following criteria. All scenes covering each field region were included (note that there is some overlap between scenes, so study sites may be included in more than one scene). Data from Landsat 4/5 TM and Landsat 7 ETM+ were included, both of which follow the same bands of spectral response (USGS, 2017). The date range selected depended on the study region: I only selected dates subsequent to restoration where relevant (details given in respective chapters). TM data is available for the period 1982–2013; ETM+ data has been collected since 1999 (although images after 2003 have some missing data due to the Scan Line Corrector failure; USGS, 2018). I further filtered the results to include only daytime scenes and those with <30% cloud cover.

All images meeting the above criteria were downloaded for analysis as Level 1 Data products. The Level 1 data are response scores in each spectral band, following pre-processing by USGS to ensure consistency and quality (USGS, 2017). The first step was to apply the formula for modified Normalised Difference Water Index (mNDWI) (Xu, 2006) to each pixel based on the response scores to the Green (Band 2; 0.52-0.60µm) and Middle Infrared¹ (MIR; Band 5; 1.55-1.75µm) spectral bands:

$$\frac{\textit{Green} - \textit{MIR}}{\textit{Green} + \textit{MIR}}$$

mNDWI gives a score for each pixel, with higher values more likely to be water. I then applied a threshold of zero to each pixel, to classify the pixel into a binary of “water” or “not water” (Xu, 2006). All individual scenes were then overlaid, and the mean value was taken for each pixel. This mean value was used as the Flood Risk Score for each pixel, and represents a gradient from “never water” (Flood Risk Score = 0) to “always water”

¹ Also known as Shortwave Infrared (SWIR) in some Landsat documentation.

(Flood Risk Score = 1). For analysis, I then calculated the area-weighted mean Flood Risk Score for each study site (as some pixels are not fully contained within the study site).

Flood Risk Score was significantly positively correlated with the water depth measured in the field in all three of my study regions (Figure 2.3). This correlation was much stronger in France and Germany than in Ukraine, possibly because in France and Germany there tended to be a stronger contrast between terrestrial habitats and aquatic habitats than in Ukraine, where there was a more gradual transition including many wetland habitats with dense emergent or floating vegetation, or even flooded forests with water under closed canopy woodland.

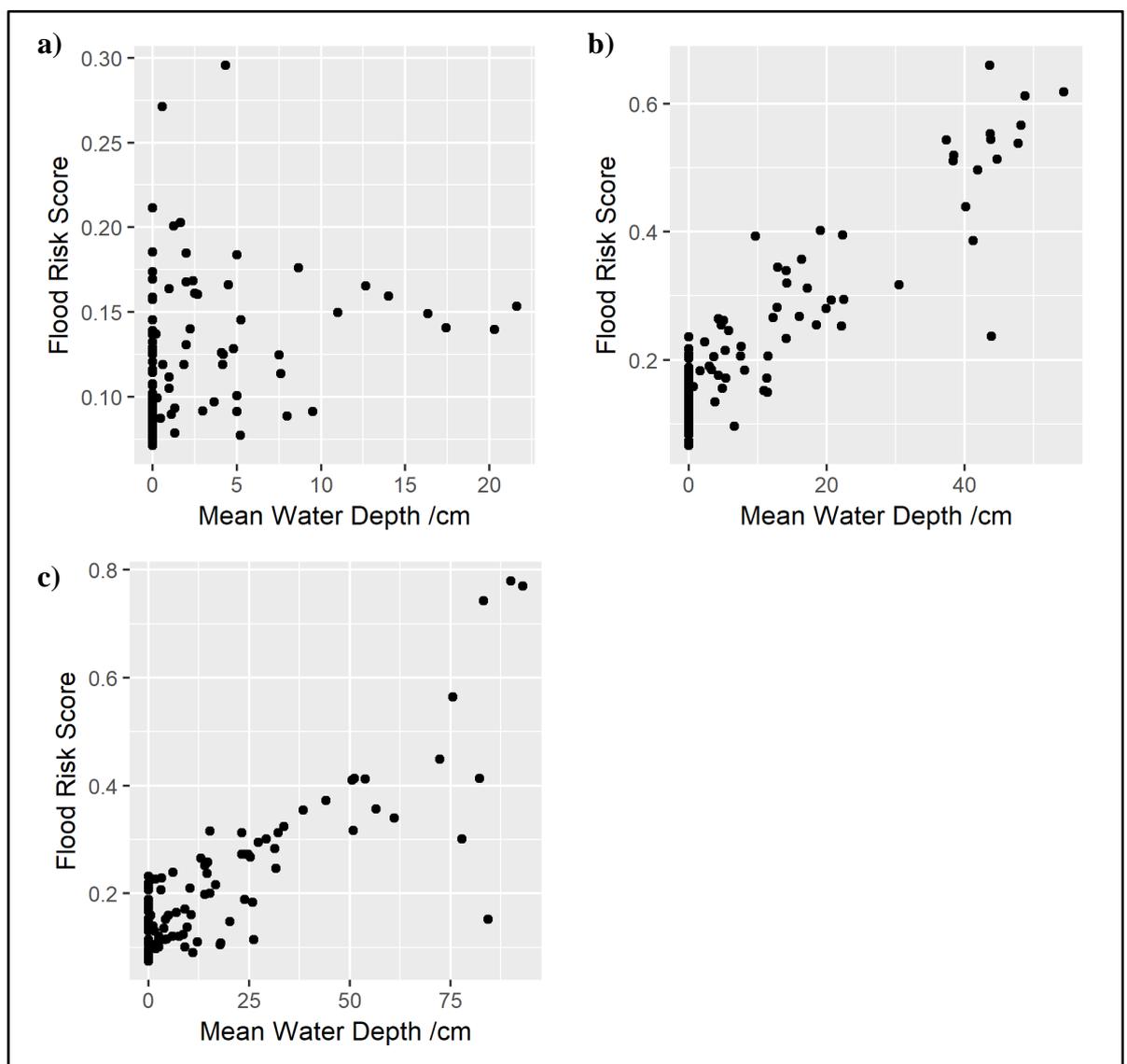


Figure 2.3 – Flood Risk Score was positively correlated with water depth in all three study regions: **a)** Ukraine (Pearson’s $r = 0.21$, $n = 92$, $p < 0.05$); **b)** France (Pearson’s $r = 0.91$, $n = 120$, $p < 0.001$); **c)** Germany (Pearson’s $r = 0.83$, $n = 112$, $p < 0.001$). Each point is a study site.

2.3.7.1 An alternative to Flood Risk Score: Global Surface Water

A recent study (Pekel *et al.*, 2016) performed a conceptually similar operation to my Flood Risk Score on a global scale, albeit with several methodological differences. In brief, they used the entire Landsat archive from 16 March 1984 to 10 October 2015; water was distinguished from not water using an ensemble of expert system, visual analytic and evidential reasoning models. Their “Water Occurrence” layer is directly comparable to my Flood Risk Score, ranging from 0% (never water) to 100% (always water). I therefore considered the option of using this published and publicly available dataset instead of my own Flood Risk Score. To inform this decision, I compared my own Flood Risk Score to the Global Surface Water Occurrence Layer (GSW OL) for all of my study regions. As with Flood Risk Score, I calculated the area-weighted mean GSW OL pixel value for each of my study sites to create a “GSW OL score”.

In Ukraine, the GSW OL produced a very different result to my Flood Risk Score, giving almost all pixels within my study sites a score of zero, and as a result not correlating with either Flood Risk Score or water depth as measured in the field (Figure 2.4). Looking at the GSW OL across the study region, it appears that it did a very poor job of identifying water within PSNPP in general, with the majority of pixels having a zero occurrence score. While the GSW OL did pick out the major, permanent water bodies, it suggested that water never occurs within most of PSNPP. In contrast, my Flood Risk Score gave most of PSNPP an intermediate score, corresponding to partial water occurrence (Figure 2.5). Given the nature of PSNPP as a wetland system, the GSW OL scores seem implausible.

In France, the results of the GSW OL were more in line with both my Flood Risk Score and field-measured water depths, correlating positively with both of them (Figure 2.6). However, the GSW OL scores were nevertheless heavily skewed towards zero, with 89 out of 120 (74%) of my sites having a GSW OL score of zero.

In Germany, the results were very similar to France. Overall there were positive correlations with both Flood Risk Score and field water depth, but the GSW OL scores were again zero for many sites (Figure 2.7).

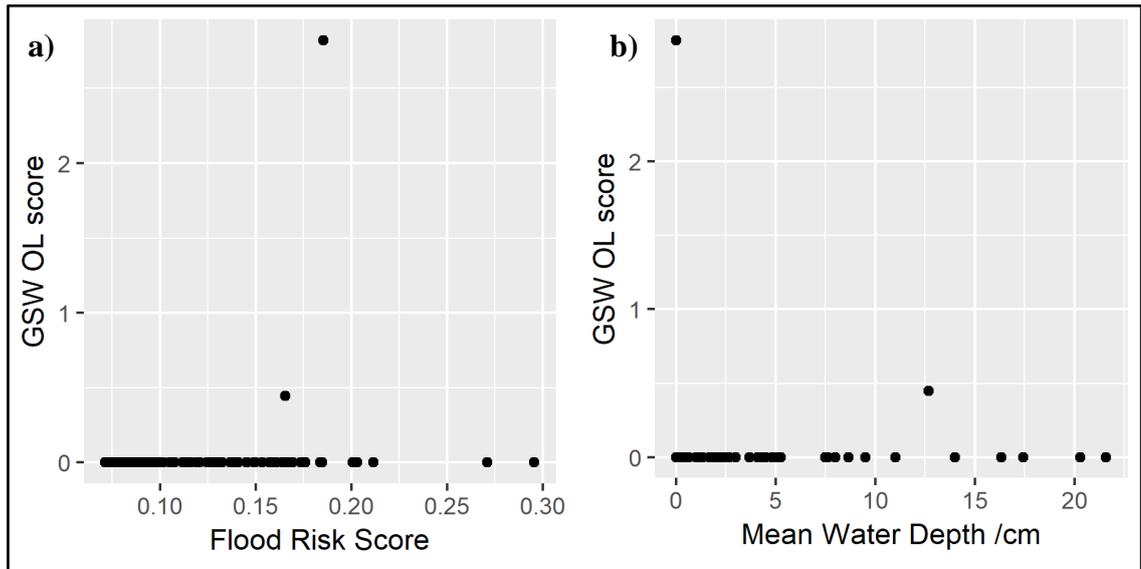


Figure 2.4 – For my Ukrainian study region, neither Flood Risk Score nor water depth were correlated with GSW OL scores. **a)** Flood Risk Score (0-1) and GSW OL score (%) (Pearson's $r = 0.164$, $n = 92$, N.S.). **b)** Water depth (cm) and GSW OL score (%) (Pearson's $r = -0.024$, $n = 92$, N.S.). Each point is a study site.

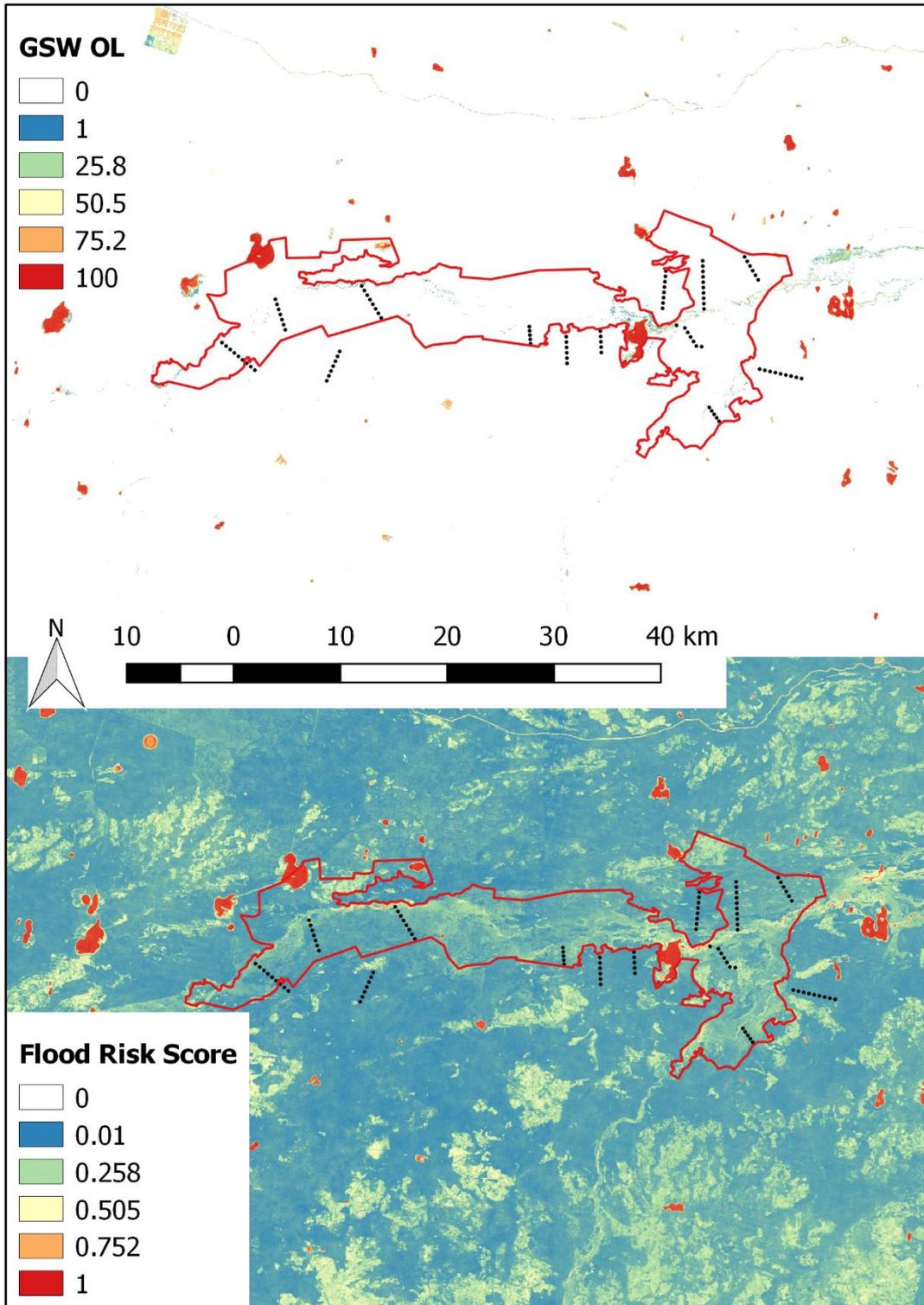


Figure 2.5 – Maps of Ukrainian study region showing GSW OL scores (top) and my Flood Risk Score (bottom) on the same colour scale. Red outline shows PSNPP; black dots are study sites. Orientation and scale are the same in both maps.

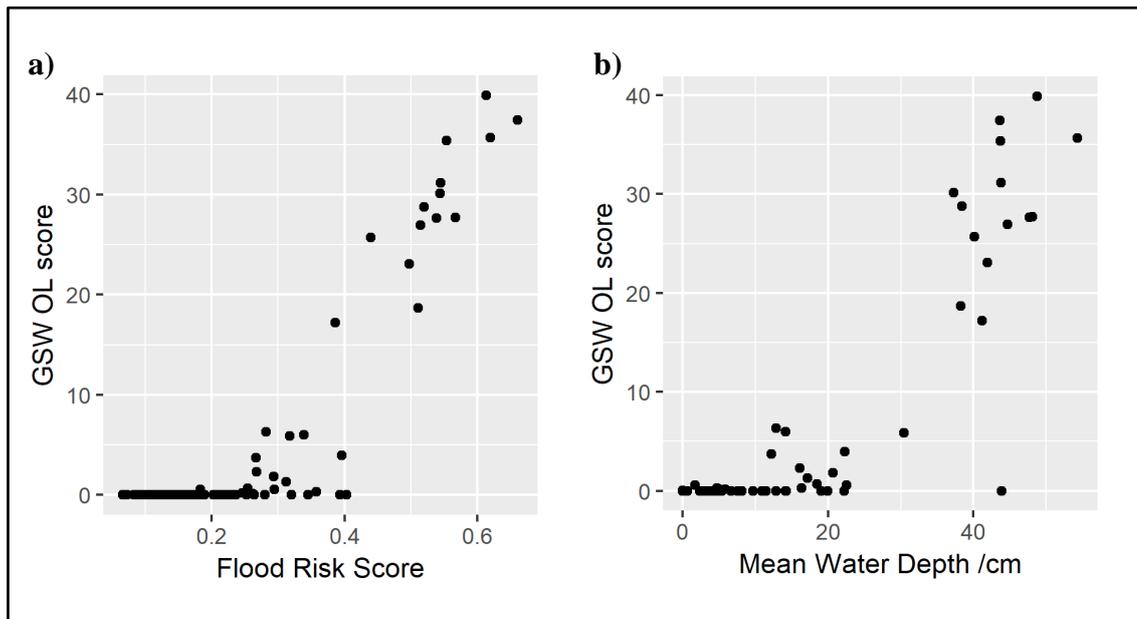


Figure 2.6 – For my French study region, both Flood Risk Score and water depth were positively correlated with GSW OL scores. **a)** Flood Risk Score (0-1) and GSW OL score (%) (Pearson’s $r = 0.872$, $n = 120$, $p < 0.001$); **b)** Water depth (cm) and GSW OL score (%) (Pearson’s $r = 0.867$, $n = 120$, $p < 0.001$). Each point is a study site.

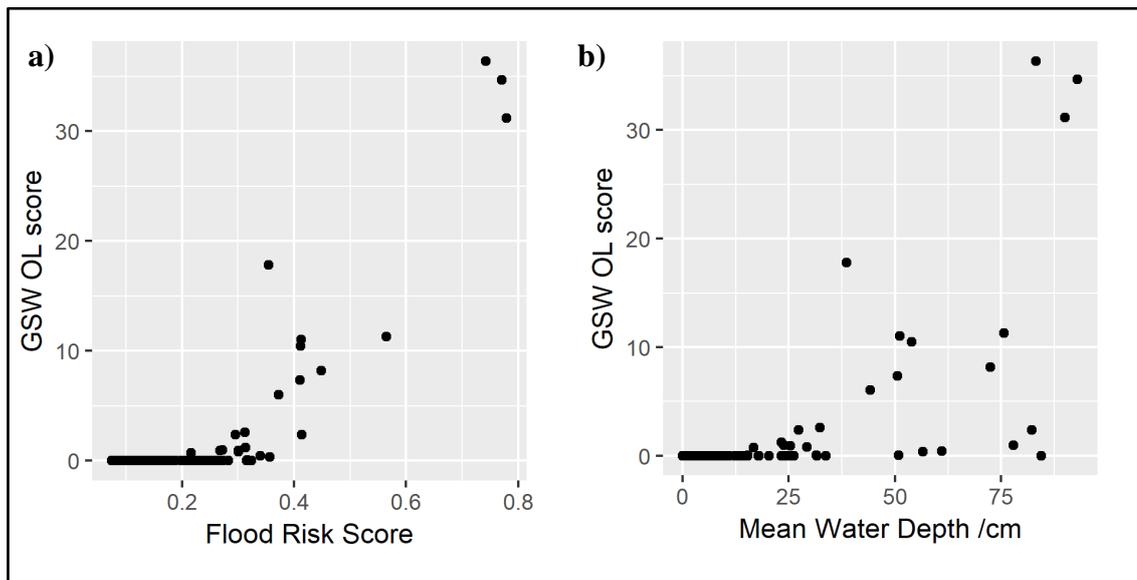


Figure 2.7 – For my German study region, both Flood Risk Score and water depth were positively correlated with GSW OL scores. **a)** Flood Risk Score (0-1) and GSW OL score (%) (Pearson’s $r = 0.828$, $n = 112$, $p < 0.001$); **b)** Water depth (cm) and GSW OL score (%) (Pearson’s $r = 0.667$, $n = 112$, $p < 0.001$). Each point is a study site.

Overall, the above results indicate that my own Flood Risk Score is the more informative measure, at least for my study regions and for the purposes required for this thesis. The strong positive correlation in wetter sites in both France and Germany would suggest both Flood Risk Score and the GSW OL are identifying similar patterns in surface water

presence for relatively wet sites. My Flood Risk Score continues to discriminate between sites towards the drier end of the scale, whereas the GSW OL gives many sites a score of zero, which is much less useful for comparing between sites. This suggests to me that the GSW OL is less sensitive to water in relatively dry areas compared to Flood Risk Score, which could result from the algorithms used by Pekel *et al.* (2016) having a high threshold for categorizing a pixel as water. With particular regards to Ukraine, vegetation may be a particular issue for the GSW OL. Large areas of the park have standing water, but are also covered with emergent vegetation (sedges, reedbed and willow scrub in particular). These areas appear to frequently have a zero score on the GSW OL but a positive score using my Flood Risk Score metric. I therefore feel that this not only supports my Flood Risk Score as being a reliable indicator of inundation frequency, but also indicates that my Flood Risk Score is the more useful and has greater discriminatory power than the GSW OL.

2.4 Analysis

The analyses carried out vary slightly by study region, and therefore complete details are given in subsequent chapters. However, there were commonalities, and the general approach was similar across study regions. The analyses introduced here were carried out on a region-by-region basis and are detailed in Chapters 3, 4 and 5; in Chapter 6 I present the results from a trait-based analysis using data from all study regions which is not described further here but fully elaborated in that chapter.

I carried out a range of analysis to characterise the habitats and vegetation structure, and address some of the following questions: are species' population densities associated with vegetation structure? Does vegetation structure differ between habitat categories? Are differences in vegetation structure associated with differences in the disturbance regime, as measured on transects or flood disturbance as measured by water depth in the field or Flood Risk Score?

In each study region, I was interested in how bird and butterfly species' population densities vary between different categories or habitats, primarily between farmland and floodplains. For most species, this was answered by using Generalised Linear Models (GLMs) to quantify the effect of habitat category. Both bird and butterfly population densities are based on count data, but the data were consistently over-dispersed to be modelled using Poisson error structures and so quasi-Poisson error structures were used

instead (Crawley, 2013). However, for species which were only observed in one habitat, I was unable to fit GLMs to compare between habitats and so I used simple randomization tests with 100,000 repeats to determine the significance of the difference in population densities between the two habitats (Manly, 2007). The randomization test is less powerful than the GLM as it is entirely non-parametric, and it is also unable to account for differences in detectability. It was therefore only used when the GLM was not an option. For plotting purposes, the mean and standard deviation in population density were still calculated assuming a quasi-Poisson error structure.

If I observed an HNV species to have higher population densities in a floodplain than the surrounding farmland, this may be because of a high density in the floodplain (supporting my hypothesis) or simply due to a low density in the farmland (providing no support). I therefore compared my results for birds, in wetland and agricultural land, to the results of previous work in Poland (Feniuk, 2015). As complete raw data for Poland were unavailable, I used a one-sample t-test to compare my density estimates to those from Poland, in both “natural” habitats and farmland. Note that the natural habitats surveyed in Poland tended to be small patches, and not subject to completely natural disturbance regimes. This comparison is most relevant for my Ukrainian region, as this is geographically and ecologically most similar to the Lubelskie region used in that previous study. However, for completeness I have included this comparison in all my study regions. This comparison does not completely eliminate rival hypotheses, but it does provide additional context and support to my conclusions which would not be possible from considering my results in isolation.

2.4.1 Identifying HNV species

There is broad agreement that the concept of High Nature Value farmland is useful, that it applies to agricultural systems which have high biodiversity, and that some of that biodiversity is tightly associated with HNVf. However, there is no agreement about a strict definition or list of associated species (Andersen *et al.*, 2003; EEA, 2004; Paracchini *et al.*, 2008; Lomba *et al.*, 2015; Strohbach *et al.*, 2015). Approaches to identifying HNVf may take a landscape-based approach (on the assumption that the characteristic biodiversity is the result of certain patterns in land cover and usage), or they may take a biodiversity-based approach and identify HNVf as areas which support certain indicator species. Furthermore, both approaches typically use expert opinion to decide which landscapes or species qualify. Another approach is that used by Claire Feniuk in the

Lubelskie region of Poland (Feniuk, 2015). Feniuk defined “low-yield farmland (LYF) preferring species” as species whose highest population densities (D_{\max}) occurred in farmland with a yield less than $33 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ (33% of the regional maximum yield observed), and where population densities in both zero-yielding natural habitats and high yielding ($>50 \text{ GJ ha}^{-1} \text{ yr}^{-1}$) farmland were less than 50% of D_{\max} (Figure 2.8). This methodology has two key benefits over other published approaches: it is based on quantitative evidence (rather than expert opinions) and it targets species which are at risk from both abandonment and intensification, as either would result in the yield changing outside the defined range, and hence in a reduction in a species’ population density. The biggest drawback is that it is based on spatially- and temporally-restricted fieldwork, and so may not extrapolate to other regions or years. Different regions may have different pools of species, and even species which are common across regions may have different behaviours across their range. Furthermore, this approach did produce some results which may be unintuitive, in particular including as HNV species some birds which are reportedly widespread and common in Europe such as Magpie, House sparrow, Blue tit and Mute swan (Snow, Perrins & Gillmor, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018).

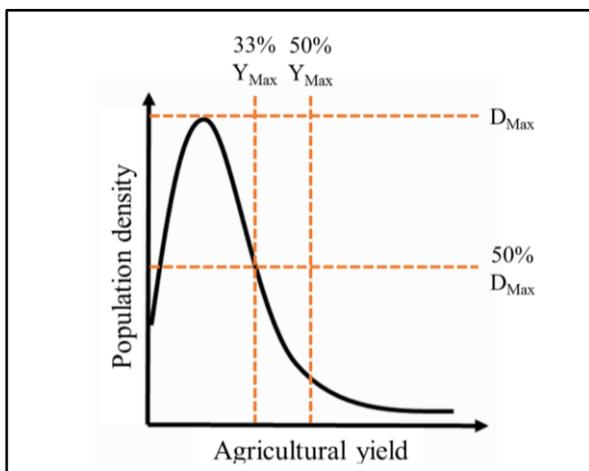


Figure 2.8 – Schematic for identifying HNV species based on density-yield curves. HNV species were defined as having their maximum population density D_{\max} at a yield less than 33% of the regional maximum yield (Y_{\max}) and having population densities of less than 50% of D_{\max} in both zero-yielding natural baseline habitats and at yields above 50% of Y_{\max} . From Feniuk (2015)

Overall, I felt that the approach taken by Feniuk had the greatest objective merit and the work presented in Feniuk (2015) is a useful proof-of-concept, but the spatial and temporal restrictions in that data and the ensuing idiosyncratic results meant I felt it was not appropriate to apply this list to my study. Instead, I have chosen to use the list of HNV

species given in Paracchini *et al.* (2008). For birds, this list was compiled using the following procedure:

- The starting point was the list of 173 European birds identified as priority species of agricultural and grassland habitats by Tucker & Evans (1997), based on their threat status and the importance of these habitats to them during their annual cycle.
- Species that do not occur regularly in the wild in the EU-27 were excluded.
- Species for which agricultural and grassland habitats are considered to be relatively unimportant (i.e. used by less than 10% of the European population) were excluded.
- Species restricted to montane grasslands were excluded, on the grounds that the factors affecting this habitat type are different to those affecting other agricultural habitats (e.g. arable, steppes, wet grassland, rice cultivation, perennial crops and pastoral woodland).
- Species listed on Annex I of the EC Birds Directive, and/or considered to have an Unfavourable Conservation Status in Europe (BirdLife International 2004), were retained.
- Species considered to have a Favourable Conservation Status in Europe (BirdLife International 2004), but to be concentrated in Europe and have a medium or high dependence on agricultural and grassland habitats (i.e. used by more than 10% of the European population) were retained.
- The resulting list was checked by the EEA, who then circulated it for consultation around national Member State experts involved in the HNV farmland project.
- The EEA collated Member State feedback, and the species list was revised accordingly.

The result of this exercise was a list of 119 bird species considered to be associated with HNV farmland (full list in Appendix 2). While this list was the result of a detailed and rigorous process, there are nonetheless caveats to its use. Firstly, the final stage of the exercise involved circulating an initial list for feedback from experts. This introduces a degree of subjectivity and unrepeatability into the results, as even experts' opinions are influenced by personal experiences and biases. Secondly, the list is presented as a pan-European list of HNV species, but that is not necessarily the most sensible approach. Both species' habitat preferences and the nature of HNV farming systems vary across Europe, so different species might be more or less closely associated with HNV farmland in

different parts of Europe. However, despite those limitations the resulting list did appear to be a sensible attempt at identifying bird species associated with HNV farmland.

A list of butterfly species thought to be associated with HNV farmland was given in the same document (Paracchini *et al.*, 2008). For butterflies, the approach taken was:

- An initial list of species was composed of all species which met at least two of the following criteria:
 - Species is restricted to Europe (Range Affinity 4 in Van Swaay & Warren, 1999).
 - Species is listed in Appendix II of the Bern Convention and/or the Habitats Directive.
 - Species is threatened according to the recent Red Data Book of European butterflies (Van Swaay & Warren, 1999) or the IUCN Red List of threatened animals.
- Species which woodland is their main habitat were then excluded from the list.

The result was a list of 27 butterflies species (full list in Appendix 2). While this list was the most appropriate one I could find, I did note that it focuses on range-restricted species which tend to be tightly associated with specific regions and farming systems, and may miss some more widespread species. As indicator species, these species were selected to minimise commission errors in identifying HNVf (i.e. anywhere these species are found is very likely to be HNVf); other species might be less ideal indicators but still show a strong association with HNVf.

2.4.2 Boxplots

While most of the graphs that I have used in this thesis are unambiguous or described in their caption, boxplots (also known as box-and-whisker diagrams) are used frequently and the exact interpretation needs to be specified. To minimise repetition, this specification is given here and is not detailed in the caption of individual boxplots. All boxplots in this thesis are generated by the *geom_boxplot* function from the *ggplot2* package (Wickham, 2009) and follow the following protocol: the central bold line is the median; the lower and upper “hinges” of the box are the 25th and 75th percentiles of the data, respectively (the height of the box therefore represents the Inter-Quartile Range, IQR); the “whiskers” extending from the top and bottom of the box extend to the highest and lowest (respectively) data points within 1.5xIQR of the upper and lower

(respectively) hinge. All data points beyond the whiskers are plotted as separate points. An example boxplot is shown in Figure 2.9.

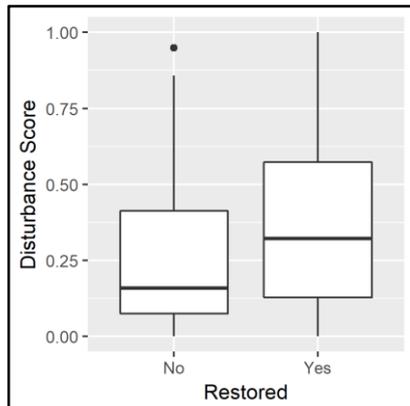


Figure 2.9 – An example boxplot. The central bold line is the median. The lower and upper “hinges” of the box are the 25th and 75th percentiles of the data, respectively (the height of the box therefore represents the Inter-Quartile Range, IQR). The “whiskers” extending from the top and bottom of the box extend to the highest and lowest (respectively) data points within 1.5xIQR of the upper and lower (respectively) hinge. All data points beyond the whiskers are plotted as separate points.

2.5 Conclusion

In this chapter, I have outlined and justified the methods used for the majority of this thesis. These methods enabled me to estimate population densities of birds and butterflies in each study site, along with habitat and environmental variables associated with each study site. Comparisons across study sites (but within study regions) then enabled me to address the questions posed, regarding the types of sites that individual species prefer, and to further consider how the characteristics of those sites might influence species’ preferences.

The next three chapters apply these methods to my three study regions. The general methods outlined here form the basis of the methods used in each region, but details specific to each region are fully elaborated in the relevant chapter.

I have chosen to consider each region largely independently for analysis, due to the geographical distances between them along with ecological differences. Despite this, the results from each region have an important role to play in the overall argument of this thesis, namely the value of flood disturbance, and restoring flood disturbance where it has been lost, for conserving biodiversity, including biodiversity more commonly associated with HNVf.

3 UKRAINE

3.1 Introduction

As outlined in Chapter 1, if floodplain restoration is to be useful for the conservation of HNV species, then a key prediction is that natural floodplains will support populations of those species. My first field season was primarily aimed at testing this prediction by comparing a natural floodplain to HNVf. If the hypothesis is correct, a reasonable number of HNV species will have population densities in the floodplain that are equal or higher to densities in HNVf. There are also many species which are not strongly associated with HNVf, including both generalist species and specialists associated with a range of non-HNVf habitats, and these species' responses to habitat type are also of interest, both from pure ecological and from conservation perspectives. While farmland species are declining faster than species associated with other habitats in Europe, many other species are declining too, including wetland specialists (BirdLife International, 2013; Burns *et al.*, 2013).

Across most of western Europe, a long history of human modification of the landscape means very few unaltered floodplains remain, and those that do tend to be only small fragments of much larger areas (Tockner & Stanford, 2002). However, despite a similarly long history of human land use, farther east in Europe the landscape tends to be less completely modified, and some areas of nearly-natural floodplain remain (Čížková *et al.*, 2013). One such example is encompassed by Pripjat-Stokhid National Nature Park (PSNPP) in Ukraine.

Located in the north-west corner of Ukraine (Figure 3.3), PSNPP covers an area of 39,315 ha. Some human activity occurs in PSNPP: there are small areas of agricultural land within the park borders, and some areas have paths for recreational use which are also used for small-scale resource extraction (firewood, fish, berries). With these exceptions, the park is a natural landscape. Of particular importance, the rivers (the Pripjat and the Stokhid, which have their confluence in the park) are not regulated or restricted in any way within the park, and are able to exhibit natural dynamics (Richards

et al., 2002). The result is a natural mosaic of habitat types, ranging from woodland through scrub to reedbeds and sedge meadows (Figure 3.1).



Figure 3.1 – An example of the landscape within Pripjat-Stokhid National Nature Park. Note the variety of habitat types, caused by variation in topography and hydrology.

The surrounding landscape consists primarily of small-scale and extensive agriculture (Figure 3.2). Following the collapse of the Soviet Union, large “collective” farms ceased and the land was distributed to households (Hostert *et al.*, 2011). As such, each household has a small plot on which they typically grow a mosaic of crops, primarily for consumption within the household, with some surplus sold. Use of chemical fertilisers and pesticides is low due to their high price relative to local incomes. In addition, many households have livestock: pigs and chickens are often kept in gardens and fed scraps, while cattle are grazed on common land (pers. obs.). This landscape, with its high heterogeneity and low chemical inputs, shows many of the characteristics of HNVf. Yields are also low. Informal discussions with a small number of farmers suggest that typical yields are around $50 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ averaged across a range of crops, although this is considerably above the national average values reported by FAOSTAT of $35.5 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ (FAO, 2015). As most agriculture is carried out for subsistence consumption, farmers’ production estimates may be less accurate than if produce were sold on the market. For reference, mean wheat yield in the UK in 2015 was approximately $130 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ (DEFRA, 2016; USDA, 2018).



Figure 3.2 – A typical agricultural area within my study region. Note the small plot sizes, diverse crops and hay meadow.

This region enabled me to look at a number of key questions. How do habitats differ between the floodplain and surrounding HNVf landscape? Are these habitat differences associated with differences in biotic (for example browsing) and abiotic (particularly flood-based) disturbance processes? How do population densities of species, particularly HNV species, compare between the floodplain and the surrounding HNVf? To answer these questions, I first characterised the habitats and vegetation structures of each of my study sites, and compared these between agricultural and wetland sites. I also looked for correlations between habitat and vegetation structure and forms of disturbance. I then investigated the associations between species' population densities and habitat and vegetation structure. I compared species' population densities between agricultural and wetland sites, and to contextualise those results I then also compared bird species' population densities in wetland and agricultural sites against reported densities in natural baseline habitats and low-yielding farmland in Poland.

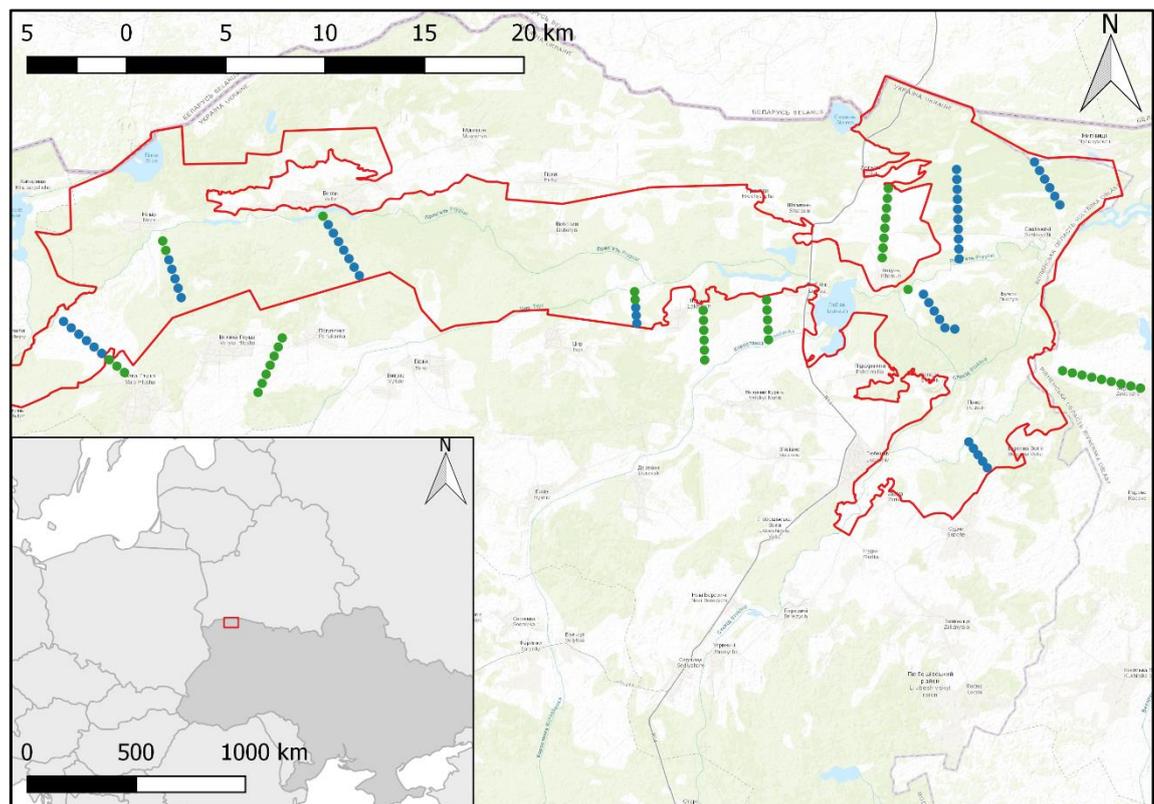


Figure 3.3 – Main: Pripyat-Stokhid National Nature Park (red outline) and study sites (blue dots = wetland sites; green dots = agricultural sites) spaced 400m or 500m apart along transects. Inset: The study region was located in the north-west of Ukraine (dark grey shading); red box shows area of main panel.

3.2 Methods

3.2.1 Field methods

I needed to sample both HNV agricultural sites and wetland sites. I therefore selected 92 study sites across the study region, of which 48 were wetland sites (all located within PSNPP) and the other 44 were agricultural sites. Mostly these were outside PSNPP, although some small agricultural areas within PSNPP were also sampled (Figure 3.3). For logistical purposes, sites were arranged along 13 transects, although sites were spaced sufficiently to consider each site independently. Study points (the central point of each study site) were spaced by 500m in most cases, although for short (<2.5km) transects, this was reduced to 400m to increase the number of sites per transect. Even so, this is still double the minimum point count spacing of 200m for independent bird counts recommended in the literature (Bibby & Etheridge, 1993; Sutherland, 1996). To further demonstrate independence, I tested for spatial autocorrelation in species counts and habitats, and found that only 14 out of 85 bird species and eight out of 39 butterfly species showed spatial autocorrelation in total count, where as seven out of 15 habitat classes

showed spatial autocorrelation (Moran's I $p < 0.05$ after Bonferroni correction for multiple testing). This suggests that, where it exists, spatial autocorrelation in species' counts is better explained by sites close together having similar habitats, rather than a lack of independence in field counts of species.

Within the wetland area, I wanted to capture a gradient from highly flood-disturbed areas nearest the river, to rarely flood-disturbed areas at the edge of the park. I designated eight transects within the park. These transects were located opportunistically but spread out across the park (Figure 3.3). These transects were aligned approximately perpendicular to the nearest river channel, and spanned, to the greatest extent possible, from the river to the edge of the park (Figure 3.4). The length of each transect therefore varied with this distance (1.6km to 4km). Position along transect was not considered as a variable in its own right, but rather it was assumed that the gradient of flood disturbance would be reflected in the other variables recorded for each site, such as Flood Risk Score. Therefore, the results are not dependent on the transects each representing a complete gradient.

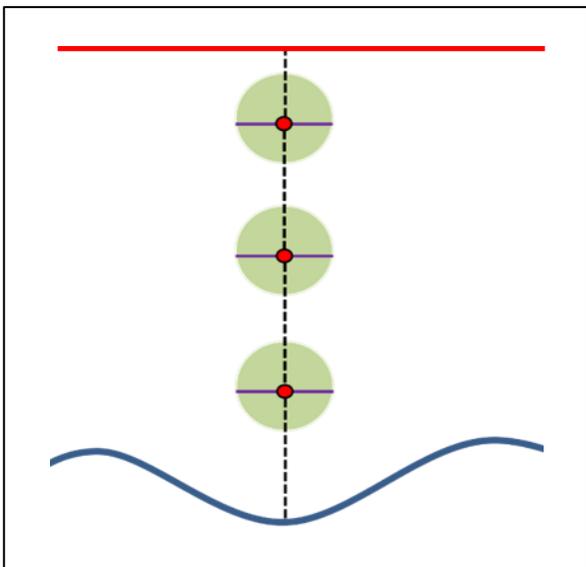


Figure 3.4 - Illustrative typical sampling design (not to scale) of wetland transects. Transects (dotted black line) ran approximately perpendicular to the river channel (blue line) to the edge of the park (red line). Sample points (red dots) were evenly spaced along the transect by 500m (or 400m for short transects). Bird surveys were carried out at the sample point. Butterfly and disturbance surveys were carried out over 200m transects running perpendicular to the main transect and passing through the sample point at the midpoint (purple lines). Habitats were mapped over a 100m radius around the sample point (green area).

I selected five transects in the agricultural landscape. Transects were located in areas of continuous farmland (avoiding areas of forestry or villages) and spread out to span

roughly the same area as the wetland transects. Transects were aligned approximately parallel to the nearest wetland transect (Figure 3.3). The length of agricultural transects was constrained by availability of continuous farmland (2km to 4km).

At each study site, I carried out bird point counts, butterfly transects, disturbance transects and habitat mapping, as detailed in Chapter 2. For birds, I used distance sampling to estimate detection radii and population densities, as detailed in Chapter 2. I visited all sites at least three times, spread over the field season (early April to late June). I carried out bird surveys 3-5 times (mean 3.62) per site. I carried out butterfly surveys whenever weather permitted, although the more stringent weather requirements (see Chapter 2) meant that the number of repeat butterfly surveys per site was lower than for birds, with only 1-3 (mean 2.61) counts per site. Disturbance surveys were carried out twice per site, on my first and last visit to each site. Habitat mapping was carried out once, and all habitat surveys were completed within a two-week period to minimise the variation in plant growth.

3.2.2 Analysis

As my habitat and vegetations structure data, and my disturbance data were both highly dimensional, I first carried out a Principal Components Analysis on each of these in order to reduce dimensionality and produce metrics of habitat and vegetation structure, and disturbance data, which could be used for further analysis. As shown below, the results of these PCAs led me to use one component to describe the vegetation and habitat structure (Veg.PC1) and two components to describe the disturbance regime (Disturbance PC1 and Disturbance PC2).

I used Landsat data to calculate Flood Risk Score over the entire study region, using the methodology described in Chapter 2. Unlike subsequent chapters (where the study regions were the locations of restoration projects), this study region has not been subject to major change over the period for which Landsat data is available, and therefore I did not limit the date window when searching for Landsat images, instead searching the entire archive (search carried out October 2017). In total, this yielded 489 individual Landsat images covering the period 1984 – 2017.

To quantify how wetland and agricultural sites differed, I compared the distribution of habitat types, Veg.PC1, Disturbance PC1, Disturbance PC2, Flood Risk Score and water depth between wetland and agricultural sites. To compare the distribution of habitat types,

I carried out a MANOVA with the site type (wetland or farmland) as the predictor variable and the area of each habitat type in each site as the response variables. For each of the other variables, I used the Shapiro-Wilk Test to determine whether to use a Welch's t-test (for normal distributions) or the Wilcoxon Rank Sum test (otherwise) to determine significant differences.

I wanted to investigate whether disturbance processes could explain some of the variation observed in habitats and vegetation structure. I looked for correlations between Disturbance PC1, Disturbance PC2, Flood Risk Score and water depth, and Veg.PC1 within wetland sites. I only considered wetland sites as vegetation structure in agricultural sites is primarily controlled by human activity, and so I would not expect any meaningful associations between my measures of biotic and abiotic disturbance and vegetation structure in agricultural sites. While the data collected are insufficient to definitively identify causal relationships, correlations may indicate interesting associations.

I used GLMs to model bird and butterfly species' responses to both Vegetation PC1 and the mean height of the vegetation. In all cases, the GLM used a quasi-Poisson error structure on the raw count data, a log link function and offset by the log of sampling effort. For birds, sampling effort was number of visits multiplied by estimated detection area (from distance sampling). For butterflies, sampling effort was simply number of visits. All butterfly transects were 200m long and 5m wide and therefore the area surveyed did not vary between sites.

For both birds and butterflies, I compared population densities in wetland versus agricultural sites. For most species, I used GLMs, which followed the same protocol described above, except with site category (wetland or agricultural) as the explanatory variable. For species which were observed only in either wetland or agricultural sites, I was unable to fit GLMs to compare between habitats and so used a randomization test to determine the significance of this difference.

I compared bird population densities to those in eastern Poland based on species-specific density-yield functions presented in Feniuk (2015). These functions allow estimation of population densities at any agricultural yield up to the maximum potential yield, defined as 1.25x the maximum observed yield. Feniuk (2015) defined "low-yielding farmland" as farmland with a yield <33% of the maximum potential yield in the region. Across sites meeting this criterion the mean yield was 8 GJ ha⁻¹ yr⁻¹ (taken across a 1km² farmland landscape, including non-productive areas). I therefore used Feniuk's density-yield

functions to calculate the estimated population density of each observed species at a yield of $8 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ (to compare to my farmland sites), as well as those at yield of $0 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ (to compare to my wetland sites). The baseline habitats in Poland were far smaller than PSNPP and embedded within a more managed landscape and so not exposed to a comparable natural disturbance regime. From the available data it was not possible to calculate the error associated with these density estimates in Poland. Instead I compared my densities with these using one-sample t-tests, treating the Polish densities as known values. Only species for which data were available from both studies were included in these analyses. One other issue is that, because the Polish estimates for zero-yielding sites were based on modelled density-yield curves, they can be positive even for species never observed in baseline habitats. By using one sample t-tests, this means that if a species was not observed in either Ukrainian wetland or Polish baseline habitats but is modelled as having a positive density at zero yield in Poland it will return a (misleadingly) significant t-test result. In the absence of access to the raw survey data I therefore manually set to zero any density estimate in Poland that was less than one-tenth of the minimum of the estimated density of any species observed in either wetland or farmland in Ukraine (i.e. whose estimated Polish density was less than $0.0176 \text{ birds km}^{-2}$). This eliminated most cases where the observed density in Polish baseline habitats was in fact zero, whilst retaining estimates for species where a very low, but positive, density is genuinely plausible.

I carried out two additional analyses to check the sensitivity of my results to the choices of Polish baseline and farmland sites. For some species, the maximum population density observed in Polish farmland occurred at a different yield. In Appendix 3 I have included the results from an alternative version of the analysis using the maximum density observed in Polish farmland, at any yield. This method biased the results towards finding higher densities in Poland, but nonetheless did not alter my overall conclusions. Secondly, as well as using an area-weighted average density for the Polish baseline habitats (based on forest soils being three times as extensive as wetland soils, as in Feniuk, 2015) I investigated the effect of comparing my Ukrainian data with density estimates based on sites with wetland soils only in Poland. The results from this analysis are also presented in Appendix 3 and showed broadly similar patterns to the results presented here, and so do not alter my overall conclusions either.

Finally, I calculated the Flood Risk Score for Feniuk's sites in the Lubelskie region. As this region spans the intersection of several Landsat scenes, and because the edges of scenes were most affected by the Scan Line Corrector failure (USGS, 2018), I only considered Landsat TM images rather than TM and ETM+. In this case, 490 suitable Landsat scenes spanning the period 1992 – 2011 were available. I did not have exact coordinates for individual study sites, and the location of sites was therefore extracted visually from Figure 2.10 in Feniuk (2015). I compared Flood Risk Score between baseline sites in Poland and wetland sites in Ukraine, and between all farmed sites in Poland and agricultural sites in Ukraine. In both cases, I used a weighted Welch's t-test to compare Flood Risk Score, using the same weightings by soil type as were applied to density-yield functions (Feniuk, 2015), such that the results are comparable with the weighted density-yield functions outlined above.

3.3 Results

3.3.1 Habitats and disturbance

3.3.1.1 Habitat and vegetation structure PCA

The proportion of variance in the data explained by each component declined rapidly, with the first two components explaining 27.9% and 14.8% of the variance, respectively. All other components explained less than 10% of the variance each and were therefore not considered further. Figure 3.5 shows the loadings of each of my measurements of habitat and vegetation structure on the first and second PC axes, along with the positions of all of the region's study sites on those axes. Looking at the positions and major habitats of each of the study sites, it appears that the first axis represents a gradient from open habitats (for example meadows) through to closed habitats (for example woodland). This is reflected in the weightings of structural variables too: mean cover at 1m, 2m, 5m and 10m are all strongly positively weighted on this first axis, and greater cover at each height is associated with closed habitats. The interpretation of the second axis is less clear, but it may be picking out "scrubbiness", with scrubby habitats scoring positively on this axis. However, scrubby habitats also tend to be intermediate between closed and open habitats, so this axis does not add much information: study sites with a positive PC2 weighting tend to have PC1 weightings close to zero. As such, PC1 can be used on its own without loss of information. Given this, I chose to use the PC1 scores for each site as the sole metric of habitat and vegetation structure for analysis, hereafter "Veg.PC1".

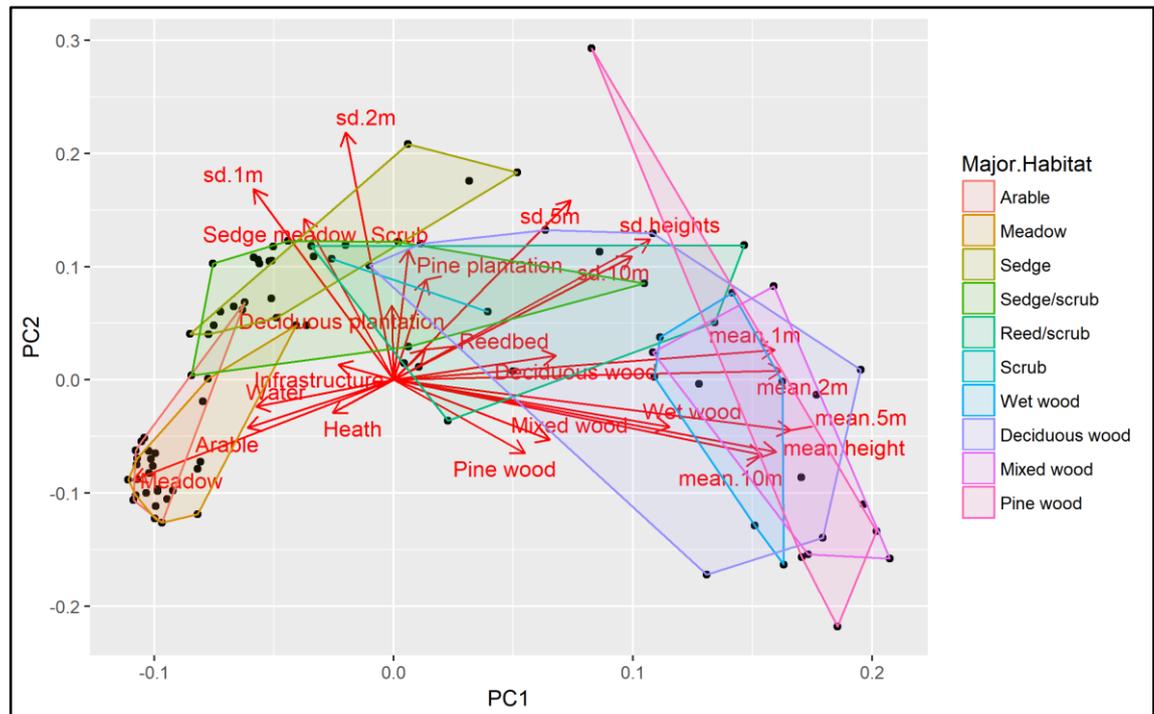


Figure 3.5 – Axes 1 and 2 of Principal Components Analysis on habitat and vegetation data. The length and direction of red arrows indicate the weightings of each habitat variable (see Chapter 2 for details). Black dots indicate scores of study sites. Coloured shapes indicate show the space occupied by sites within a major habitat category; these major habitat categories are purely a visual aid and were not used in classification.

3.3.1.2 Disturbance

I classified signs of disturbance into seven categories: Beaver, Boar, Deer, Elk, Other animal signs, Fire and Human (see Appendix 1). Browse Score was also included as a separate category. I carried out a pairwise correlation test across all disturbance categories. As this was purely exploratory, I did not carry out a correction for multiple comparisons. Most of the categories were uncorrelated across sites, except for Boar, Deer and Browse, which were all significantly positively correlated with each other. Elk was also positively correlated with Other animal signs (Figure 3.6). Due to the high dimensionality and correlated structure of the disturbance data, I carried out a Principal Components Analysis on these data.

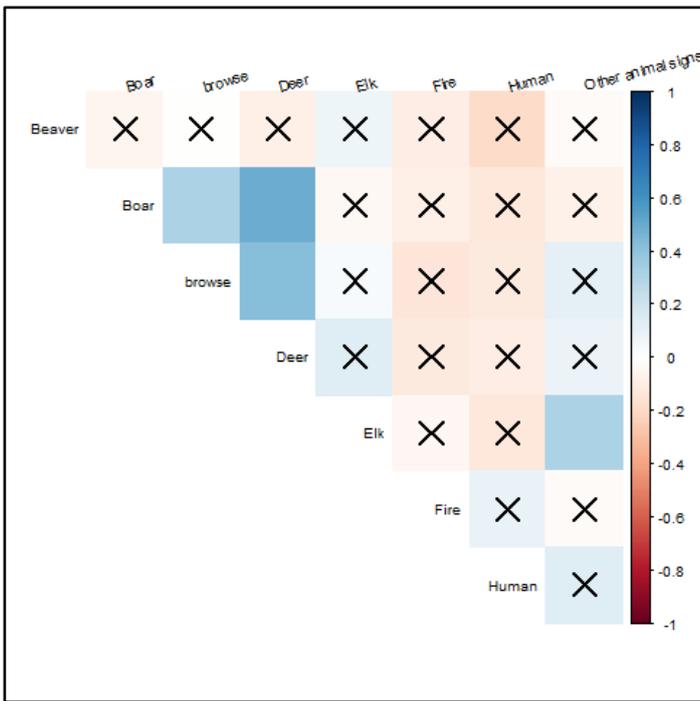


Figure 3.6 – Correlation plot of different categories of disturbance across study sites (n = 92). The colour of squares indicates the correlation coefficient. X indicates non-significant ($p > 0.05$) correlations.

In this PCA, the proportion of variance explained by each component dropped off rapidly, with the first component explaining 37.3% of the variance, and the second only 16.5%. The loadings of each disturbance category along with the positions of each study site (and their major habitat) on the first two axes are shown in Figure 3.7. There was significant overlap between different major habitats within this space, suggesting that major habitat type does not have a strong relationship with the prevailing disturbance regime. Fire was the single most heavily weighted type of disturbance on the first axis. Human disturbance was also positively weighted on the first axis, suggesting that this axis might give an indication of the level of “abiotic” (Fire and Human) disturbance, and that such abiotic disturbance is largely independent of “biotic” disturbance (Deer, Elk, Browse and Other animal signs) disturbance. On the second axis, Elk, Other animal signs, Deer and Browse were the most heavily weighted variables (in that order). These variables all indicate biotic disturbance, especially by browsing mammals. This suggests that sites’ scores on the second axis may indicate the level of browsing and abundance of large herbivorous mammals.

While the second component explained much less variance than the first, I decided that, considering the patterns of loadings and the positioning of sites, both the first and second components provided useful information about the disturbance regime of each site, so I

used both Disturbance PC1 and Disturbance PC2 in the following analyses. Because these are orthogonal to each other they were treated as independent variables for analysis.

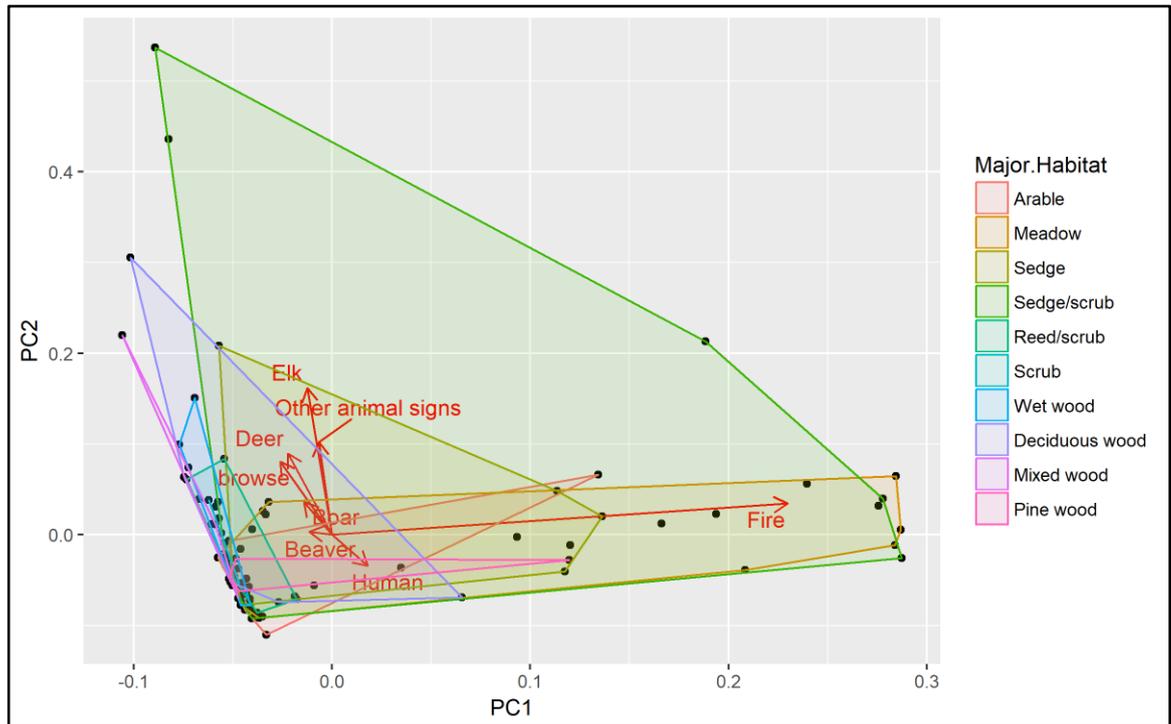


Figure 3.7 – Axes 1 and 2 of Principal Components Analysis on disturbance data. The length and direction of red arrows indicate the weightings of each disturbance variable. Black dots indicate individual study sites. Coloured shapes indicate show the space occupied by sites within a major habitat category – note that these major habitat categories are purely a visual aid and were not used in classification.

3.3.1.3 Flood Risk Score

Another aspect of disturbance is the degree of flood disturbance. Figure 3.8 shows the Flood Risk Score across the entire study region. Large, permanent water bodies have high Flood Risk Scores (≈ 1) as do some sections of the river channel. Within PSNPP, much of the area has an intermediate Flood Risk Score (0.2-0.5). Agricultural areas tend to have low Flood Risk Scores (< 0.2).

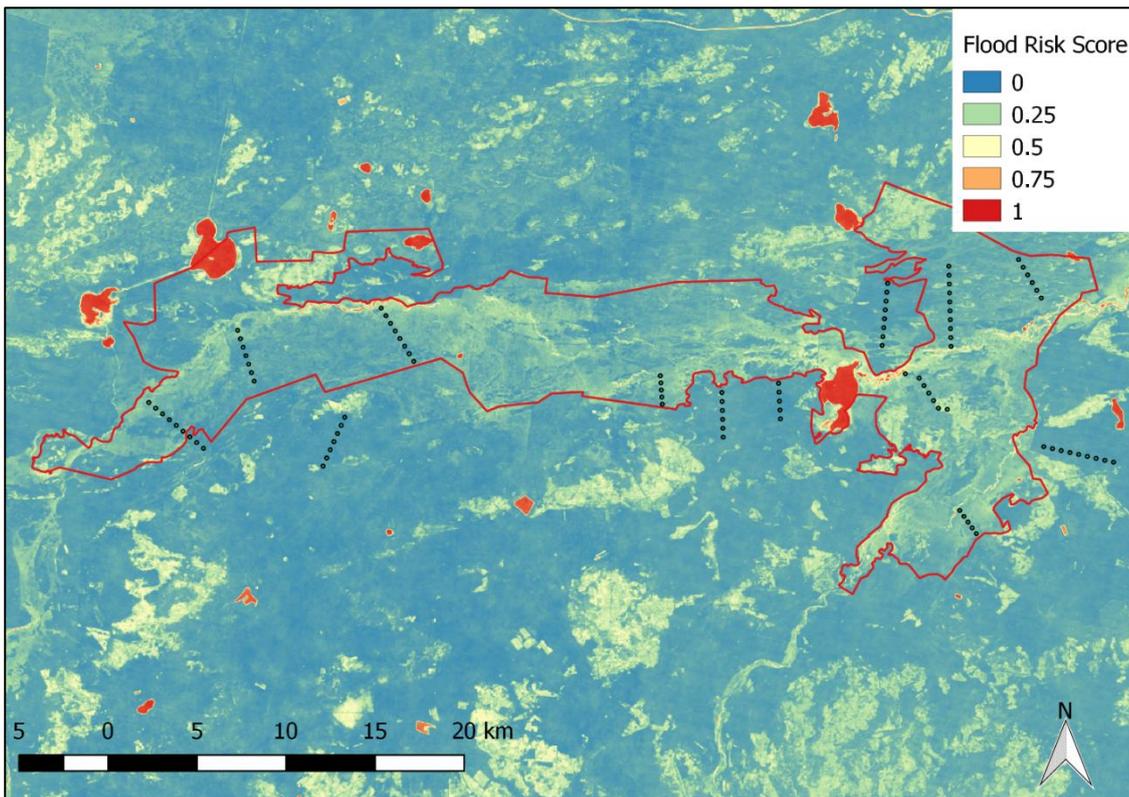


Figure 3.8 – Flood Risk Score across the study region, calculated as the mean occurrence of water across 489 Landsat images taken between 1984 and 2017. Colour indicates Flood Risk Score from 0 (no water occurrence) to 1 (permanent water occurrence). PSNPP is outlined in red. Study sites are marked with dots (not to scale).

3.3.2 Do farmland and wetland differ in habitats, vegetation structure or disturbance processes?

3.3.2.1 Habitats

The proportion of habitats differed significantly between agricultural and wetland sites (MANOVA $df = 77, p < 0.001$). Figure 3.9 shows the overall proportion of habitats in the two sites. Meadow habitats covered the largest area of agricultural sites, followed by Arable, Sedge meadow and Scrub. In wetland sites, Wet wood, Scrub and Sedge meadow covered the largest area. Natural woodlands (Deciduous wood, Pine wood and Mixed wood) were all more common in wetland sites than agricultural sites.

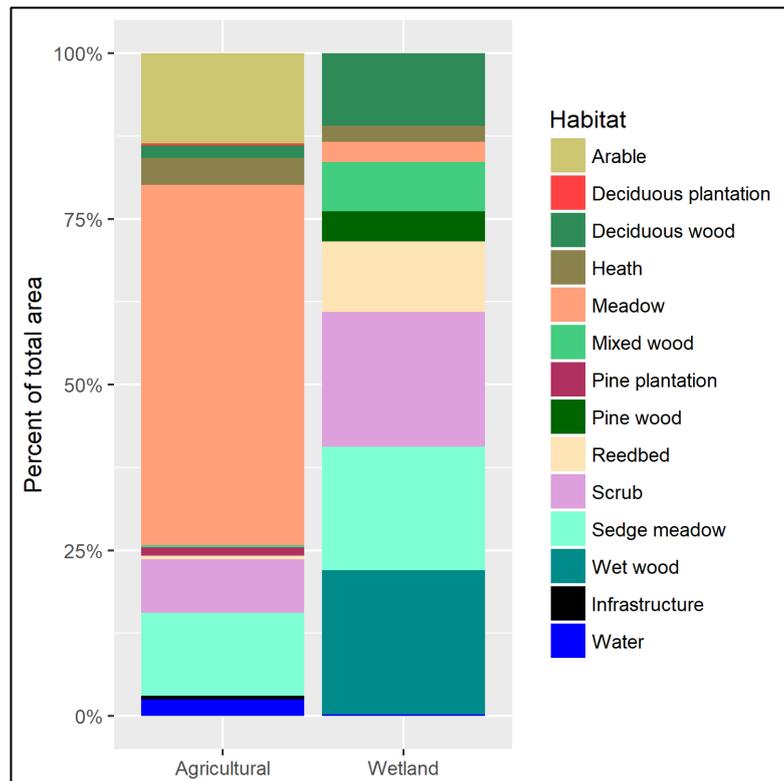


Figure 3.9 – Agricultural and wetland sites differ significantly in their habitat composition (MANOVA residual df = 77, $p < 0.001$)

3.3.2.2 Vegetation structure and disturbance

Wetland sites had significantly higher Veg.PC1 scores, indicating that they had more closed habitats ($W = 117$, $n = 92$, $p < 0.001$; Figure 3.10). This result is as expected given the distribution of habitats types (above). Most of my agricultural sites were very open, being mostly arable plots or meadows, with only occasional hedges and small patches of natural habitat. While some wetland habitats are relatively open (for example sedge meadows) the wetlands contained far more closed habitats, mostly scrub and woodland.

Agricultural sites had significantly higher Disturbance PC1 scores than wetland sites ($W = 1768$, $n = 92$, $p < 0.001$; Figure 3.10). However, wetland sites had significantly higher Disturbance PC2 scores ($W = 691$, $n = 92$, $p < 0.01$; Figure 3.10). This highlights that while both agricultural and wetland sites are subject to disturbance, the types of disturbance are very different between the sites. Disturbance PC1, which was higher in agricultural sites, gives high weight to fire and human disturbance, whereas PC2, which is higher in wetlands, gives high weight to forms of disturbance associated with wildlife. This makes intuitive sense as agricultural land is dominated by human activity, and fire is often used as a management tool. In the wetland, however, human activity is very low, fires are uncommon, and wildlife is abundant.

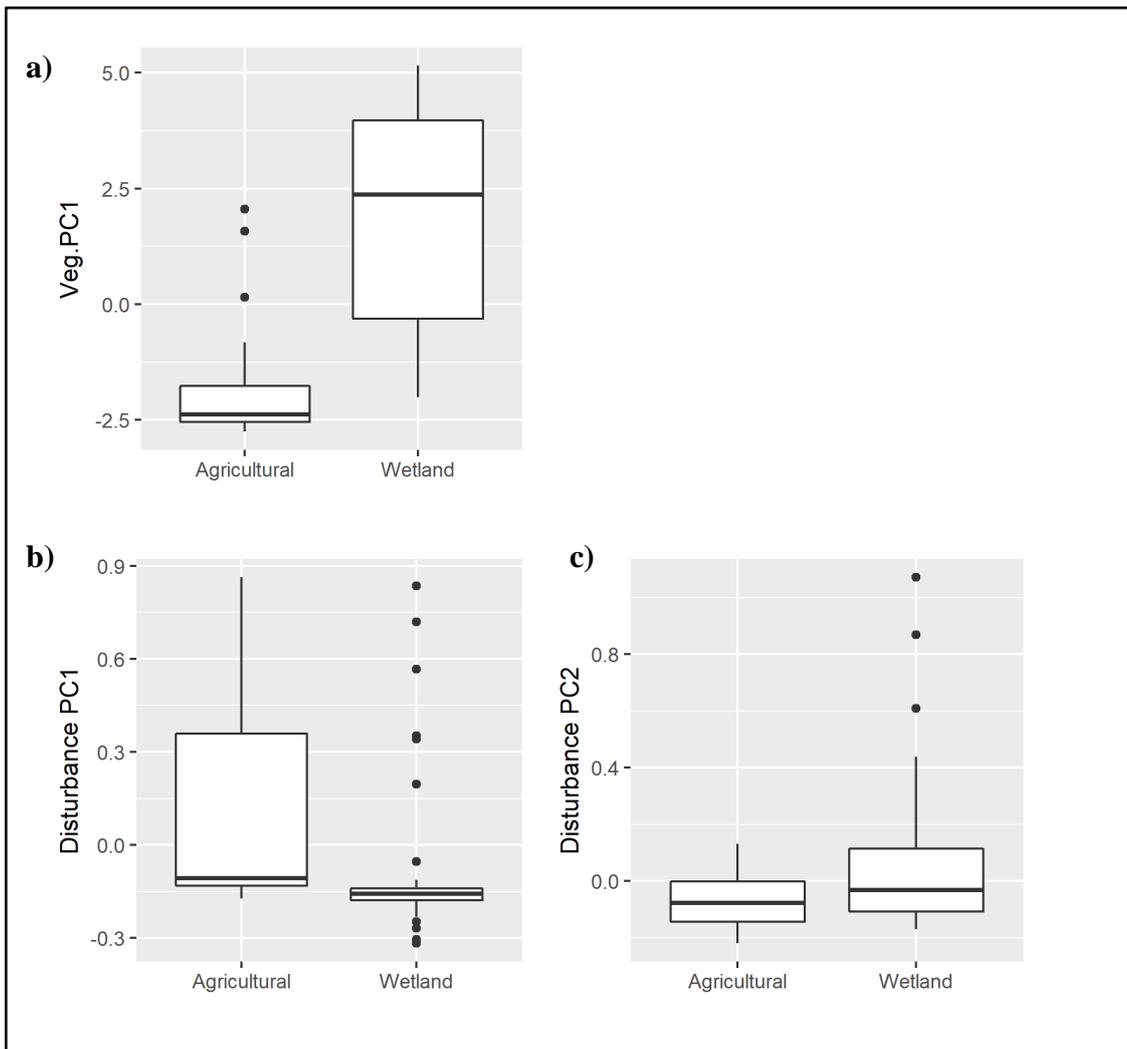


Figure 3.10 – a) Wetland sites have significantly higher Veg.PC1 than agricultural sites ($W = 117$, $n = 92$, $p < 0.001$). **b)** Wetland sites have significantly lower Disturbance PC1 than agricultural sites ($W = 1768$, $n = 92$, $p < 0.001$). **c)** Wetland sites have significantly higher Disturbance PC2 than agricultural ($W = 691$, $n = 92$, $p < 0.01$). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Disturbance PC1 scores are associated with disturbance by fire and human activities while Disturbance PC2 scores are associated with disturbance by wildlife (browsing, signs of deer and elk). See Chapter 2 for details of boxplots.

3.3.2.3 Flood Risk Score and water depth

Wetland sites had significantly higher Flood Risk Scores and significantly higher water depths than agricultural sites ($W = 744$, $p < 0.05$ and $W = 488.5$, $p < 0.001$, respectively, $n = 92$; Figure 3.11). These results confirm my impressions from the field. In most agricultural sites, there was typically no standing water except for drainage ditches, ponds and the like, which typically covered only a small area of the site in total. Some agricultural sites contained wet meadows, but these were relatively few.

It is important to note that agricultural sites are managed by people. As such, the significant differences observed in disturbance regimes and vegetation structure between agricultural and wetland sites are not the result of variation in natural processes. Furthermore, it cannot be argued that any of the differences are causally linked. For example, it cannot be suggested that agricultural sites had lower Veg.PC1 (more open habitats) because they had a lower Flood Risk Score. Rather both the habitat structure and flood regime in those sites are predominately controlled by human management. In the following section, I only consider wetland sites, where natural processes dominate.

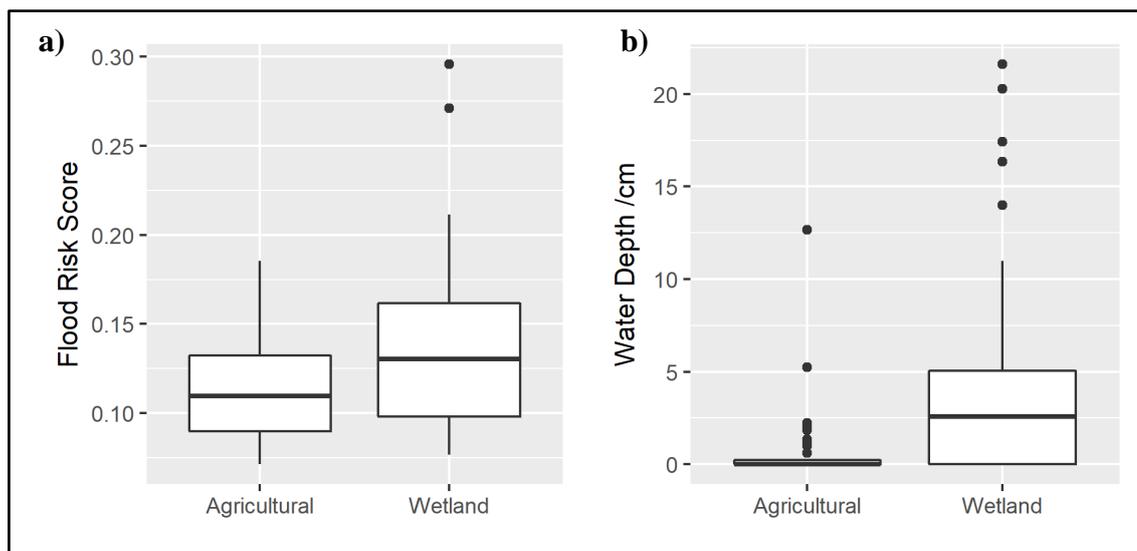


Figure 3.11 – **a)** Wetland sites had significantly higher Flood Risk Scores than agricultural sites ($W = 744$, $n = 92$, $p < 0.05$). **b)** Wetland sites had significantly higher water depth than agricultural sites ($W = 488.5$, $n = 92$, $p < 0.001$). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). See Chapter 2 for details of boxplots.

3.3.3 Are disturbance and flooding regimes associated with vegetation structure?

This section aimed to identify possible associations between natural disturbance processes and vegetation in my wetland sites. There was a significant negative correlation (Pearson's $r = -0.530$, $n = 48$, $p < 0.001$) between Disturbance PC1 and Vegetation PC1 (Figure 3.12). However, there was no correlation between Disturbance PC2 and Vegetation PC1 (Pearson's $r = 0.0718$, $n = 48$, N.S.). As fire and, to a lesser extent, human activity were most strongly weighted on PC1, and biotic disturbances such as browsing and beaver damage were more strongly weighted on PC2, one interpretation is that fire creates open habitats, whereas biotic disturbance has less of an effect on vegetation structure. The reverse is also possible, that open areas are more prone to fire. In other

systems, it has been shown that a positive feedback cycle exists, with fires creating open habitats, which are more prone to fire and so remain open (Bond & Keeley, 2005; Archibald *et al.*, 2013; Ratajczak *et al.*, 2014). Most wetland sites had low Disturbance PC1 scores; the observed correlation is driven by a small number of sites which had positive Disturbance PC1 scores and negative Veg.PC1 scores. There are also limitations of the method. For example, evidence of fire (for example burnt vegetation) is unlikely to remain obvious for more than a year or so, whereas vegetation structure may change over much longer timescales. In particular, closed habitats may take a long time to develop after disturbance has created an open patch.

I found a significant negative correlation between Flood Risk Score and Veg.PC1 (Pearson's $r = -0.503$, $n = 48$, $p < 0.001$; Figure 3.12). This suggests wetter places (higher Flood Risk Score) tend to have more open habitats (lower Veg.PC1). This fits with the hypothesis that flood disturbance is associated with more open habitats. However, there could be alternative explanations for the observed results. For example, closed habitats may make it harder to detect water using satellite data and so the Flood Risk Score may be biased towards lower scores in more closed habitats, where water is less likely to be visible from above. There was no significant correlation between water depth and Veg.PC1 (Pearson's $r = -0.077$, $n = 48$, N.S.; Figure 3.12). This may be because water depth was a "snapshot" and may therefore be less reliable than the long term pattern identified by Flood Risk Score. In particular, unusually dry weather conditions lasting since the winter in the year that I carried out fieldwork (pers. obs.) may have influenced the results. However, my experience from the field tended to agree with the lack of correlation. It is easy to assume that "wetlands" are open habitats such as reedbeds or bogs, as is commonly the case in Britain. But floodplain forests are a natural habitat that ought to be widespread, if not for human modification of the landscape (Richards *et al.*, 2003; Hughes, del Tánago & Mountford, 2012). In PSNPP, such wet woodlands were extensive, and remained wetter longer into the summer after more open habitats had begun to dry considerably (pers. obs.).

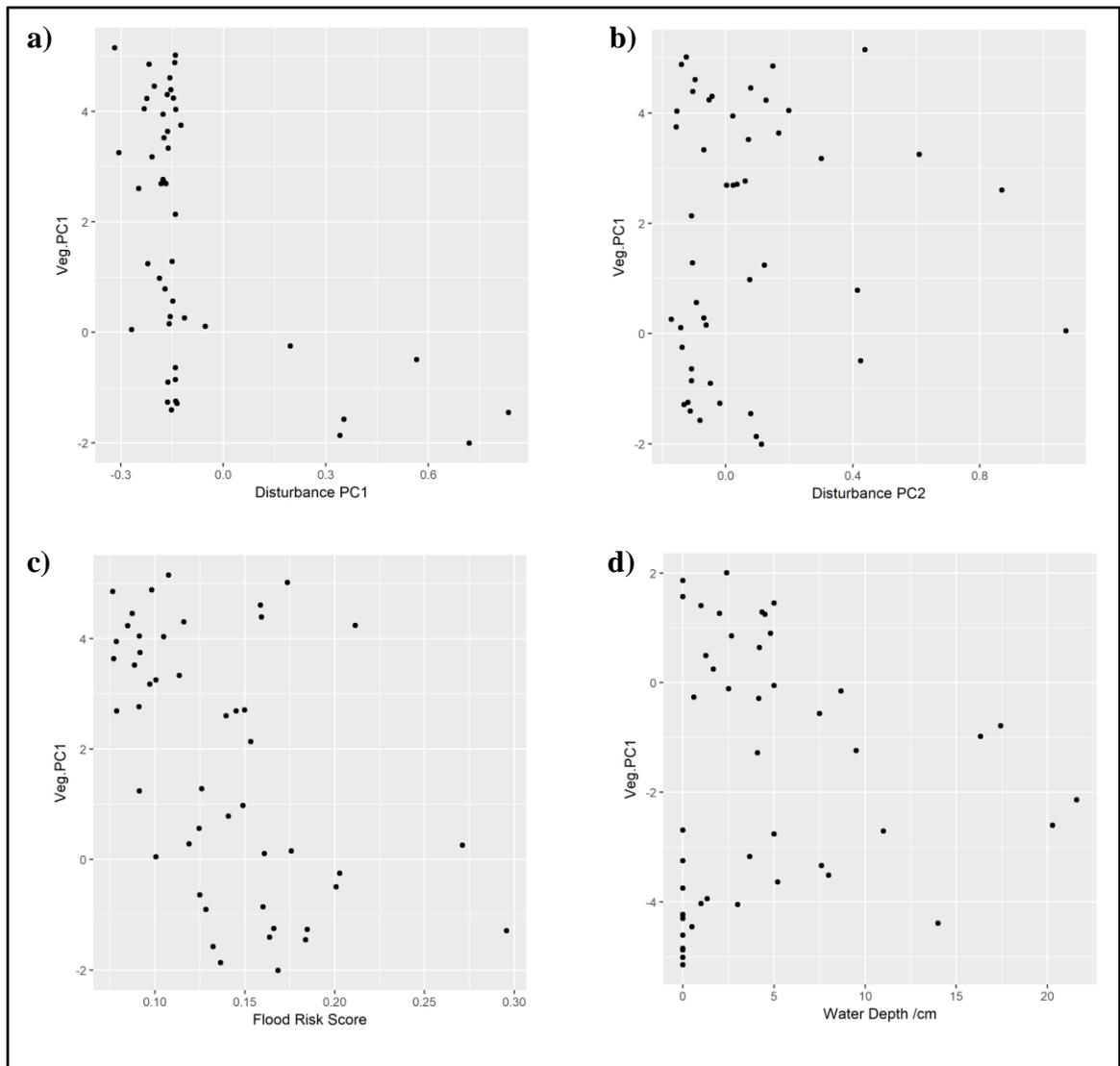


Figure 3.12 – **a**) Disturbance PC1 was negatively correlated with Veg.PC1 (Pearson's $r = -0.530$, $n = 48$, $p < 0.001$). **b**) Disturbance PC2 was not correlated with Veg.PC1 (Pearson's $r = 0.0718$, $n = 48$, N.S.). **c**) Flood Risk Score was negatively correlated with Veg.PC1 (Pearson's $r = -0.503$, $n = 48$, $p < 0.001$). **d**) Water depth was not correlated with Veg.PC1 (Pearson's $r = -0.077$, $n = 48$, N.S.). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Disturbance PC1 scores are associated with disturbance by fire and human activities while Disturbance PC2 scores are associated with disturbance by wildlife (browsing, signs of deer and elk). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). Points represent individual sites.

3.3.4 How are species' population densities related to vegetation structure?

The relationship between species' population densities and the first component of the vegetation PCA (Veg.PC1) is shown for birds (Figure 3.13) and butterflies (Figure 3.14); positive PC1 scores are associated with closed habitats, so a more positive model estimates indicates population densities tended to be higher in more closed habitats.

The relationship between species' population densities and the mean height of the vegetation is also shown for birds (Figure 3.15) and butterflies (Figure 3.16). Again, more positive model estimates indicate the population densities tended to be greater in sites with greater vegetation heights.

Looking at individual species, the results seem to fit well with their known ecology (van Swaay, Warren & Loïis, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). For example, woodland birds tend to have positive estimates for both Veg.PC1 and mean height (for example flycatcher species, Woodlark, several tit species) whereas farmland and wetland birds have negative estimates (for example Black-tailed godwit, Grey heron, Lapwing). The same holds true for butterflies, with species such as the Speckled wood having positive estimates, and several copper and blue species having more negative estimates.

There is a strong agreement between the models based on Veg.PC1 and those based on mean height, which is to be expected given that mean height was strongly weighted on Veg.PC1. However, modelling with Veg.PC1 appears to provide greater discrimination between species, which is especially apparent among the species with positive estimates for the relationship with mean height.

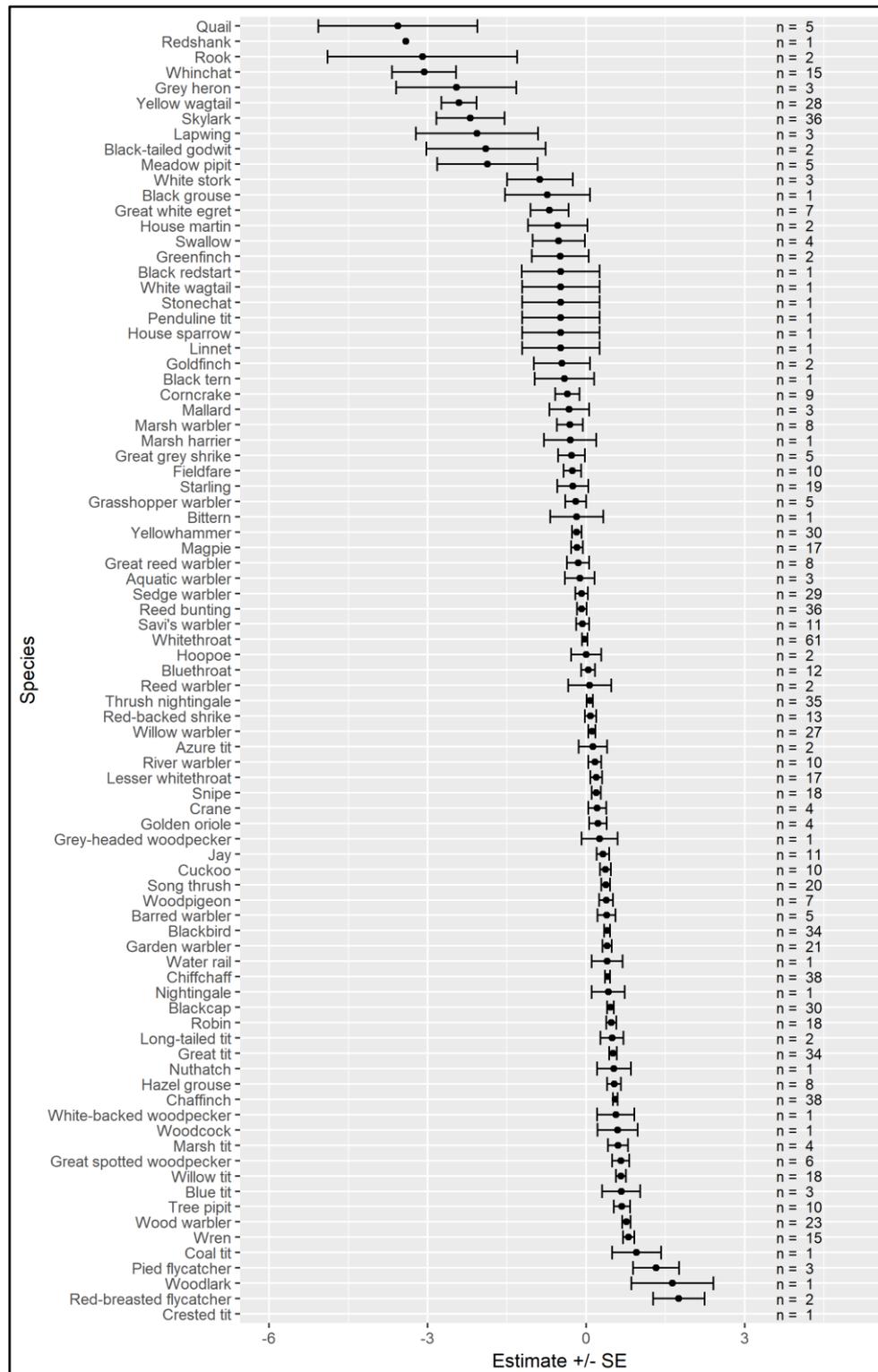


Figure 3.13 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species' population density and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more negative estimate indicates that species had higher population densities in sites with a lower Veg.PC1 (i.e. prefers more open habitats). There were 92 sites; n values on the figure indicate the number of sites with at least one observation for that species.

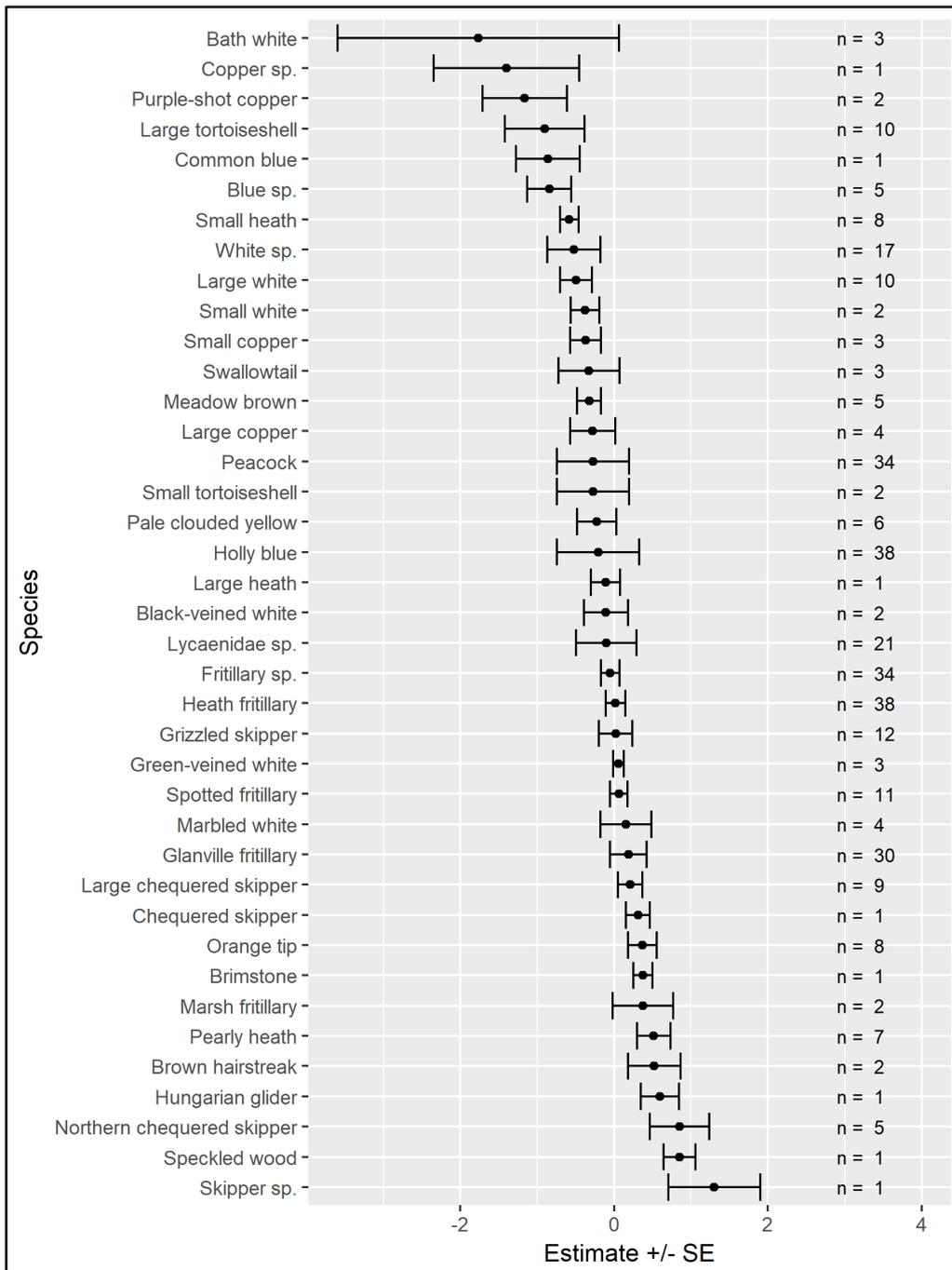


Figure 3.14 – Modelled estimate of the slope \pm 1 Standard Error (SE) of the relationship between butterfly counts and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more negative estimate indicates that species had higher counts in sites with a lower Veg.PC1 (i.e. prefers more open habitats). There were 92 sites; n values on the figure indicate the number of sites with at least one observation for that species.

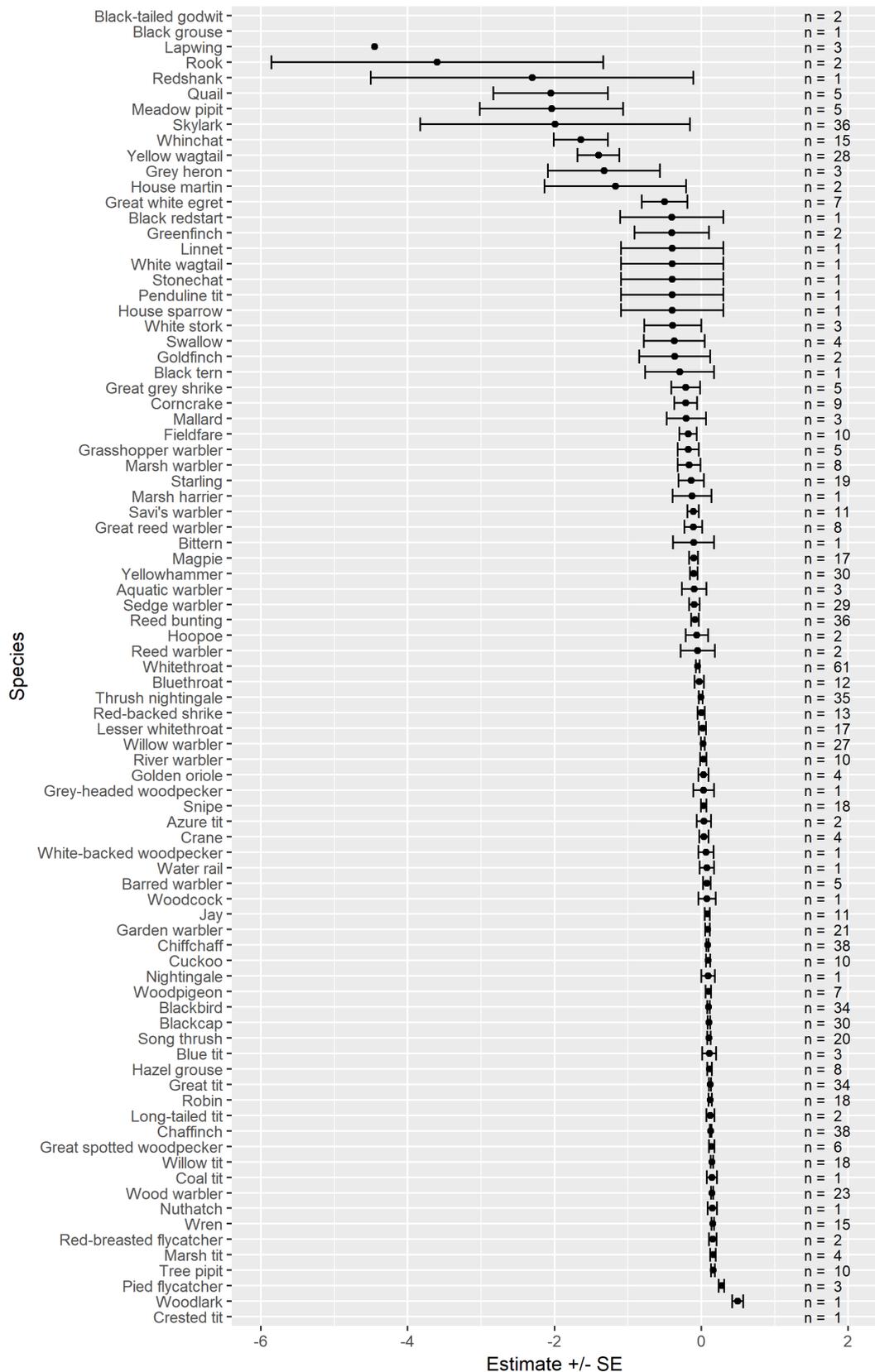


Figure 3.15 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species’ population density and the mean height of the vegetation in each site. A more negative estimate indicates that species had higher population densities in sites with lower vegetation heights. There were 92 sites; n values on the figure indicate the number of sites with at least one observation for that species.

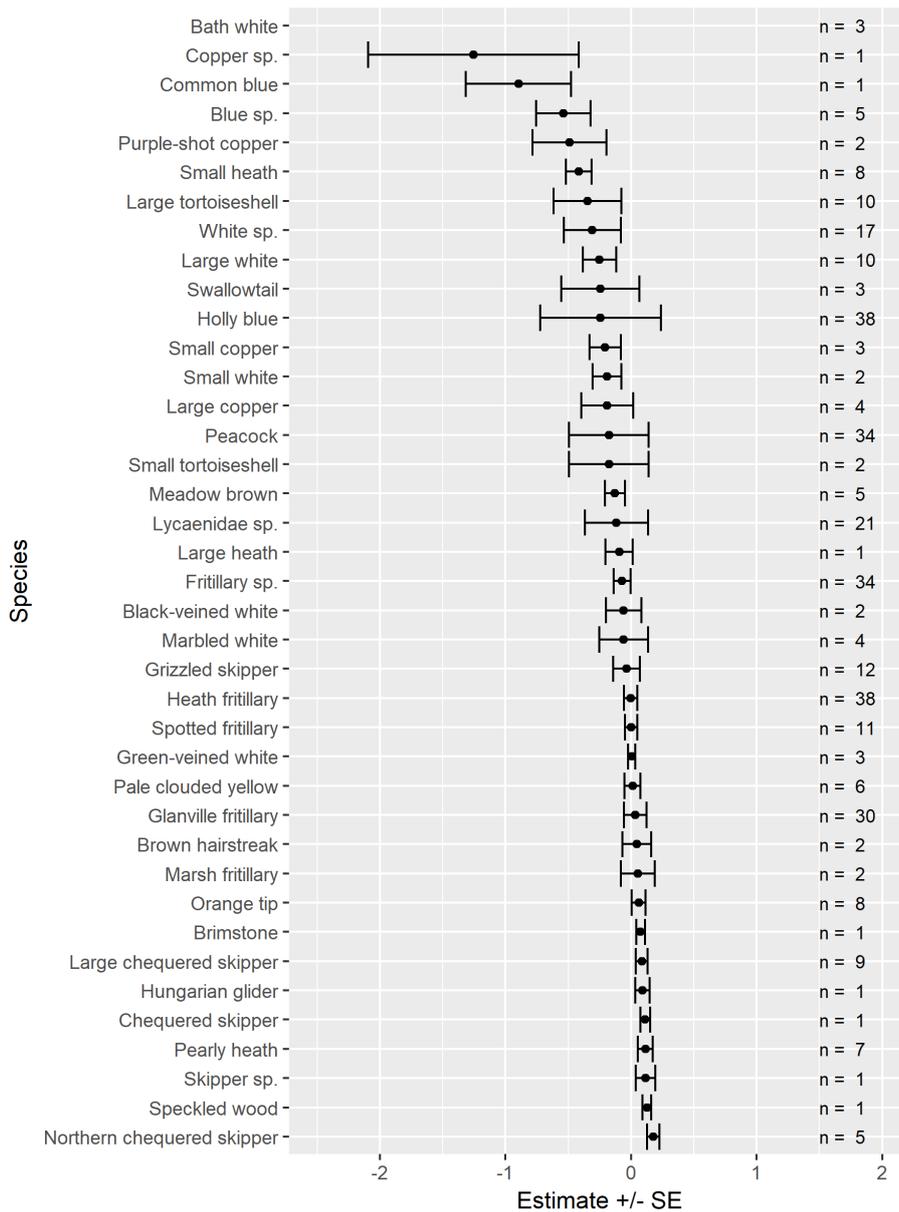


Figure 3.16 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between butterfly species’ population density and the mean height of the vegetation in each site. A more negative estimate indicates that species had higher population densities in sites with lower vegetation heights. There were 92 sites; n values on the figure indicate the number of sites with at least one observation for that species.

3.3.5 Species’ population densities compared in wetland and agricultural land

3.3.5.1 HNV bird species

Figure 3.17 shows the population densities of HNV bird species in the wetland of PSNPP and in the surrounding HNV farmland. As described in Chapter 2, these species are widely recognised as being indicative of HNV farmland. My results, however, show diverse patterns. Of particular note, two species (Reed bunting and Snipe) had

significantly higher population densities in the wetland than in the surrounding agricultural landscape. A further 19 species showed no significant preference. While for some of those species (for example Hoopoe) there were simply too few observations to draw any strong conclusions, for others (for example Whitethroat) there were ample data and these results provide robust evidence that population densities were similar in both wetlands and HNVf. In both cases, these results suggest the species in question are not dependent on HNVf but can in fact thrive in natural habitats. The remaining six species fitted the pattern expected of HNV species, with higher population densities in the agricultural landscape than in the wetland.

Across all bird species (HNV and non-HNV) only four were listed as threatened on the EU Red List For Birds (BirdLife International, 2015), but all of these are HNV species: Aquatic warbler, Black-tailed godwit, Great grey shrike and Lapwing (all listed as Vulnerable). Of these, Lapwings showed a significant preference for agricultural sites while Aquatic warblers, Great grey shrikes and Black-tailed godwits showed no significant preference. While four species is too small a sample to draw conclusions, these results do not suggest any simple association between threat status and habitat preference.

3.3.5.2 Non-HNV bird species

Looking at non-HNV birds (Figure 3.18), 20 species showed a significant preference for wetland, 38 showed no significant difference in densities across habitat types, and none preferred agriculture. That far more species had significantly higher population densities in wetland than in farmland highlights the importance of natural habitats for biodiversity. This remains true even if the results for HNV species (above) are also counted. Non-HNV species include wetland specialists (for example Savi's warbler), generalists (for example Jay), and farmland species somewhat tolerant of more intensive farmland (for example Starling). As such, these results highlight the diversity in species' habitat requirements, ranging from species which were abundant in wetland but never found in agricultural land (for example Wren) to species showing the opposite pattern (for example House martin).

None of these species are considered threatened on the EU Red List for Birds (BirdLife International, 2015); the only species not classified as Least Concern was the Meadow pipit, which is listed as Near Threatened. Meadow pipits were only observed in agricultural sites but this was not a significant preference.

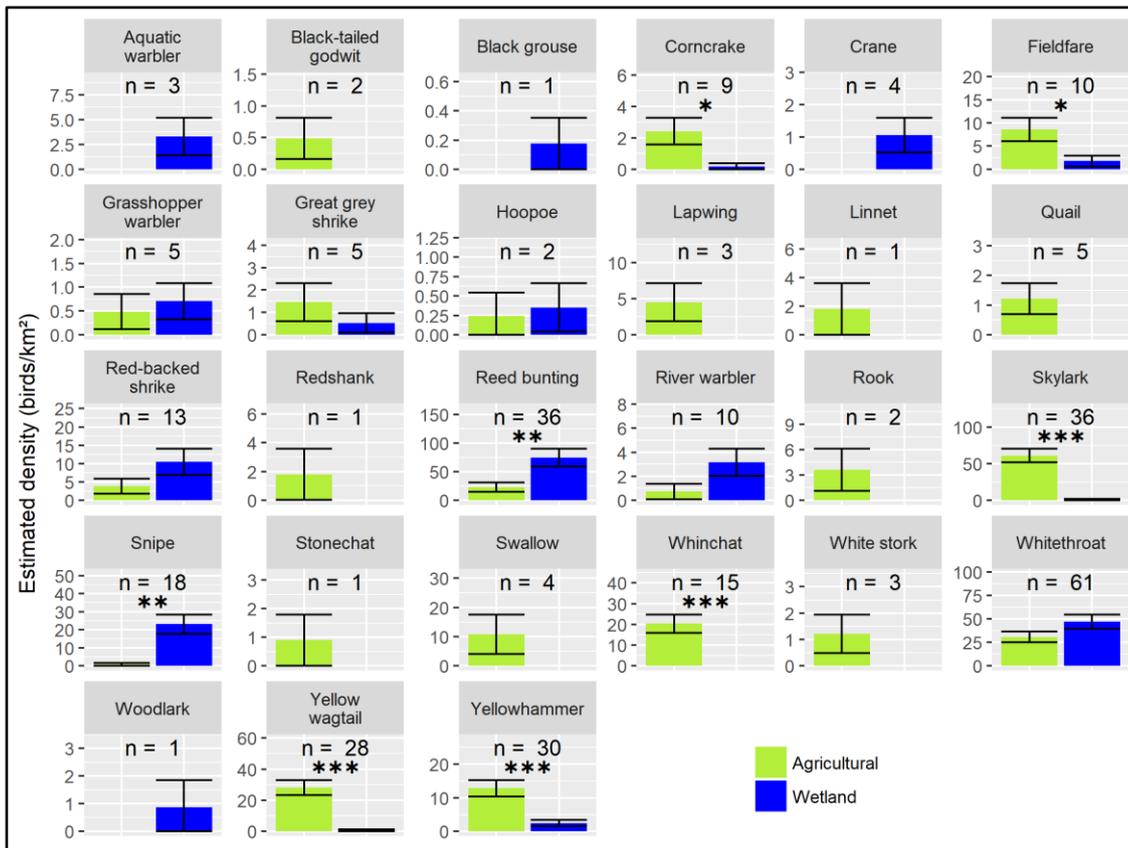


Figure 3.17 – Population density of HNV bird species in Agricultural (green) and Wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. There were 44 Agricultural sites and 48 Wetland sites; n values in the figure refer to the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either Agricultural or Wetland sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.3.5.3 Butterflies

Figure 3.19 shows the results for all butterfly species and species groups (i.e. observations that could not be identified to species level). Only one HNV indicator species (Marsh fritillary) was observed and so I have not separated the plots into HNV and non-HNV species. Interestingly, the Marsh fritillary was only observed in a wetland site (although this was not a significant result), although with only one HNV species it is clearly impossible to draw conclusions about the utility of wetlands for HNV butterflies in general. There was also only one species listed on the EU Red List for Butterflies (van Swaay *et al.*, 2010), the Large heath (Vulnerable), and this showed no significant preference. Overall, eight species of butterfly had significantly higher densities in farmland, 12 species showed no significant difference in density between farmland and wetland and only one preferred the wetland.

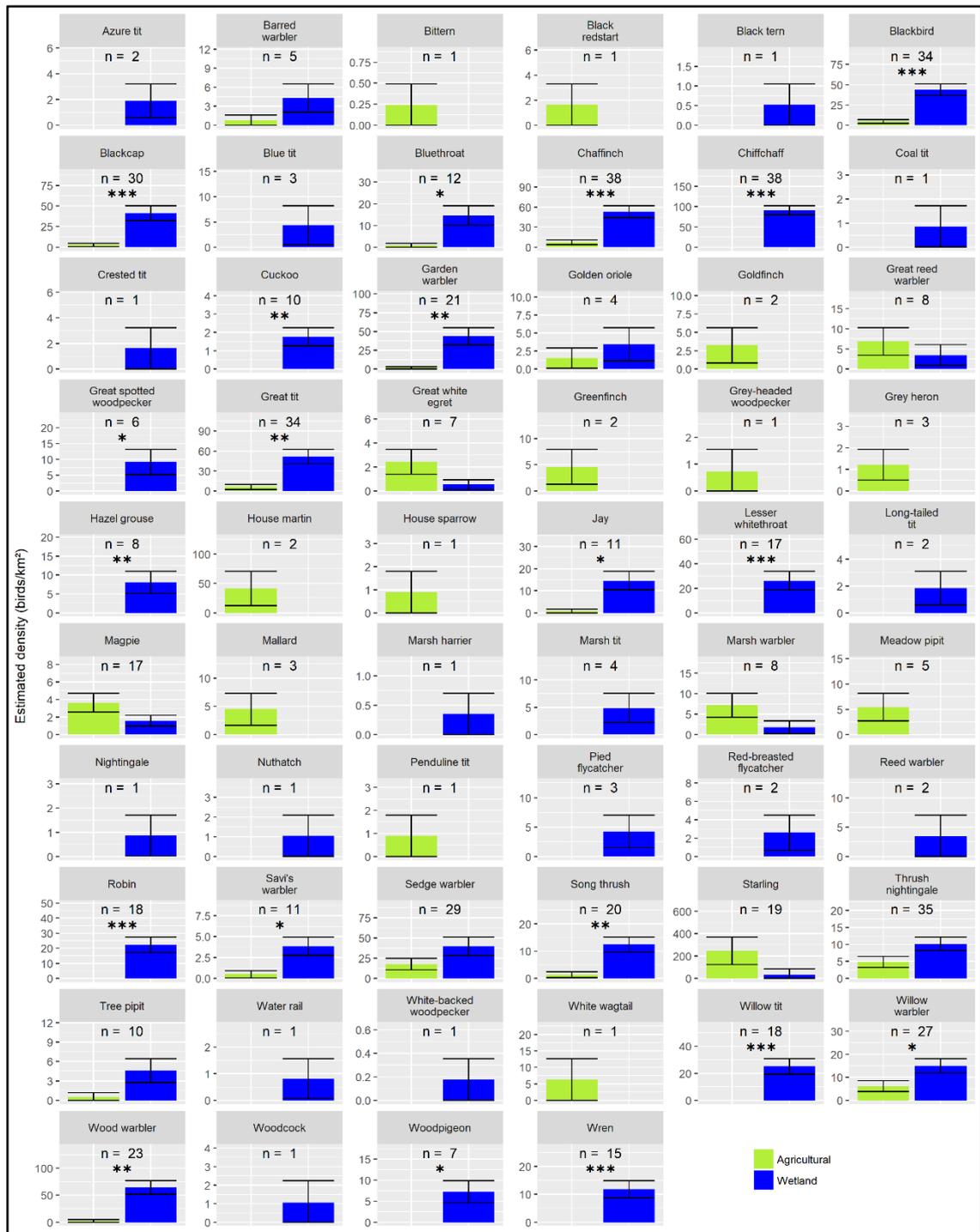


Figure 3.18 – Population density of non-HNV bird species in Agricultural (green) and Wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. There were 44 Agricultural sites and 48 Wetland sites; n values in the figure refer to the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either Agricultural or Wetland sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

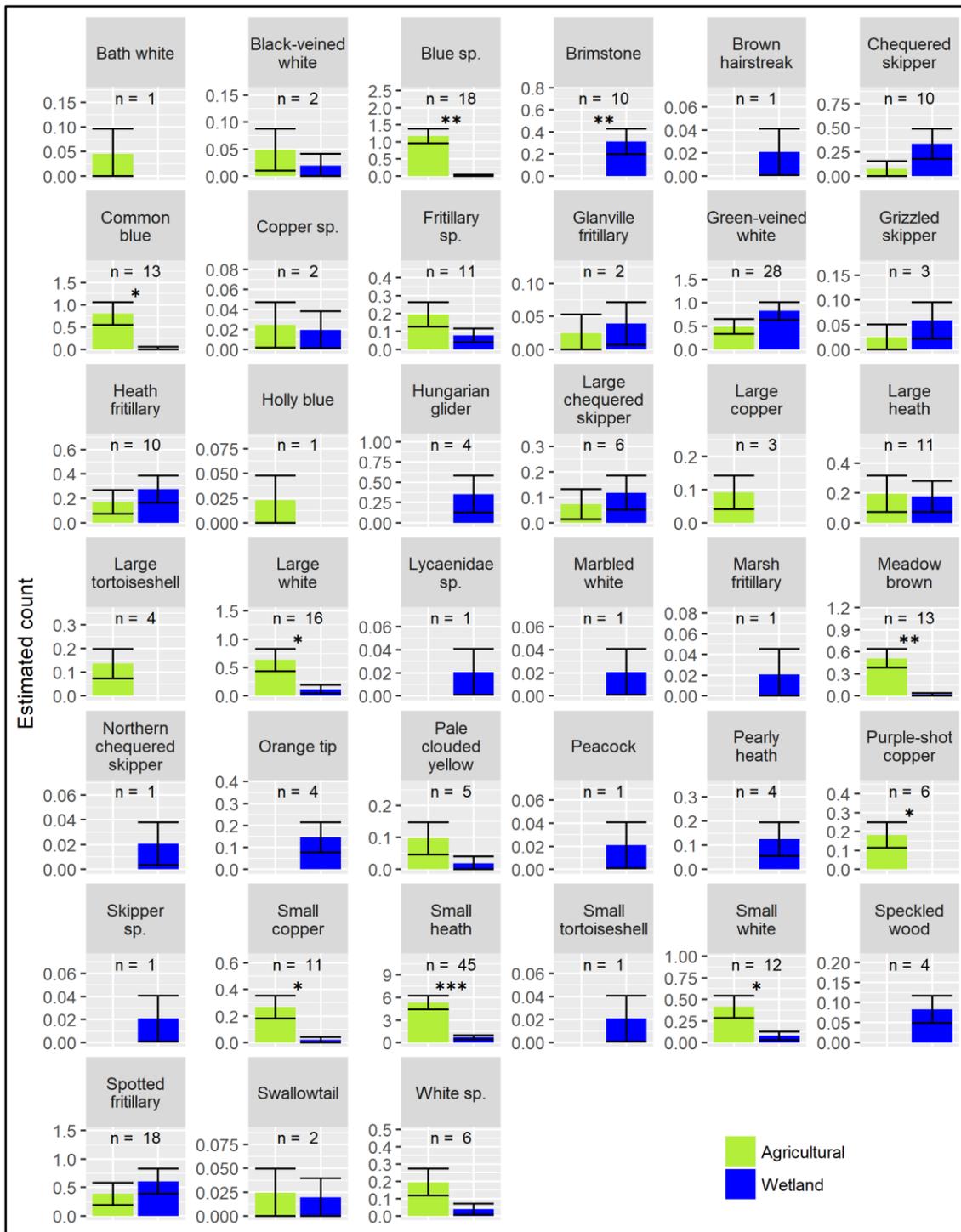


Figure 3.19 – Estimated counts per 200m transect of butterfly species in farmland (green) and wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. There were 44 Agricultural sites and 48 Wetland sites; n values in the figure refer to the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either Agricultural or Wetland sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.3.6 Comparisons with Polish results

While I found several HNV species of bird to prefer wetland to the surrounding agricultural land, this could be the result of population densities being unusually high in the wetland (as predicted from my hypothesis) or unusually low population densities in the surrounding agricultural land, or both. As described in Chapter 2 and the methods of this chapter, in an attempt to separate these possibilities I have compared my results to previous work in the Lubelskie region of Poland. Of all my study regions, the Ukrainian study region is the closest and ecologically most similar to this previous study region. A comparison of bird densities between my study region and the Lubelskie region may therefore shed further light on patterns seen in Ukraine, although with the caveat that the Lubelskie region of Poland is not necessarily any more ‘typical’ than my study region in Ukraine.

3.3.6.1 HNV birds

Looking first at birds classified as HNV species, Figure 3.20 shows that, in most cases, population densities are similar in low-yielding farmland in Poland and in farmland in my study region in Ukraine. In many cases, the central estimate from Ukrainian farmland is higher than that from Polish farmland, even if this difference is not significant. This suggests that the agricultural system present in my Ukrainian study site is an example of High Nature Value farmland, at least to the same extent as low-yielding farmland in Poland. Therefore, in most cases my previous results cannot be explained by low population densities in farmland in Ukraine compared to Poland. A small number of species do have significantly different densities in the two sets of farmland; perhaps these species have specific habitat requirements that are more common in one agricultural system or the other, such as wet grassy meadows favoured by the Black-tailed godwit (Melman *et al.*, 2008); nonetheless, such species are the exception.

The patterns in Polish baseline habitats versus Ukrainian wetland are less clear. A simple tally of significant differences was close to a tie, with seven species showing significantly higher populations in Poland versus six in Ukraine. However, looking more closely at the data, there are important differences to pick out. Several species which were found in low densities, or not at all, in “natural” baseline habitats in Poland had high population densities in Ukrainian wetland, such as Red-backed shrike and Whitethroat. This indicates that “natural” habitats in the two areas, which are only around 100km apart, are very different. Baseline habitats in Poland cannot be described as truly “natural”; I believe

the key driver of this difference is the large scale flood disturbance that exists in PSNPP but is largely suppressed in baseline habitats in Poland. Furthermore, many species have higher central estimates of population density in Ukraine than in Poland, albeit with sufficient error that this is not significant, which suggests those species do benefit, to some extent, from the natural flood regime in Ukraine. Several of the species which had higher population densities in Polish baseline habitats than Ukrainian wetland had relatively low densities in both regions, and higher densities in farmland (for example Corncrake, Whinchat). This also agrees with my previous results (above) that while flood disturbance benefits some HNV species, it does not benefit all of them.

3.3.6.2 Non-HNV birds

Figure 3.21 shows the results for all non-HNV bird species. Species' population densities in both sets of farmland tended to be similar, with a few exceptions. Of these, more species had significantly higher population densities in Polish than Ukrainian farmland, although in several cases the population density in farmland in both countries is close to zero (for example Coal tit, Lesser whitethroat). On the other hand, more species had significantly (and in some cases dramatically) higher population densities in Ukrainian wetland than in baseline habitats in Poland (for example Blackbird, Blackcap, Chiffchaff). With such a diverse set of species (the only commonality is that they were not classified as HNV species) a range of patterns is to be expected. To the extent that it is possible to generalise, these results suggest that Ukrainian farmland is similar in terms of value to biodiversity to low-yielding Polish farmland, but that non-HNV bird population densities in PSNPP are often much higher than in baseline habitats in Poland.

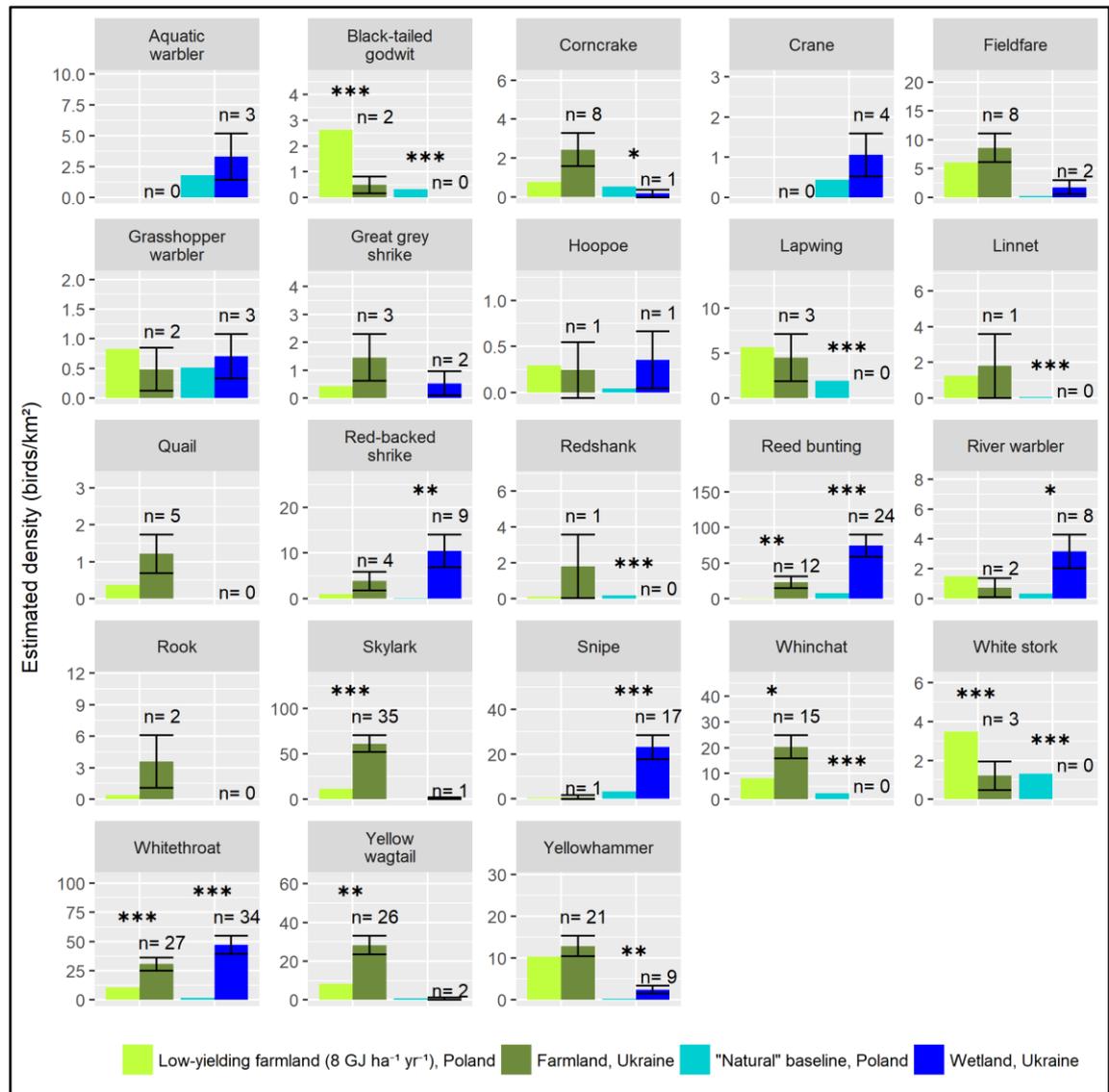


Figure 3.20 – Estimated population density of HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from Feniuk (2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine (* p<0.05, ** p<0.01, *** p<0.001). There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

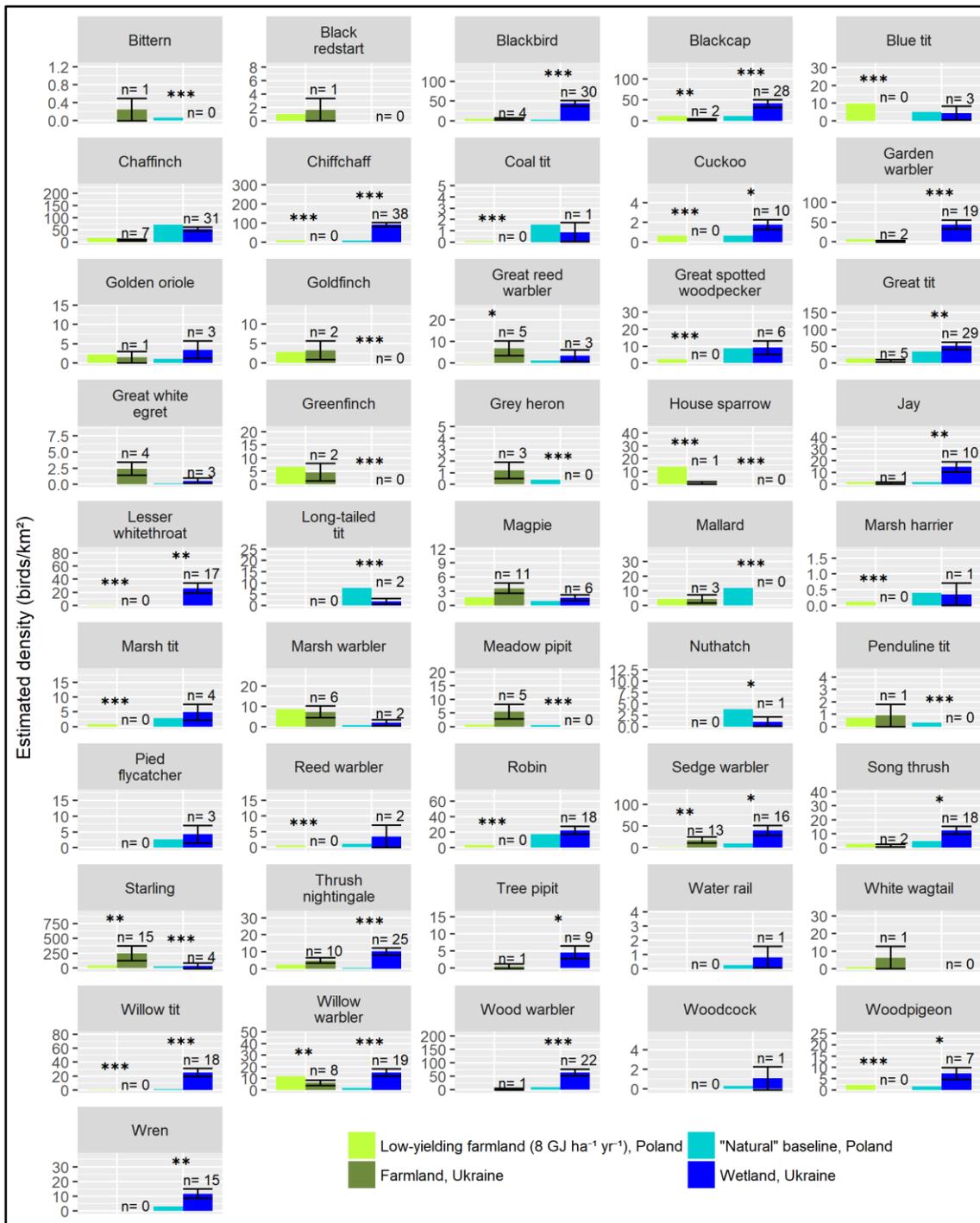


Figure 3.21 – Estimated population density of non-HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from Feniuk (2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate \pm one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

3.3.6.3 Flood Risk Score

There was no significant difference between the Flood Risk Score in baseline sites in Poland and wetland sites in my study region in Ukraine ($t = 1.79$, $df = 9.55$, N.S.; Figure 3.22). This is contrary to the expectation that my Ukrainian sites have greater flood disturbance. Farmed sites in Poland did have a significantly higher Flood Risk Score than agricultural sites in Ukraine ($t = 2.59$, $df = 18.5$, $p < 0.05$; Figure 3.22). Note that farmed sites in Poland refers to mosaic landscapes which have some agricultural production, but may also include non-productive areas (Feniuk, 2015).

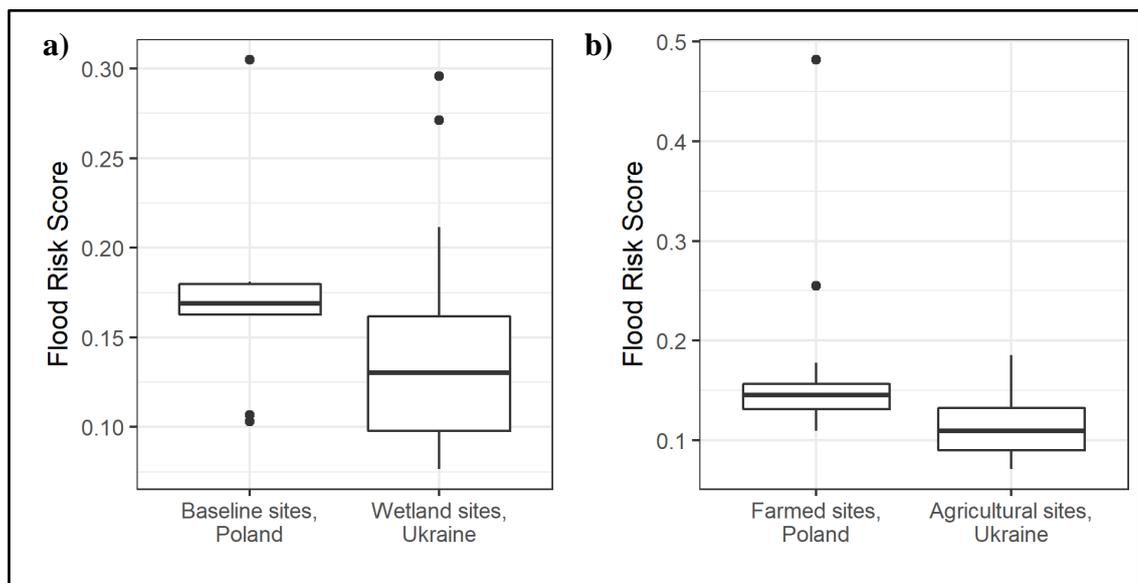


Figure 3.22 – a) There was no significant difference in Flood Risk Score in baseline/wetland sites between the Lubelskie region of Poland (Feniuk, 2015) and my study region in Ukraine ($t = 1.79$, $df = 9.55$, N.S.). b) Flood Risk Score was significantly higher in farmed sites in the Lubelskie region of Poland (Feniuk, 2015) than agricultural sites in my study region in Ukraine ($t = 2.59$, $df = 18.5$, $p < 0.05$). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated).

3.4 Discussion

In this chapter, I have examined habitats, disturbance processes and biodiversity in one of the best preserved examples of a natural floodplain in Europe: Pripjat-Stokhid National Nature Park (PSNPP) in Ukraine. Overall, my results demonstrate the value of wetland habitats for biodiversity, and demonstrate that they can support population densities of HNV species which are as high, or higher, than the population densities in HNVf. Furthermore, I have found evidence that the disturbance regime plays a role in modifying the habitat, which in turn leads to variation in species' population densities.

I compared population densities of species of bird and butterfly within the wetland to the surrounding agricultural landscape. Overall, my results highlight the importance of natural habitats for biodiversity, especially for birds. More species of bird had higher population densities in Ukrainian wetland than in the surrounding low-yielding farmland, and many species were not recorded in the agricultural landscape at all. Conservation of natural habitats, including wetland, is therefore essential for biodiversity. Looking just at HNV bird species, there were several species which had higher, or equal, population densities in the wetland to the surrounding farmland. Moreover, by directly comparing density estimates to estimates from Poland, it is evident that, in almost all cases, this was not because the characteristics of the farmland made it particularly unsuitable for those species (species typically had similar densities in Ukrainian as in Polish farmland) but rather that many species had high densities in Ukrainian wetland, higher than they did in Polish baseline habitats (albeit in some cases these differences were not significant). This suggests that the characteristics of natural habitats differ between these regions. The differences between these study regions may be because PSNPP is a large protected area subject to a natural flood regime along with other forms of biotic disturbance such as browsing, whereas the natural habitats sampled in Poland were on a smaller scale and not subject to the same disturbance.

However, across both birds and butterflies in Ukraine, there were still many species, including some HNV species and the majority of all butterfly species, which had higher densities in farmland than wetland. Some species were never observed in the wetland. Wetland restoration would therefore not be a useful conservation strategy for all species, including some HNV species. Nevertheless, if the hypothesis that these species depend on disturbance (be it natural or anthropogenic) is correct, then restoring other disturbance processes may benefit them. While the landscape and habitats of PSNPP are dominated by flood disturbance, other natural habitats dominated by fire, or grazing, or both might provide suitable habitat for other HNV species (Fuhlendorf *et al.*, 2009; Archibald *et al.*, 2013; Navarro *et al.*, 2015; Regos *et al.*, 2016). Further work is needed to establish the biodiversity impacts of restoring those and other disturbance processes at the landscape scale.

To further understand what was driving these patterns, I investigated the responses of birds and butterflies to variation in habitat and vegetation structure. I found different species have different preferences: some prefer open habitats, others closed habitats,

while some are more generalist. Furthermore, these preferences correspond well with what is known about species' preferences (Snow *et al.*, 1998; van Swaay *et al.*, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). This is therefore a clear indicator that my bird and butterfly surveys, and habitat mapping, were reasonably robust and accurate in estimating species' abundances and describing habitats in a biologically relevant way. I further tested this by using vegetation mean height as the explanatory variable instead of Veg.PC1 and found similar results. Both Veg.PC1 and vegetation mean height have strengths and weaknesses as descriptors of the habitat, and my results suggest neither one is obviously more useful than the other.

Wetland sites clearly differ from agricultural sites in terms of their vegetation structure and disturbance regime. Focusing on the wetland sites (where natural processes might be expected to show stronger relationships with habitats) there was some evidence that disturbance processes were driving vegetation structure. Both Disturbance PC1 and Flood Risk Score were significantly correlated with Veg.PC1, suggesting that disturbance from fire and flooding can both create open habitats. However, the high variance unexplained by the correlation, and the lack of correlation between water depth or Disturbance PC2 with Veg.PC1, all suggest that the drivers of vegetation structure are diverse and incompletely captured by the variables I studied, in the way I studied them. Furthermore, at the moment these results remain correlational and cannot exclude alternative explanations, including the possibility that certain types of disturbance such as fire are more common in open habitats (Bond & Keeley, 2005; Archibald *et al.*, 2013).

The results from calculating Flood Risk Score indicated that this metric is useful in determining flood disturbance, with permanent water bodies clearly picked out and having a score close to one, intermediate values across much of the floodplain, and typically low values in agricultural areas. However, there is also evidence that this approach has limitations. While large, permanent water bodies were clearly distinguished, river channels were not so clear, possibly because the channels are quite narrow (my experiences in the field suggest often <10m) and so only partially fill each Landsat pixel. Furthermore, the river channels may be obscured by emergent, floating or overhanging vegetation, none of which should be classified as water by the mNDWI method (Xu, 2006). Finally, the rivers are dynamic, and the exact course of the main channels may have altered even within the timescale of the satellite data used. The presence of emerging or floating vegetation may also obscure standing water in the floodplain surrounding the

river channels, again leading to an omission error in detecting the presence of water (Figure 3.23). In addition to technical limitations in calculating Flood Risk Score, there are limitations in the use of Flood Risk Score as a metric of flood disturbance. Agricultural land was often drained using artificial ditches, which were often substantial in width and so the water in them could have been detected (pers. obs.), which could lead to a high Flood Risk Score within agricultural areas despite water being constrained to those ditches and not the result of flooding (although note that some agricultural land consisted of wet meadows and therefore not all high Flood Risk Scores in agricultural land are misleading). A more general limitation stems from Flood Risk Score being a measure of the proportion of time a parcel of land is inundated with water. Rather than long term inundation, flood disturbance could be created by rapid, high energy but infrequent flood events (Richards *et al.*, 2002; Parajka *et al.*, 2010). Furthermore, Flood Risk Score also does not account for differences in subterranean water levels or hydrological connectivity, both of which have been shown to affect the vegetation and can be considered as components of the flood disturbance regime (Richter *et al.*, 1998; Powell, Jakeman & Croke, 2014; Hester *et al.*, 2016).



Figure 3.23 – Emergent, floating or overhanging vegetation may prevent the detection of water when using satellite data.

However, the proposed differences in disturbance regime between my study region and that in Poland were not reflected in Flood Risk Score, for which I found no difference between baseline sites in Poland and wetland sites in Ukraine. As described above, this may reflect limitations of the Flood Risk Score metric, especially in sites with a high degree of vegetation as was the case in PSNPP. Other forms of disturbance may also be important, but I do not have comparable data for these from Poland. Nonetheless, these results do suggest that if wetland restoration can recreate wetlands comparable to PSNPP, then doing so would benefit biodiversity immensely, including both species previously found to prefer natural habitats (Feniuk, 2015) and HNV species (Paracchini *et al.*, 2008). In terms of farmland, the agricultural sites in my field region in Ukraine appeared to broadly similar to low-yielding farmland in Poland in terms of bird species' population densities. Farmed sites in Poland did have a slightly higher Flood Risk Score than those in Ukraine. Wet meadows were an important component of the farmland in Poland (Feniuk, 2015) but formed only a small part of my agricultural study sites in Ukraine. However, this result may reflect idiosyncrasies in site selection or local patterns in agriculture, rather than widespread differences in the agricultural systems between the two regions.

3.5 Conclusion

In this chapter, I have looked at a natural floodplain wetland and the surrounding HNVf in north-western Ukraine. Across much of Europe, HNVf is declining as a result of both intensification and abandonment. This raises an important concern for the conservation of species associated with HNVf. Overall, more bird species had higher densities in the wetland than the surrounding farmland but more butterfly species preferred the farmland. Moreover, I found many bird species categorised as HNV species had equal or higher population densities in wetland than farmland, in contrast to the expectation given their presumed affiliation with farmland. By comparison with previous work in Poland, this appears to be driven more by high population densities in wetland areas rather than by low population densities in agricultural areas in my study region. This suggests that large areas of contiguous floodplain, subject to natural ecological processes including disturbance processes, can contain habitats suitable for some HNV species.

Looking at habitat and vegetation structure, I found clear associations between species and habitat structure. These associations match expectations from accounts of species' ecologies, and therefore confirm the robustness of my biodiversity sampling techniques.

There was some evidence that disturbance processes, particularly fire and flooding, could lead to more open habitats, as predicted by my hypothesis. However, it was also clear that my results did not fully explain the variance in habitats observed; this may reflect limitations of my surveys and data collection, or it may reflect that habitats are the result of complex ecological processes acting over long timescales, and therefore much more extensive study would be required to elucidate mechanisms driving patterns in habitats.

This chapter focuses on a natural floodplain, which has never been subject to significant anthropogenic influence. However, across most of Europe this type of habitat has been lost, and therefore would need to be restored. While restoration often aims to recreate a reference natural habitat, it does not always succeed. The next two chapters therefore focus on two contrasting restoration projects, and aim to understand the extent to which restoration of floodplains benefits biodiversity in the same way as do natural floodplains, and whether this is influenced by the characteristics of the restoration carried out.

4 FRANCE

4.1 Introduction

In the previous chapter, I found that a natural floodplain supported high population densities of many species of bird and butterfly, including several species more commonly associated with HNVf. I therefore concluded that a natural flood disturbance regime can create suitable habitats for those species. However, across most of Europe, rivers have been disconnected from their floodplains (Tockner & Stanford, 2002; Davidson, 2014) and most rivers around the world are subject to some form of flow regulation (Lehner *et al.*, 2011). Therefore, in order to realise these benefits across Europe, in most cases it is necessary to restore floodplains and reinstate a natural flood regime.

Over the past decade or so, deregulation of rivers and floodplain restoration have received growing attention in both policy and research, and received large amounts of funding (Poff & Hart, 2002; Bernhardt *et al.*, 2005; Bridgewater & Aricò, 2016; Angelopoulos *et al.*, 2017), although the majority of projects which are carried out are not monitored for their effectiveness (Bernhardt *et al.*, 2005; Olden *et al.*, 2014). Restoration projects vary widely in their objectives and implementation. In many cases, the strongest political driver is to reduce flood risk to urban areas (ClimateWire, 2012; Bond *et al.*, 2014; Mikus *et al.*, 2016; Potter, Ludwig & Beattie, 2016; Ahilan *et al.*, 2018), although predicting the impact of restoration on hydrology can be challenging (POST, 2011; Acreman & Holden, 2013; Alfieri *et al.*, 2016; Dixon *et al.*, 2016; Waylen *et al.*, 2018). Restoring rivers and their floodplains can also benefit biodiversity, increase water quality and amenity value, and increase carbon sequestration (Buijse *et al.*, 2002; Palmer *et al.*, 2005; Hughes *et al.*, 2012; Beyer & Höper, 2015; González *et al.*, 2015; Sutfin *et al.*, 2015; Muhar *et al.*, 2016; Schindler *et al.*, 2016).

Numerous studies have shown the impact of floodplain restoration of a wide range of taxa, including plants (González *et al.*, 2015; Sellheim, Vaghti & Merz, 2016; Toth, 2017), birds (Raven, 1986; Jonsson, Strasevicius & Malmqvist, 2012; van Turnhout *et al.*, 2012; Hagy *et al.*, 2017), carabid beetles (Görn & Fischer, 2015; Januschke & Verdonschot, 2015), aquatic invertebrates (Miller, Budy & Schmidt, 2010; Mérigoux *et*

al., 2015) and fish (Roni *et al.*, 2008; Dolédec *et al.*, 2015; Lamouroux & Olivier, 2015). However, while it has been suggested that restoring natural disturbance processes could benefit HNV species (Navarro *et al.*, 2015), to the best of my knowledge no study has yet focused on testing that hypothesis. In this and the subsequent chapter, I aim to directly test that hypothesis through studies of two regions where restoration projects have been carried out.

The first of these two projects was in France, on the river Rhône. The Rhône is one of the major rivers in Europe, flowing down from the Alps through Switzerland and France to the Mediterranean Sea, where it forms the Camargue Delta. Natural river morphology can be described as a spectrum, influenced by the surrounding geology, climate, topography, sediment load, gradient and discharge (Figure 4.1(a); Knighton & Nanson, 1993). The Rhône flows from the alps, where the landscape was formed by tectonic activity creating the mountains and subsequently modified by glacial activity (Olivier *et al.*, 2009). In my study region, the Rhône naturally varied along the spectrum of river morphologies between a braided river and a meandering river, varying over time in response to changes in sediment load and discharge (Olivier *et al.*, 2009). It is thought that immediately prior to human modification, the Rhône's natural morphology was on the cusp between a meandering and a braided river system (Michelot, 1983). As such, the Rhône naturally had a meandering main channel but also smaller channels within the floodplain, known as "floodplain channels" (Figure 4.1(b)). The Rhône would naturally have been dynamic, with the main channel migrating across the floodplain and floodplain channels being formed and subsequently abandoned in response to variation in patterns of erosion and sedimentation (Olivier *et al.*, 2009). However, since approximately 1870, human activities have had ever increasing influence over the morphology of the Rhône, both through direct works such as embankments but also through changing land use in the Rhône's catchment resulting in changing patterns of erosion and sedimentation (Fruget, 2006; Olivier *et al.*, 2009).

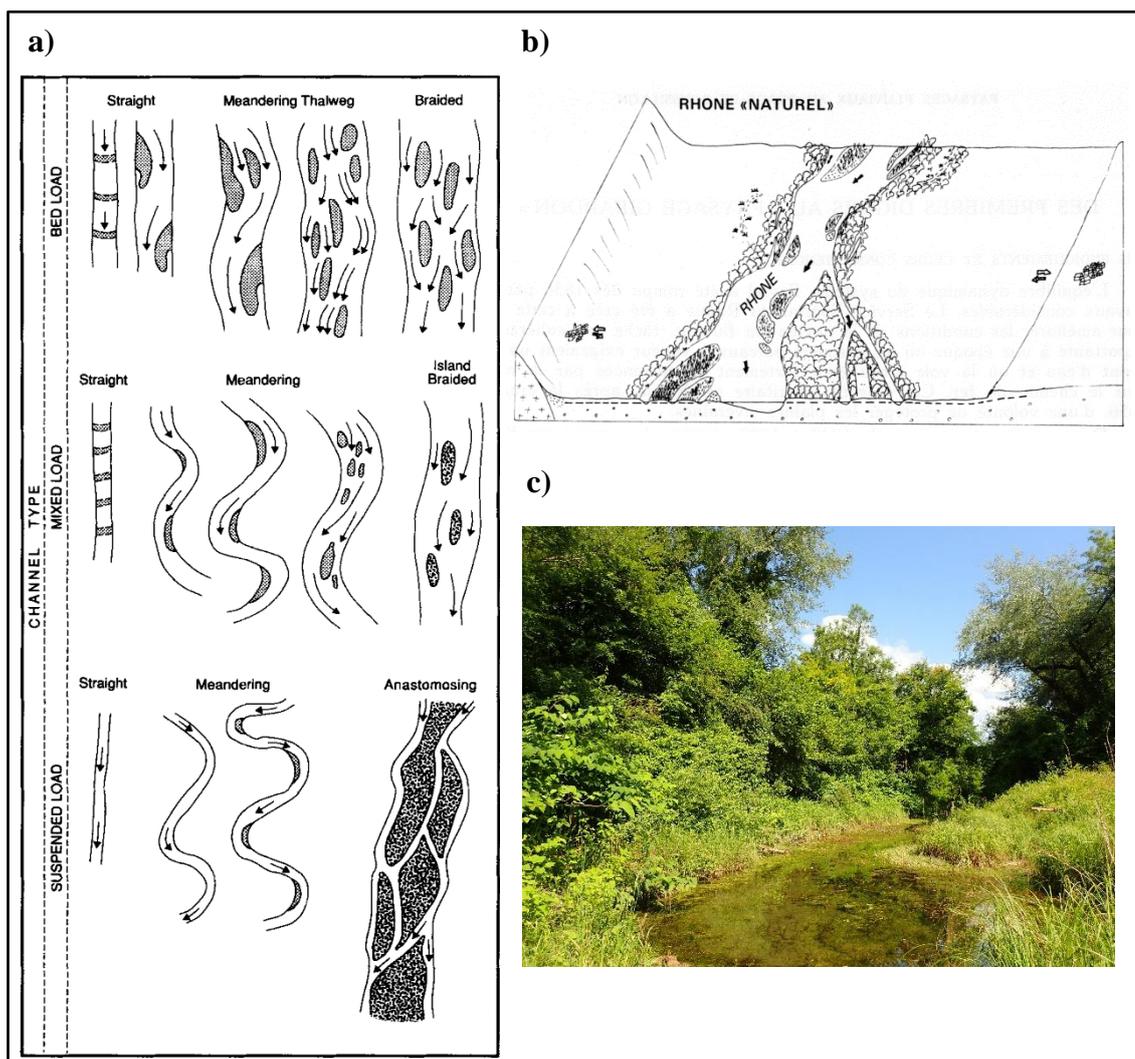


Figure 4.1 – a) The spectrum of river morphologies, from Knighton & Nanson (1993). b) Schematic of the natural morphology of the Rhône near my study region, in recent times but prior to human modification, from (Michelot, 1983). Floodplain channels are illustrated on both sides of the main channel. c) An example of a floodplain channel in my study region.

The Rhône has an extensive history of human use, being used as a major trade route since ancient times (Koch, 2006). As technology, particularly engineering, advanced, the Rhône was subject to ever greater modification. Levees were built as early as the beginning of the 19th Century to protect riverside residents from floods, followed by dykes to improve navigability (Fruget, 2006). The most substantial changes occurred after the *Compagnie Nationale du Rhône* was established in 1933, and tasked with improving navigation and generating electricity (Terrier & Bouffard, 2003). Over subsequent decades, embankments were built, the natural channel was further modified through dredging and embankment, and several sections of the natural channel were bypassed by artificial channels to facilitate hydroelectric generation (Fruget, 2006; Olivier *et al.*, 2009). In each of these sections, barrages at the upstream difffluence control the amount

of water released into the natural channel, with the remainder flowing through the artificial canal to the hydroelectric plant (Figure 4.2). These modifications have resulted in dramatic changes to the river's physical and biological processes (Ward & Stanford, 2006; Olivier *et al.*, 2009). Numerous dams regulate the flow, avoiding both extreme high and low flows; patterns of sediment erosion and deposition have been altered; large areas of riparian vegetation have been lost; and eutrophication has reduced aquatic macrophyte diversity in many areas (Fruget, 2006; Olivier *et al.*, 2009).

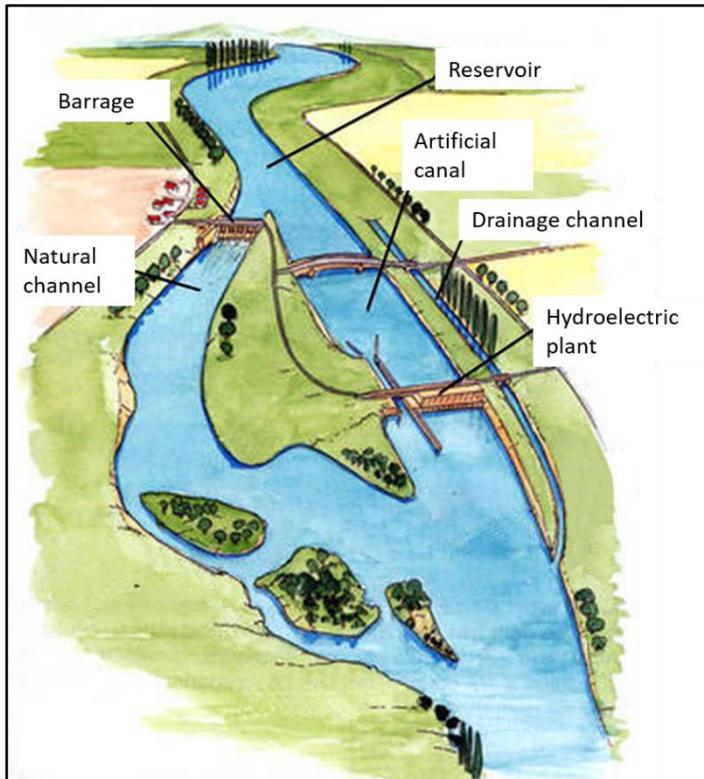


Figure 4.2 – Illustrative cartoon of typical layout. At the upstream diffidence, a barrage controls the amount of water discharged through the natural channel. The remaining discharge flows through the artificial canal and through a hydroelectric plant before re-joining the natural channel. Modified from Rottier (2013)

Following floods in the Upper Rhône in 1990, decisions were made to carry out a restoration project, with aims of both reducing flood risk and improving biodiversity (Lamouroux *et al.*, 2015). This restoration project can be broken down into two components. Firstly, the minimum discharge into the natural channel was increased. At times when total discharge of the river is low, most water is diverted through the artificial canals and hydroelectric plants, leaving very little discharge into the natural channel. The minimum level of discharge into the natural channel is mandated by law on a reach-by-reach basis and is a small fraction of the natural discharge. As a typical example, in the Chautagne reach (see below), the minimum discharge was previously set at $10\text{-}20\text{m}^3\text{s}^{-1}$,

whereas the average unregulated discharge would be $410\text{m}^3\text{s}^{-1}$. This legally mandated minimum was increased in the Chautagne reach to $50\text{-}70\text{m}^3\text{s}^{-1}$. Even at this increased level, the minimum discharge is still only a small fraction of the natural discharge, and above-minimum discharge is expected for most of the year (Lamouroux *et al.*, 2015).

The second component was active restoration of floodplain channels. As a result of channelization and the reduced discharge through the natural channel, many of these had become terrestrialised or disconnected from the main channel by the build-up of sediments. The restoration therefore aimed to reverse this by dredging or digging to reconnect the floodplain channels with the main channel and improve flow through the floodplain channels (Lamouroux *et al.*, 2015). Importantly, the potential for scientific study was considered in the planning stage, and only a subset of floodplain channels was restored, leaving the rest as unrestored controls to assess the impact of the restoration (Lamouroux *et al.*, 2015).

This project has been the focus of ongoing research to monitor the impacts of both restoring the floodplain channels and increasing the minimum flow. To date, studies have shown that restoration has led to changes in physical characteristics of floodplain channels (Riquier, Piégay & Šulc Michalková, 2015), changes in aquatic macroinvertebrate communities (with effects differing between native and alien species; Castella *et al.*, 2015; Mérigoux *et al.*, 2015; Paillex *et al.*, 2015), and changes in fish communities (Daufresne *et al.*, 2015; Dolédec *et al.*, 2015; Lamouroux & Olivier, 2015). However, these studies have focused on physical attributes and aquatic communities of the channels themselves rather than on wider ecological impacts.

I therefore aimed to investigate the impact of the restoration project on the wider ecosystem, in terms of both biodiversity and habitats, with a particular focus on the extent to which this restoration project has increased flood disturbance and thereby modified the environment in a way that benefits HNV species. Furthermore, the situation of this project enabled me to study the biodiversity and habitats of several other land cover categories. Differences between these categories may highlight which processes and environmental features most strongly influence the responses of biodiversity to floodplain restoration.

4.2 Methods

4.2.1 Field Methods

I conducted fieldwork on a section of the Upper Rhône in eastern France, between Lyon and Geneva (Figure 4.3). My study encompassed three bypassed reaches: Chautagne, Belley and Brégnier-Cordon (after the nearest towns; see Lamouroux *et al.* 2015 for more detail). The surrounding landscape is primarily agricultural, with intensive arable on the valley floors, and vineyards and livestock on the sides of valleys and higher elevations. My study sites were all located on the valley floor, in what would have been the floodplain prior to human modification. To give an indication of intensity, average yield in Rhône-Alps NUTS 2 Region for cereals is 53.7 tonnes per km² per year (EUROSTAT, 2014).

As described above, both restored and non-restored floodplain channels have been sampled for previous studies and I used the same study sites, totalling 22 restored channel sites and 33 non-restored channel sites (see Lamouroux *et al.* 2015 for further details on how these were selected). In addition to these floodplain channels, the study region has a number of different land uses which I felt may provide useful contrasts to each other. I therefore selected additional study sites in four other categories: Farm (34 sites), Main Channel (12 sites), No Channel (14 sites) and Meander (6 sites), as described below (Figure 4.4).

As I was interested in how farmland species fare in flood-disturbed landscapes, I sampled Farm sites spanning the same section of river as the floodplain channels but at least 100m from any channel. For practical reasons, all study sites were selected to be accessible, although an extensive network of tracks and paths meant that this was not too restrictive, and representative farmland could still be reached.

Floodplain channels are much smaller than the main river Rhône, and I felt that the main channel was likely to be significantly different in terms of both physical features and biodiversity. I therefore also sampled Main Channel sites, located at the edge of the main river channel, at points where the channel is bordered by natural habitat. These sites were intended to include both biodiversity associated with the Rhône itself, and biodiversity associated with habitats bordered by a large river channel. I selected Main Channel sites spanning the same stretch of river encompassing all my Floodplain Channel sites (Figure 4.3).

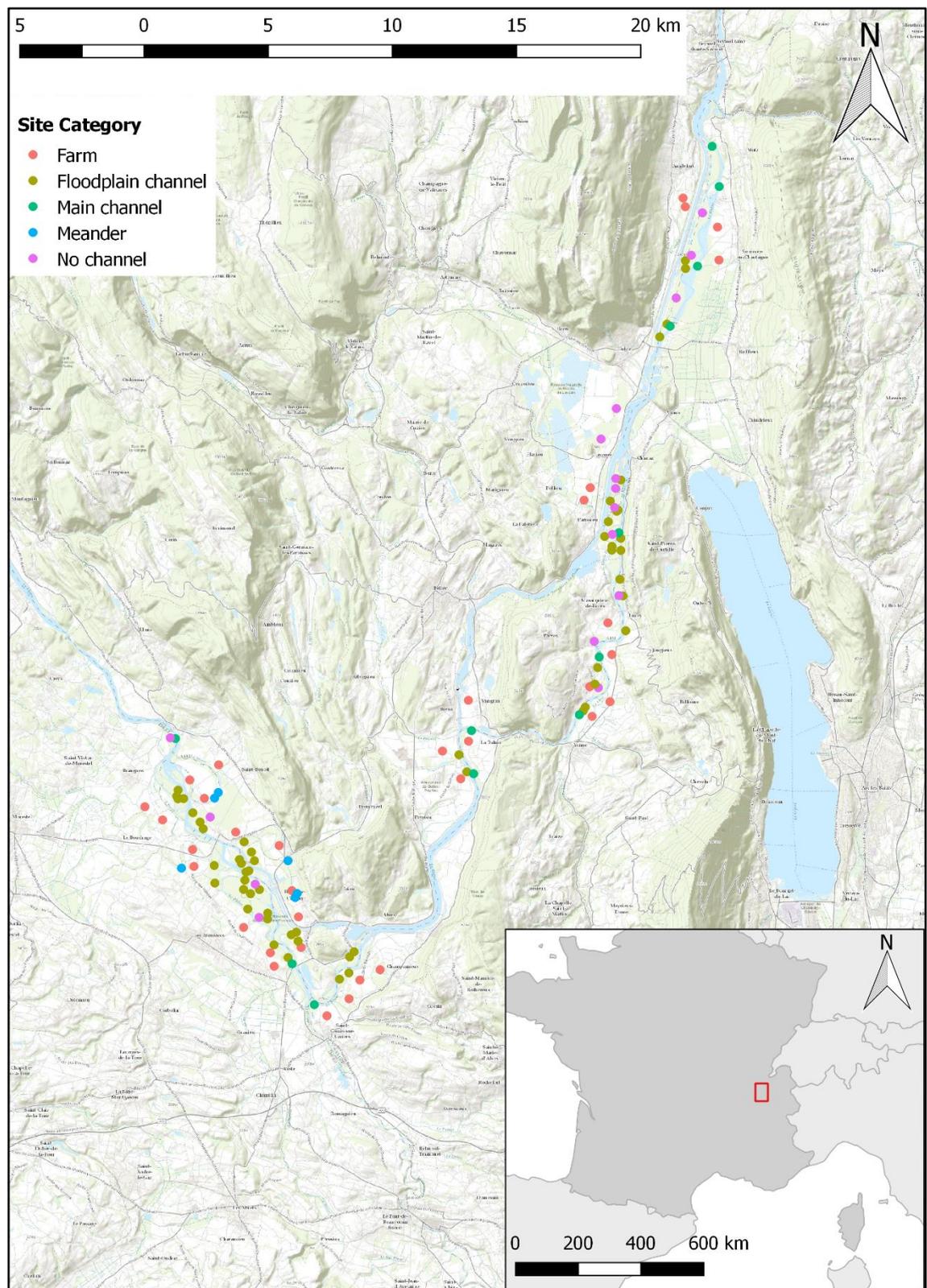


Figure 4.3 – Location of study sites. Main panel shows a topographic map of the study region with positions of individual study sites indicated by dots, coloured by category (not to scale). Inset panel shows location of study region within France (dark shading) and Europe; red box is area detailed in main panel.

Prior to channelization, the Rhône was a dynamic, meandering river. As the river shifted, old meanders became cut off, initially forming oxbow lakes and over time becoming

increasingly terrestrialised or permanent wetlands, depending on ground water supplies. These former meanders provide a contrast to floodplain and main channel sites, being lentic wetland sites fed by groundwater, rather than lotic sites fed by runoff. I therefore chose to include Meander sites to observe ecological and physical differences from my other study sites (Figure 4.3). These former meanders are also included in the ongoing research project; as with floodplain channels I based my study sites on previous sampling locations. In this case, there were two sites per meander, located near the upstream and downstream end of the meander, and all such former meanders within my study region were included (Emmanuel Castella, pers. comms. 2016).

If river channels are affecting the surrounding habitats through flood disturbance, then they should differ from otherwise similar areas lacking flood disturbance. No Channel sites were located at least 100m from the nearest channel (including the main channel, bypass canals and floodplain channels) but still within the floodplain, in areas of natural habitat, which otherwise match the habitats surrounding the main channel and floodplain channels. I selected sites opportunistically within the same region as my Floodplain Channel sites (Figure 4.3).

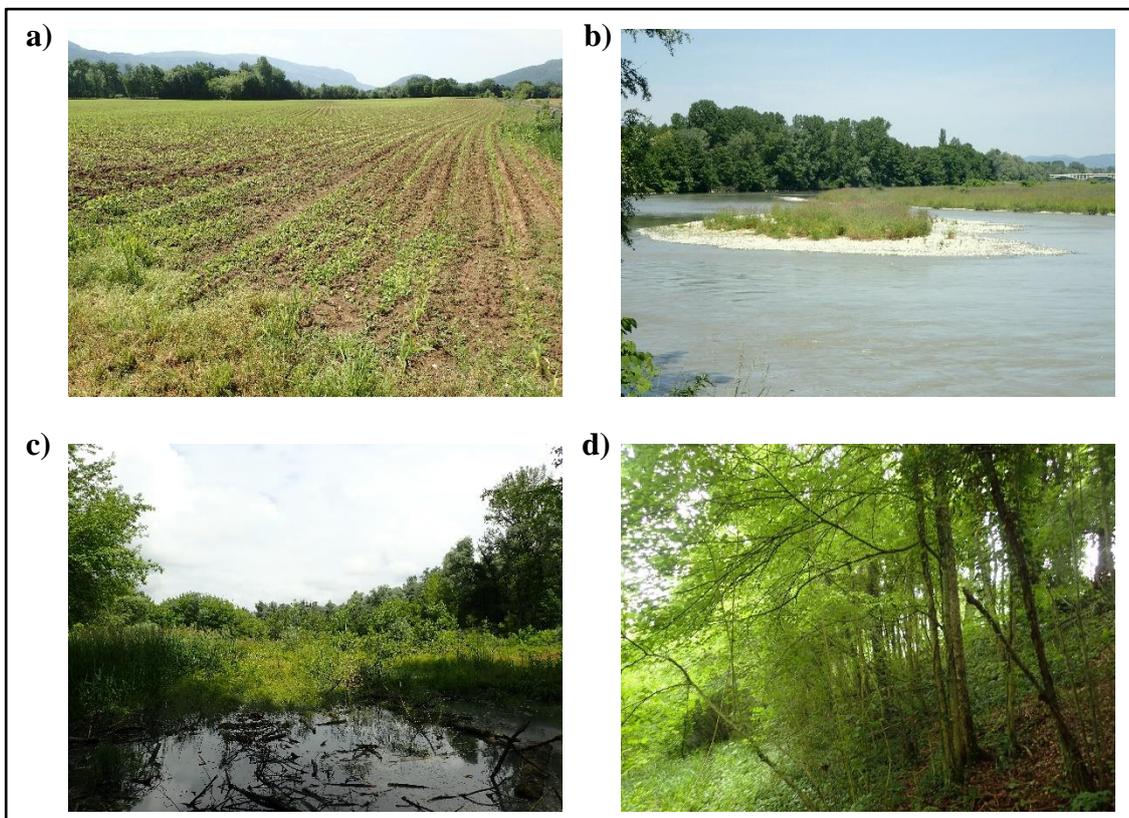


Figure 4.4 – Photographs of typical landscapes in a) Farm sites; b) Main Channel sites; c) Meander sites; d) No Channel sites.

In most sites, I carried out bird counts, butterfly transects and habitat mapping following the protocols described in Chapter 2. Bird counts were not carried out in 10 Floodplain Channel sites for logistical reasons. Butterfly transects were all 100m long, and in Floodplain Channel, Main Channel and Meander sites they followed the course of the channel in order to maximise the likelihood of detecting an effect of channel type. I tried to centre the transect around the study point (i.e. 50m on either side) but practical constraints meant this was not always possible, although transects always passed through the study point. I did not collect biotic disturbance in this field season. Most of the landscape, including “natural” habitats, was managed to some extent by humans. The most natural sites were in the *Réserve naturelle du Haut-Rhône français*, although even those sites were subject to some management. As such, I felt that anthropogenic impacts would mask any effect of biotic disturbance.

I visited all study sites several times through my field season on a rotational basis. As I was able to visit several study sites within a day, on subsequent rotations I varied the order in which I visited sites, in order to account for variation in bird and butterfly activity even within the prescribed time windows for those surveys. For most sites, I carried out bird counts three or four times (mean 3.74); however, access was limited for five sites within the *Réserve naturelle du Haut-Rhône français* which were only counted once. Due to the more restrictive weather requirements for butterflies, I was only able to carry out one to three butterfly counts per site (mean 2.49).

4.2.2 Analyses

I first characterised the habitat and vegetation structure at each site. As my habitat and vegetation structure data were highly dimensional, I carried out a Principal Components Analysis to reduce this dimensionality. As described below, I chose to use a single component (Veg.PC1) as my main metric to describe the habitat and vegetation structure.

As a metric of the long term significance of flood disturbance in each site, I used Landsat data to calculate Flood Risk Score over the entire study region, using the methodology described in Chapter 2. I limited the search to only include those images taken after restoration of the studied region was completed, in 2006. The search was carried out in October 2017. In total, I used 107 suitable images, dating from 2006 to 2017.

My study site categories were chosen based on land cover, and I therefore expected differences in the habitats and vegetation structure across them. Furthermore, I expected

them to differ in their degree of flood disturbance. To confirm and quantify this, I compared habitat types, Veg.PC1, Flood Risk Score and water depth between the different categories of study site. For habitat types, I used a MANOVA to test for a significant association. For Veg.PC1, Flood Risk Score and water depth I used Tukey's HSD test to identify pairwise significant differences. I also looked for correlations between Veg.PC1 and Flood Risk Score, and Veg.PC1 and mean water depth to investigate whether there is evidence that flood disturbance affects habitats and vegetation structure.

A central tenet of both my study and ecology more generally is that different species occupy different niches, and therefore will have different population densities in different habitats (Darwin, 1859; Elton, 1927; Begon *et al.*, 2006). In this region more than my other study regions, I was able to directly investigate the effects of land cover on species' population densities. I compared population densities between the five categories of study site (Farm, Floodplain Channel, Main Channel, Meander and No Channel), for all bird and butterfly species individually. To do this, I fitted quasi-Poisson regression models with count as the dependent variable, site category as an explanatory variable, a log link function and the log of sampling effort as an offset. All floodplain channel sites were considered together for this analysis. For birds, sampling effort was number of visits multiplied by estimated detection area (from distance sampling). For butterflies, sampling effort was simply number of visits (all transects were 100m long and 5m wide, so the area surveyed did not vary).

The previous analysis compared species' population densities across categories of land covers. However, rather than responding to category *per se*, species are likely to be responding to ecologically relevant aspects of the environment which differ between those categories. To further understand this, I investigated whether my measurements of habitat and vegetation structure could explain variation in species' population densities. To do this, I used quasi-Poisson models, similar to those described above, to determine species' responses to Veg.PC1. I also re-ran this analysis just using vegetation mean height as the explanatory variable instead of Veg.PC1 to explore whether using this raw variable offered greater clarity than the opaquely derived metric of Veg.PC1.

A key part of this study was to investigate the impacts of the restoration project itself. I therefore narrowed the focus to only consider Floodplain Channel sites, and used quasi-Poisson models, similar to those described above, to compare bird and butterfly species'

population densities in unrestored and restored channels where possible. However, I could not fit these models to species which were observed only in either restored or unrestored channels, so for those species I used a randomization test to determine the impact of restoration.

To investigate the impact of the restoration on habitats and vegetation structure, and on flood disturbance processes, I also compared restored and non-restored floodplain channels in terms of their Veg.PC1, Flood Risk Score and water depth. I used the Shapiro-Wilks test on Veg.PC1, Flood Risk Score and water depth to test for normality, and then either Welch's t-test for normal data or Wilcoxon Rank Sum Test as a non-parametric equivalent for non-normal data to compare between restored and non-restored channels.

The results of these analyses (see below) indicated that restoration of floodplain channels did not significantly affect the population densities of most species of bird or butterfly, but nonetheless many species' population densities differed between Floodplain Channel and Farm sites. Such differences could be the result of either farmland or floodplains in this region being either unusually good or unusually bad habitat for those species, in any combination. To get a better understanding of this, I present the results alongside results from natural baseline habitats and low-yielding farmland from a previous study in Poland (Feniuk, 2015), which gives an independent estimate of bird species' population densities to provide a benchmark. I compared my Floodplain Channel sites against natural baseline habitats in Poland, and my Farm study sites against the low-yielding farmland sites in Poland. Given that the restoration project did not impact the population densities of most bird species, and did not significantly alter habitats and vegetation structure, I use all Floodplain Channel sites rather than only restored ones. This study region is geographically distant and ecologically dissimilar to the Lubelskie region of Poland so the results should only be considered a rough guide to whether the population densities I observed were particularly high or low. This comparison only includes species observed in both regions, so more specialist species are unlikely to be included. Comparisons were tested using the single-sample t-test.

4.3 Results

4.3.1 Habitats and flood disturbance

The proportion of variance explained by successive principle components in my PCA of habitat and vegetation structure declined rapidly, with the first axis accounting for 28.2%

of the variance, the second accounting for 17.2% and all others accounting for less than 10%. Figure 4.5 shows variable loadings on the first two axis of the PC, along with study sites' scores. The first axis, Veg.PC1, appears to have picked out a gradient from open habitats (mostly associated with farmland) through to closed habitats (especially woodland). Variables such as cover of meadow or arable were weighted negatively, while all measures of vegetation height were weighted positively on this axis. The second axis is less clearly defined. It may be positively correlated with scrubby or structural variability: standard deviation in vegetation height across the site is positively weighted on this axis. It may also indicate amount of water as Main Channel and Meander sites mostly score positively, while No Channel sites are mostly negatively scored on this axis. Overall, these results suggest that the first principal component alone is the most useful metric of habitat and vegetation structure, and that including any further components does not add much information. Therefore, I used Veg.PC1 as the sole metric of habitat and vegetation structure for the remaining analyses.

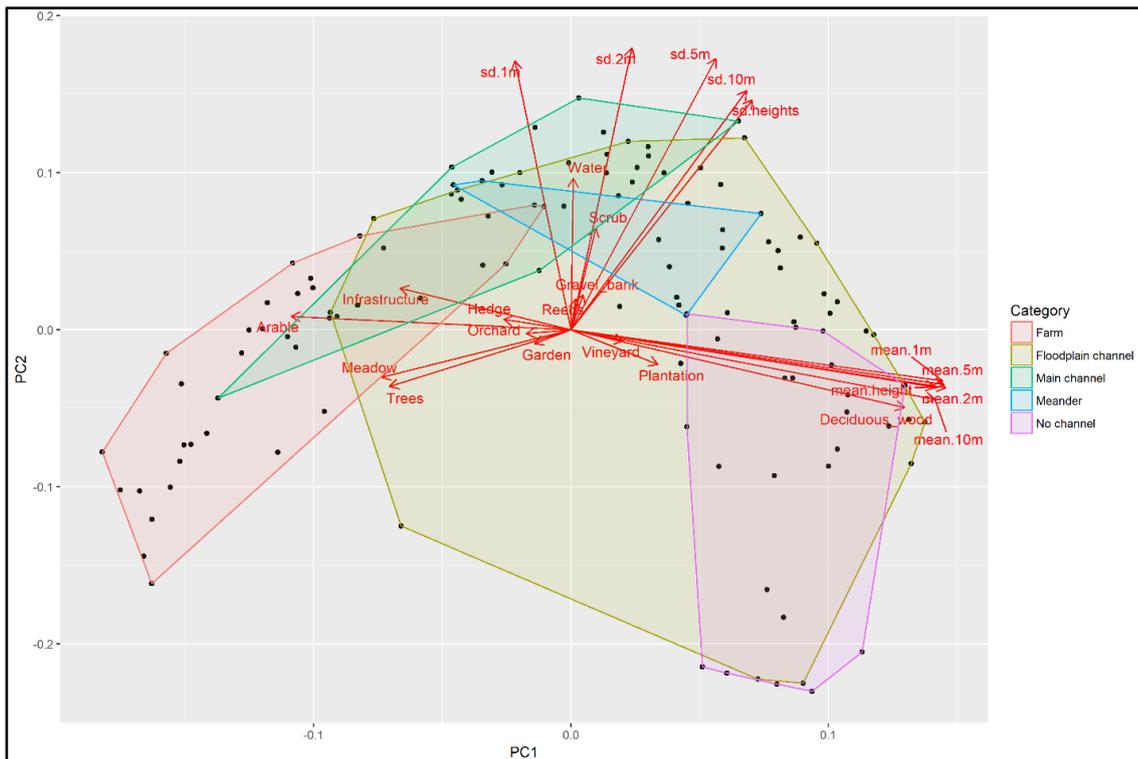


Figure 4.5 – First two axes of Principal Components Analysis of habitat and vegetation structure data. Length and direction of red arrows show the weightings of each habitat variable. Black points indicate scores of individual study sites. Coloured regions encompass all study sites in each category.

4.3.1.1 Flood Risk Score

The only type of disturbance considered for my Rhône sites was flood disturbance, as measured by Flood Risk Score and field measurements of water depth. Figure 4.6 shows

the Flood Risk Score across the entire region. The Flood Risk Score of my study sites ranged from 0.066 to 0.661, demonstrating that a wide range of flood regimes were sampled.

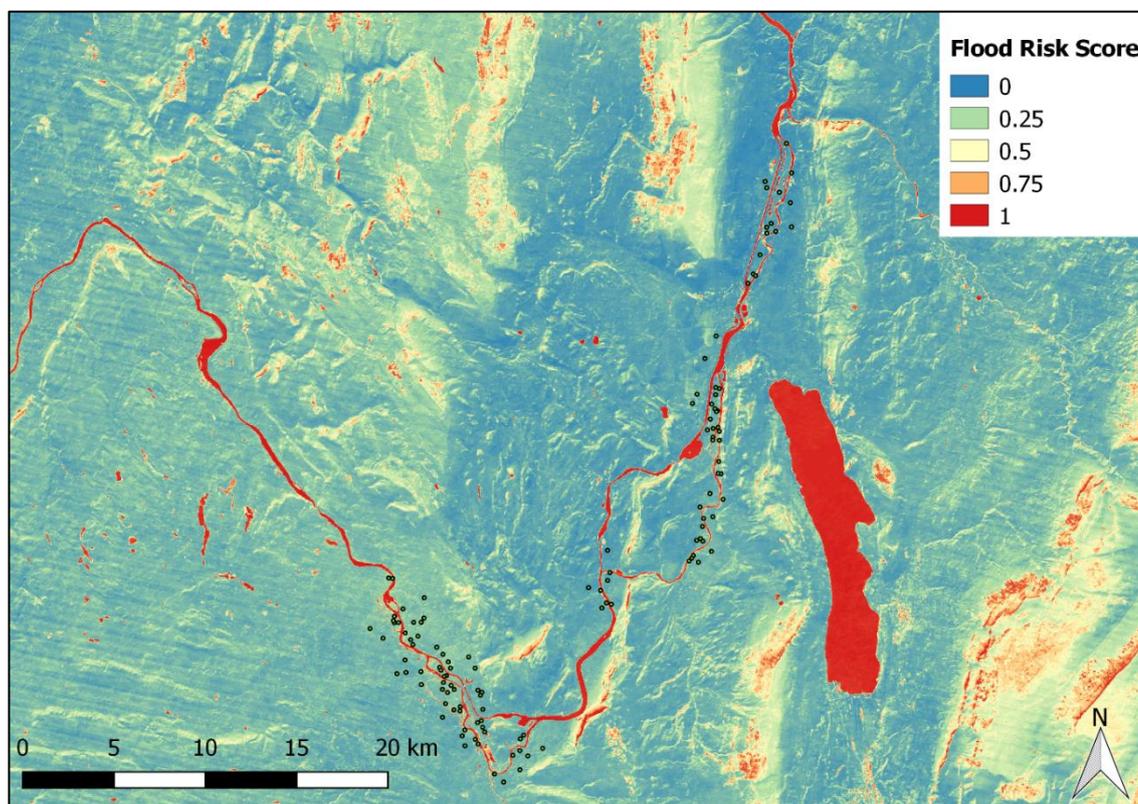


Figure 4.6 – Flood Risk Score across the study region, calculated as the mean occurrence of water across 107 Landsat images taken between 2006 and 2017. Colour indicates Flood Risk Score from 0 (no water occurrence) to 1 (permanent water occurrence). Study sites are marked with dots (not to scale).

4.3.2 Do categories of study site differ in habitats, vegetation structure and flood disturbance?

I found that the different categories of study site varied significantly in terms of their habitats, Veg.PC1 scores, Flood Risk Scores and water depths. Figure 4.7 shows the proportion of habitats in each study site category. There are clear differences between categories. Farm sites are dominated by Arable and Meadow habitats, which covered 54% and 20% of the area respectively. Deciduous woodland was present in all site categories, although it covered the greatest area of No Channel sites (79%) and the least in Farm sites (8%). Main Channel sites had the greatest area of Water, covering 43% of the area of sites in that category. Scrub was also present across all site categories, although there was less variation in the area covered by Scrub, which covered between 5% (of Farm sites) and 17% (of Meander sites) of the area. All of these results are intuitive given the nature of my site selection process, as described above.

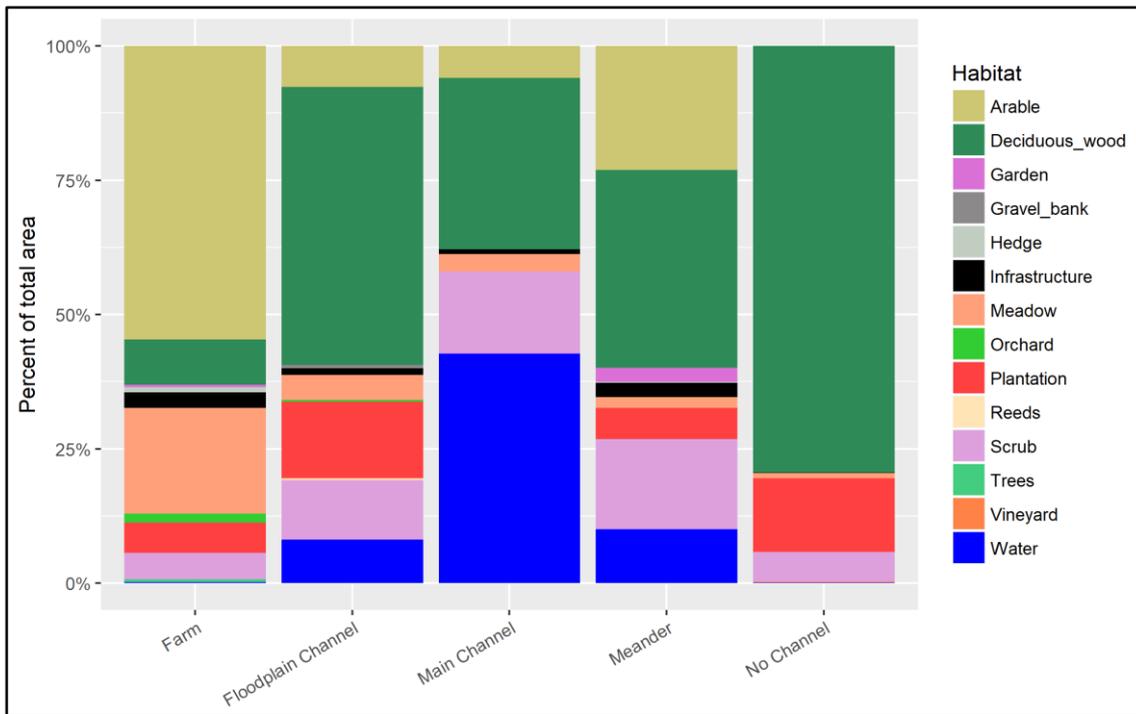


Figure 4.7 – The proportion of habitats varies significantly across the five categories of study site in my French study region (MANOVA residual df = 118, $p < 0.001$).

Farm sites had significantly lower Veg.PC1 scores than any other category, suggesting that Farm is the most open category (Figure 4.8). No Channel sites had the highest Veg.PC1 scores, suggesting the most closed vegetation structure (Figure 4.8). Main Channel sites had the highest Flood Risk Score, while Farm and No Channel sites had the lowest (Figure 4.8). The main river channel is a wide, permanent body of water, and my Flood Risk Score was able to detect this reliably, although as my Main Channel study sites were located at the edge of the channel, this only accounted for around half of each site. Floodplain Channel and Meander sites had similar, intermediate Flood Risk Scores. Note that in many cases, the water bodies in those sites were smaller than a pixel in Landsat data, being only a few meters across (USGS, 2017). Furthermore, emergent, floating and overhanging vegetation could all have reduced the likelihood of water being detected. Nonetheless, both those site categories still show significantly higher Flood Risk Scores than Farm sites, and Floodplain Channel sites were significantly higher than No Channel sites. As with the scores in Main Channel sites, this could be explained to some extent by the water in the channels themselves, and does not necessarily indicate overbank events are more common.

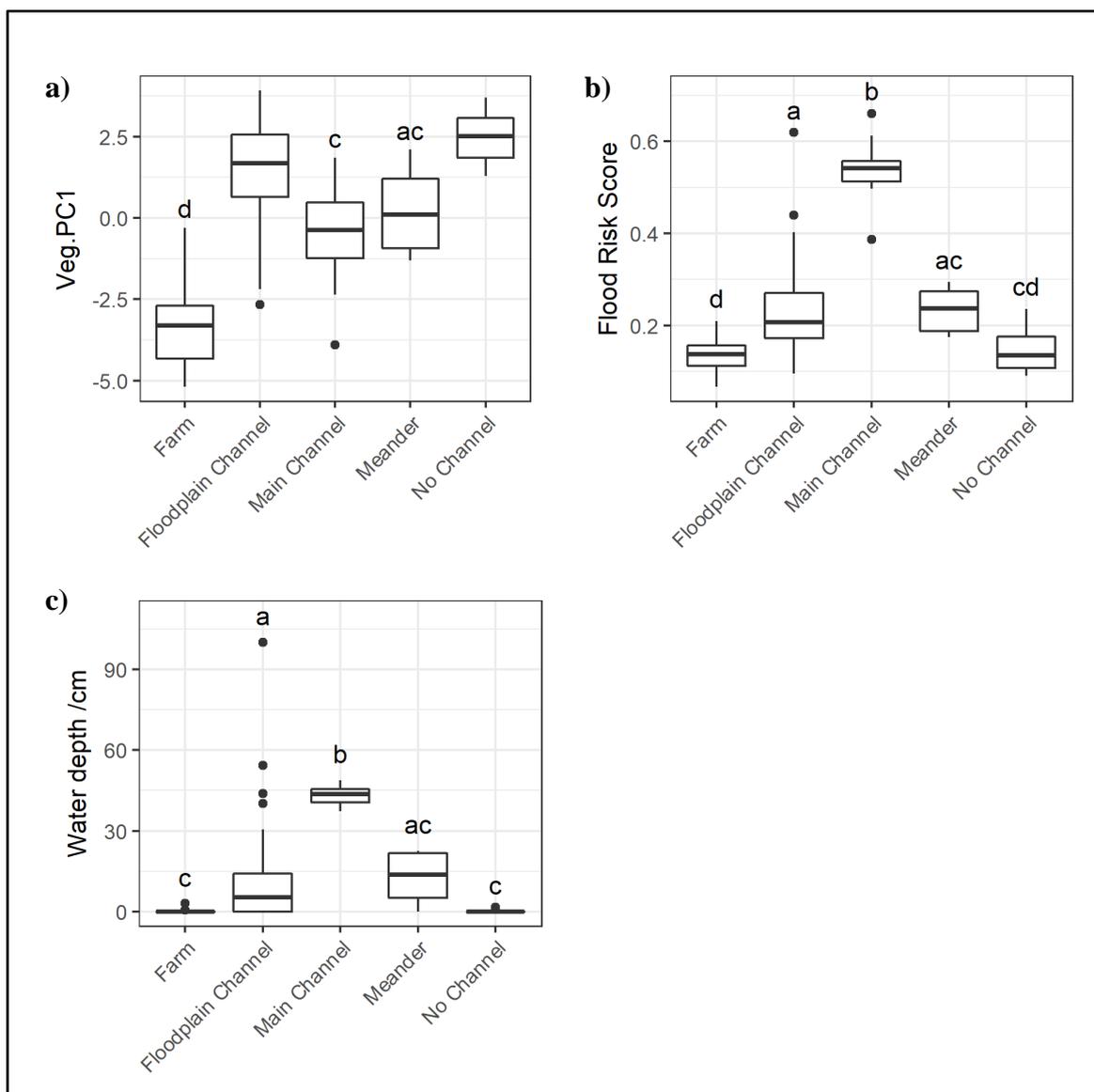


Figure 4.8 – Boxplots of **a)** Veg.PC1; **b)** Flood Risk Score; **c)** water depth in study sites of different category. In each panel, different letters are significantly different (Tukey HSD $p < 0.05$). Farm $n = 34$; Floodplain Channel $n = 54$; Main channel $n = 12$; Meander $n = 6$; No Channel $n = 14$. Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). See Chapter 2 for details of boxplots.

Both Farm and No Channel sites had very low water depth measurements in the field, with most sites having a water depth of zero (Figure 4.8). Main Channel sites had the deepest water (Figure 4.8). Note that, as described in Chapter 2, areas of water too deep to measure in the field were assigned a depth of 100cm; this applies to the main river channel in all Main Channel sites, as well as many channels and bodies of water within my Floodplain Channel or Meander sites. In these cases, the true water depth could be far deeper.

4.3.3 Are flooding regimes associated with variation in vegetation structure?

This section excluded Farm sites, as I assumed that in those sites vegetation structure is dominated by agricultural activities or other human management, and not controlled by natural processes. There was a significant negative correlation between Flood Risk Score and Veg.PC1 (Pearson's $R = -0.441$, $n = 86$, $p < 0.001$; Figure 4.9). This suggests that sites with a higher Flood Risk Score tended to be more open. This may indicate that water disturbance creates open habitats, in line with my hypothesis. However, it may be that vegetation is affecting the water levels (through, for example, greater levels of evapotranspiration in closed habitats), or that closed vegetation makes it harder for satellite imagery to detect water.

There was also a significant negative relationship between water depth and Veg.PC1 (Pearson's $R = -0.574$, $n = 86$, $p < 0.001$; Figure 4.9). This corroborates the previous result that wetter sites tend to have more open vegetation. However, in many cases the only standing water was in permanent water bodies (channels and ponds). Such permanent water bodies rarely had significant emergent vegetation, often being deep and fast flowing. This result therefore does not provide much evidence that the amount of water influences the habitat outside of the channels themselves, but rather demonstrates that channels have different vegetation structures to the surrounding landscape.

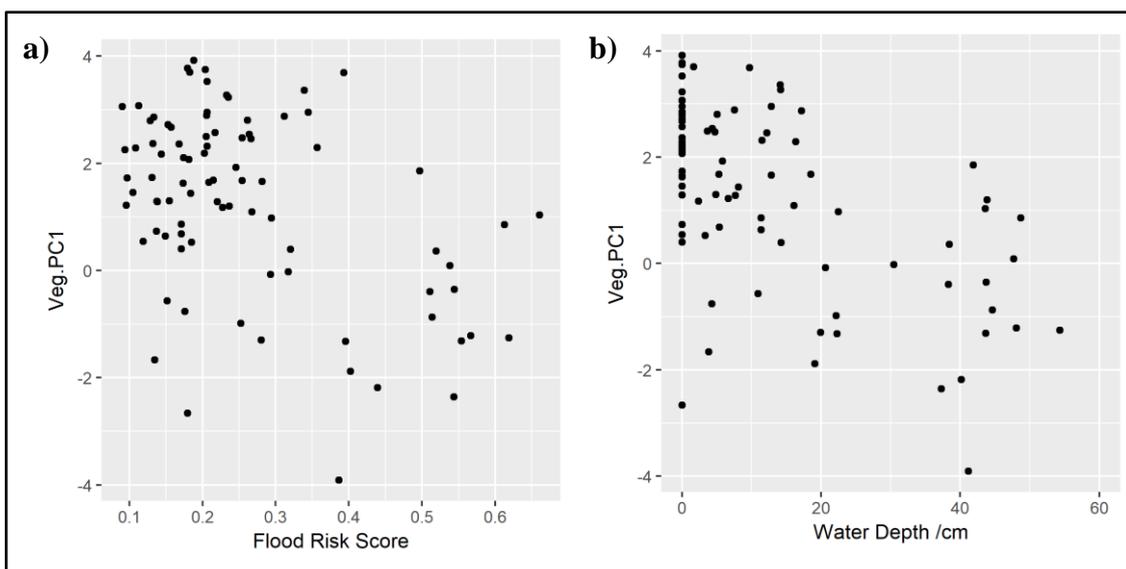


Figure 4.9 – **a)** Veg.PC1 was negatively correlated with Flood Risk Score (Pearson's $R = -0.441$, $n = 86$, $p < 0.001$). **b)** Veg.PC1 was negatively correlated with water depth (Pearson's $R = -0.441$, $n = 86$, $p < 0.001$). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). Dots are individual study sites.

4.3.4 How are species' population densities related to vegetation structure?

Figure 4.10 and Figure 4.11 show the modelled response of species of bird and butterfly, respectively, to vegetation structure. Species further right were associated with higher Veg.PC1 scores, and hence prefer more closed habitats. Figure 4.12 and Figure 4.13 show the same analysis carried out with mean vegetation height as the sole descriptor of the habitat.

These results agree well with widely reported habitat preferences. For example, woodland birds such as Nuthatch and Robin appear towards the right of both Figure 4.10 and Figure 4.12 (associated with higher Veg.PC1 scores and greater mean vegetation height), confirming their preference for closed habitats with higher vegetation, while grassland or farmland birds such as Hoopoe and Stonechat appear towards the left in both figures, preferring more open habitats and low vegetation (Snow *et al.*, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018). The same is true of butterflies, with species associated with grassy or marshy places appearing towards the left (for example Swallowtail and Small heath) while woodland species (such as Lesser purple emperor and Poplar admiral) appear further right in both Figure 4.11 and Figure 4.13 (van Swaay *et al.*, 2006; Tolman & Lewington, 2009).

Comparing the results obtained by using Veg.PC1 with those using mean height, the broad patterns are very similar, with no evidence that either metric is inherently more useful or clear.

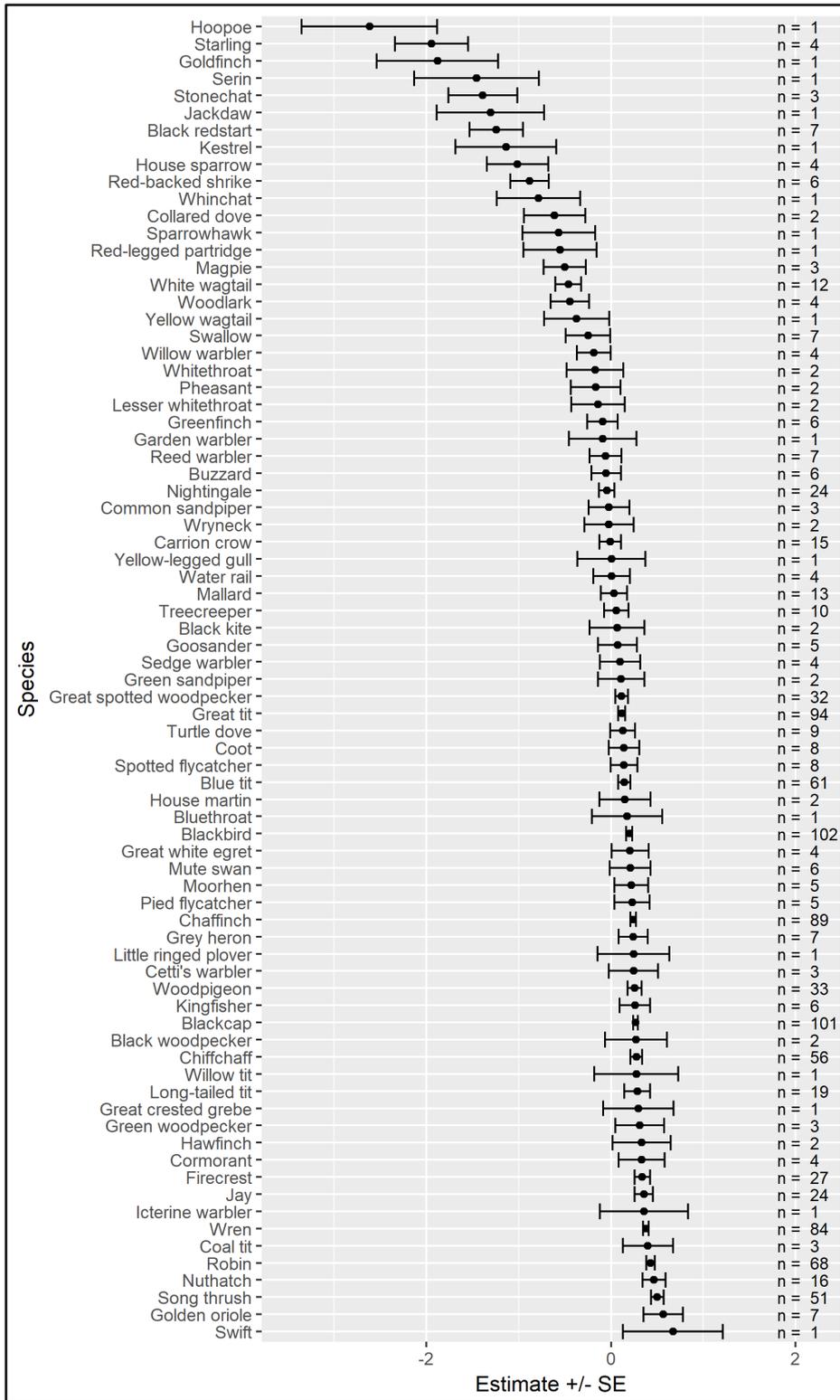


Figure 4.10 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species’ population density and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more negative estimate indicates that species had higher population densities in sites with a lower Veg.PC1 (i.e. prefers more open habitats). Models used a quasi-Poisson error structure. Birds were surveyed at 113 sites; n values in the figure refer to the number of sites with at least one observation of that species.

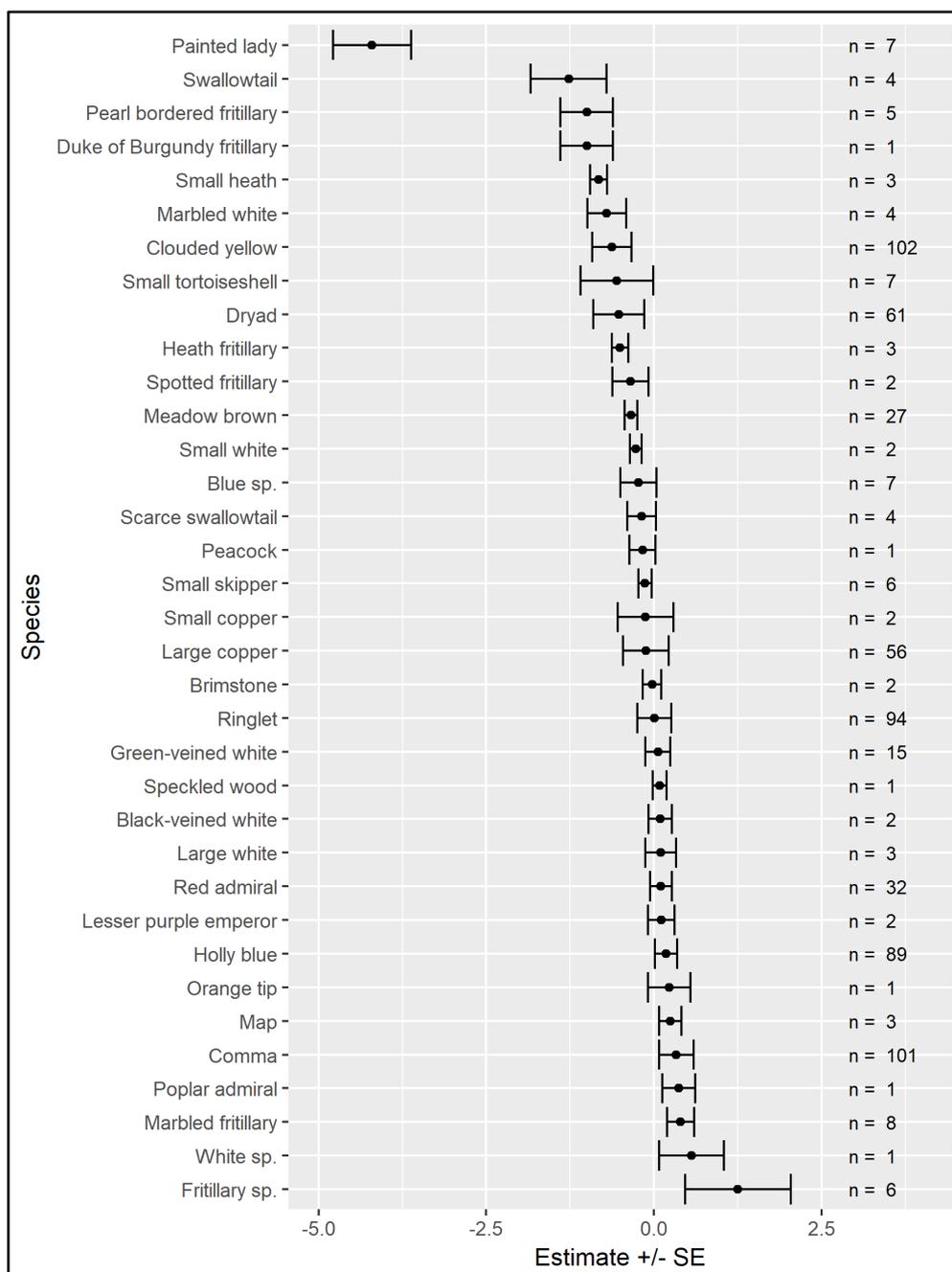


Figure 4.11 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between butterfly counts and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more negative estimate indicates that species had higher population densities in sites with a lower Veg.PC1 (i.e. prefers more open habitats). Models used a quasi-Poisson error structure. Butterflies were surveyed at 123 sites; n values in the figure refer to the number of sites with at least one observation of that species.

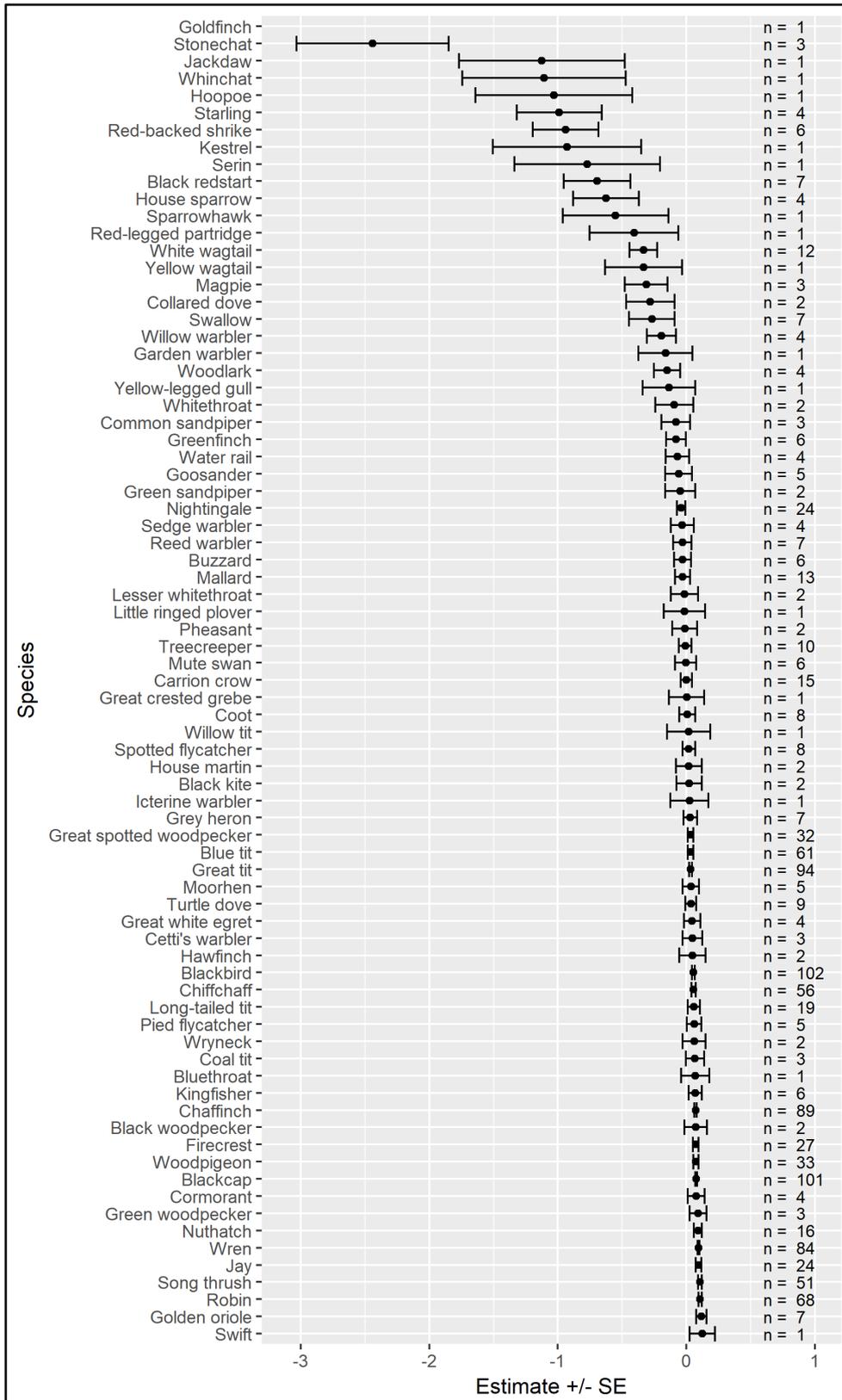


Figure 4.12 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species’ population density and the mean height of the vegetation at a site. A more positive estimate indicates that species had higher population densities in sites with a higher mean vegetation height. Models used a quasi-Poisson error structure. Birds were surveyed at 113 sites; n values in the figure refer to the number of sites with at least one observation of that species. Models failed to fit for some species.

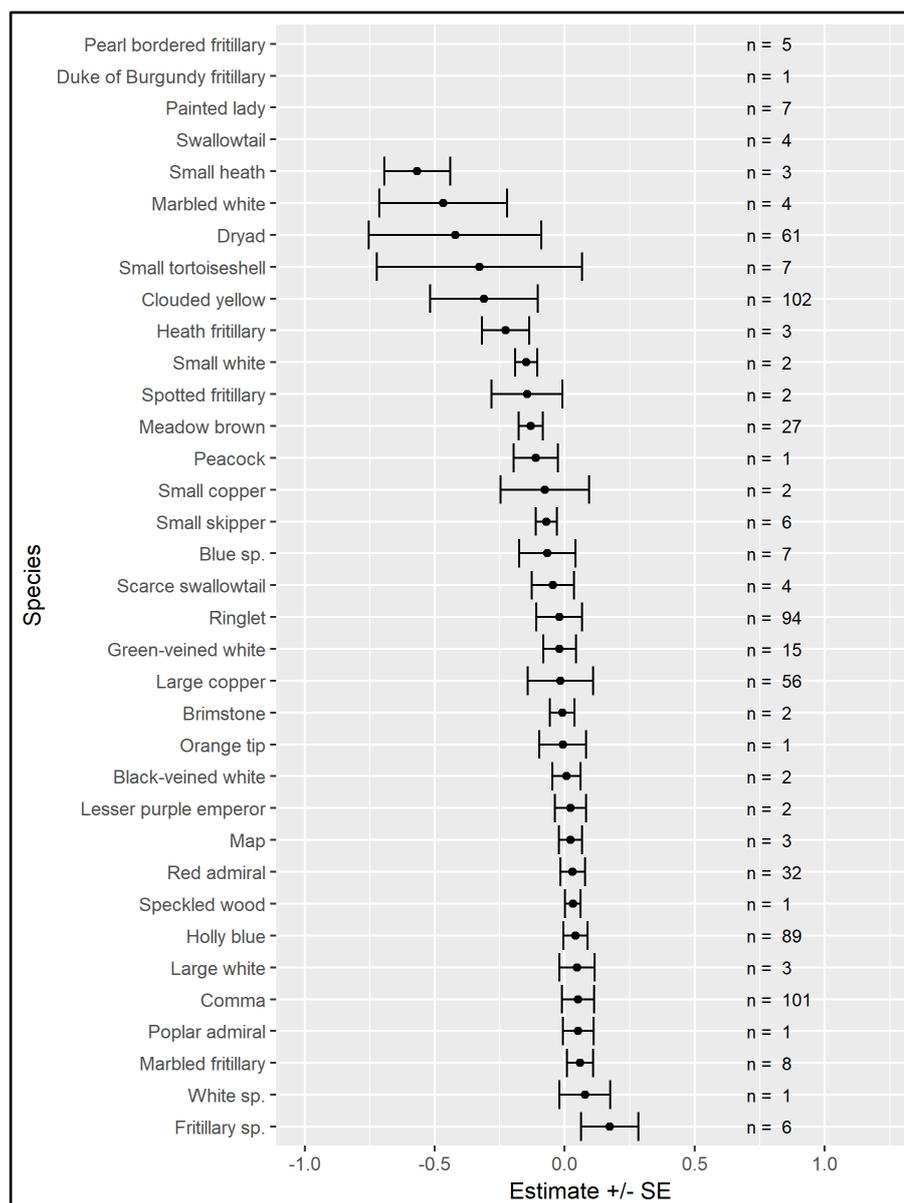


Figure 4.13 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between butterfly species' population density and the mean height of the vegetation at a site. A more positive estimate indicates that species had higher population densities in sites with a higher mean vegetation height. Models used a quasi-Poisson error structure. Birds were surveyed at 123 sites; n values in the figure refer to the number of sites with at least one observation of that species. Models failed to fit for some species.

4.3.5 How do species' population densities vary across study site categories?

4.3.5.1 Birds

The vast majority of bird species (63 out of 77) showed significant differences in population density across different categories (Figure 4.14). These results corroborate what is known about species' ecologies (Snow *et al.*, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018): farmland birds (such as Jackdaw, Yellow wagtail and Red-legged

partridge) were abundant in Farm sites, while water birds were most abundant in Floodplain Channel, Main Channel or Meander sites (for example Grey heron, Little ringed plover and Moorhen). All categories except Farm had a high proportion of woodland (see Section 4.3.1), therefore woodland birds (such as Chaffinch and Wren) were often common in any category except Farm. Larger versions of each panel showing significant differences between individual categories for each species, and the number of sites per category with at least one observation of each species are available in Appendix 4.

4.3.5.2 Butterflies

For butterflies, only nine out of 35 species showed a significant difference across categories. In general, there were far fewer butterfly observations than bird observations, which may have contributed to the smaller number of significant results. However, the significant results that do exist follow logically from species' ecologies (Tolman & Lewington, 2009); for example, Poplar admirals were most abundant in No Channel sites (which included all the poplar plantations sampled), while Small heath butterflies were abundant in Farm sites. Again, larger versions of each panel showing significant differences between individual categories, and the number of sites per category with at least one observation of each species are available in Appendix 4.



Figure 4.14 – Population density of bird species, by study site category, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. Colour of filled bar indicates site category. Stars indicate significance of ANOVA (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Number of sites per category: Farm = 34; Floodplain Channel = 45; Main Channel = 12; Meander = 6; No Channel = 16.

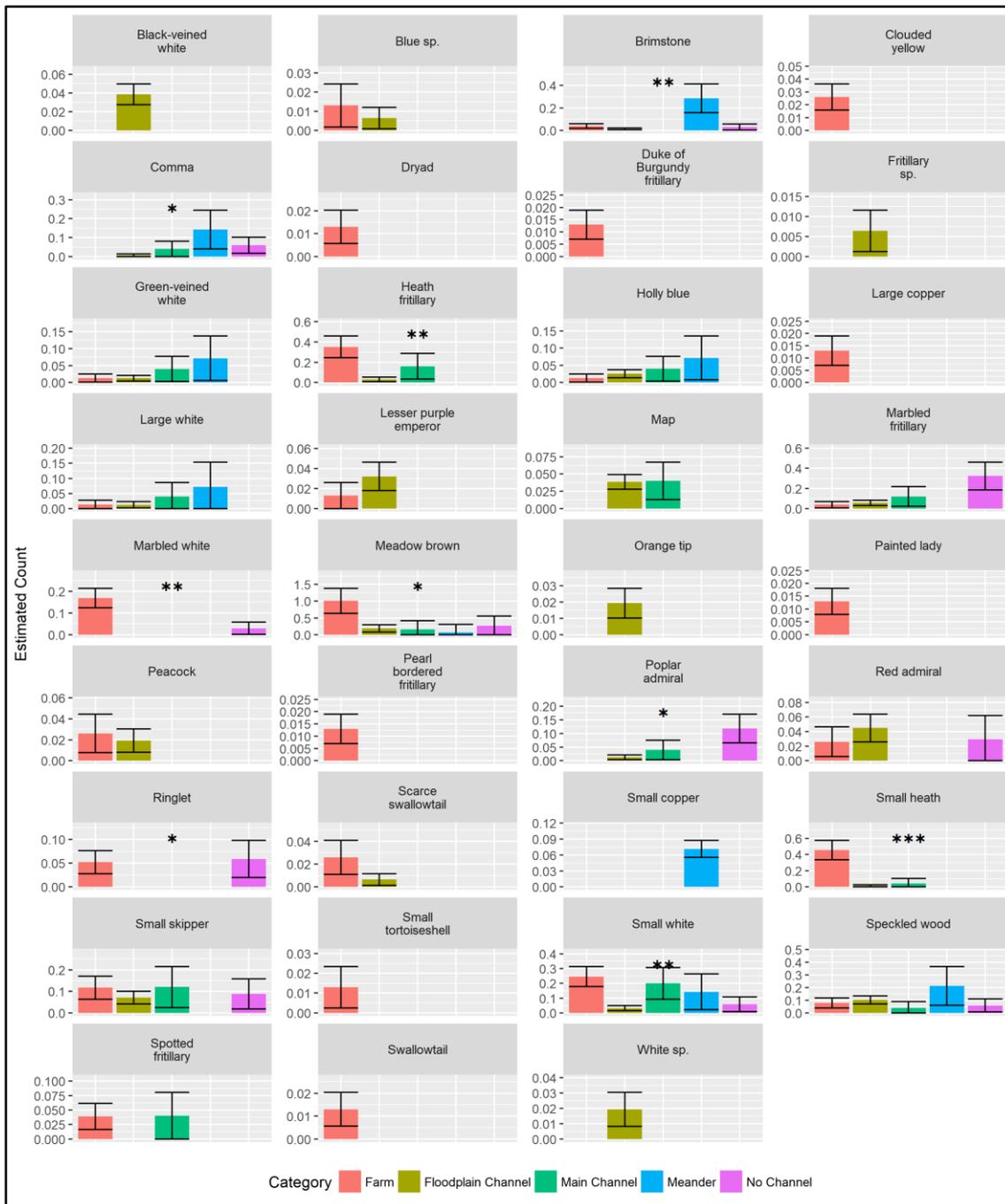


Figure 4.15 – Counts per transect of butterfly species or groups, by study site category, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. Colour of filled bar indicates site category. Stars indicate significance of ANOVA (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Number of sites per category: Farm = 34; Floodplain Channel = 55; Main Channel = 12; Meander = 6; No Channel = 16.

4.3.6 Do restored and non-restored channels differ in habitat structure or flood disturbance?

As shown in Figure 4.16, there was no significant difference in Veg.PC1, water depth or Flood Risk Score between restored and non-restored floodplain channels (Wilcoxon Rank

Sum $W = 335$, $W = 270$, and $W = 3642$, respectively; all $n = 55$, N.S.). Previous studies have shown clear differences within the channels themselves as a result of restoration (Lamouroux *et al.*, 2015), but these data suggest that the restoration has not led to an increase in flood disturbance outside the channels and therefore there has been no effect on the surrounding landscape or habitats.

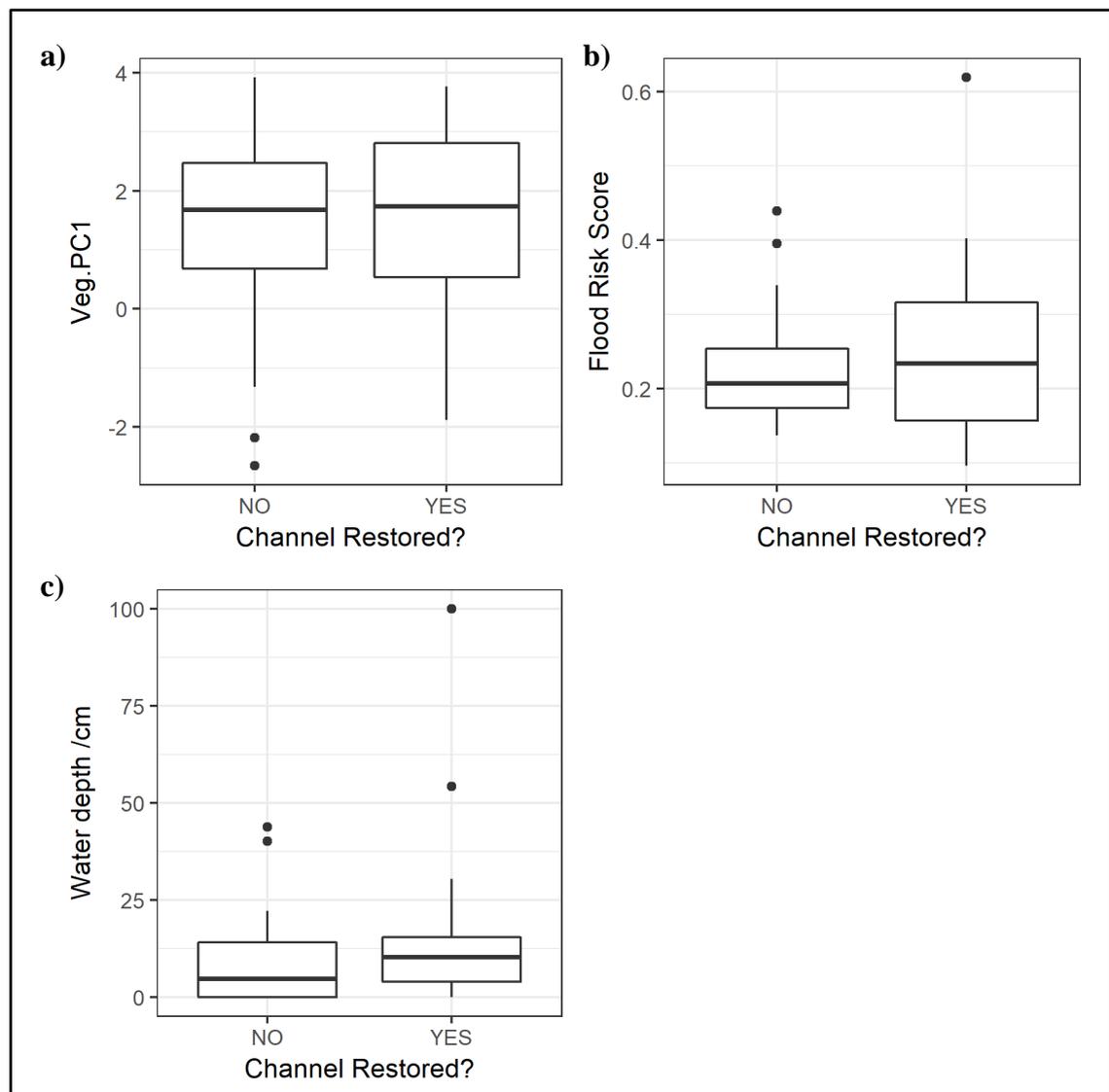


Figure 4.16 – a) Veg.PC1 did not differ between restored and non-restored channels (Wilcoxon Rank Sum $W = 335$, $n = 55$, N.S.). b) Flood Risk Score did not differ between restored and non-restored channels (Wilcoxon Rank Sum $W = 270$, $n = 55$, N.S.). c) Water depth did not differ between restored and non-restored channels (Wilcoxon Rank Sum $W = 342$, $n = 55$, N.S.). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). See Chapter 2 for details of boxplots.

4.3.7 How does restoration affect species?

4.3.7.1 HNV Birds

This similarity in the physical structure and flood disturbance regime of restored and non-restored Floodplain Channel sites was echoed in my population data. Of the seven HNV bird species observed in Floodplain Channel sites, none differed in density between restored and non-restored sites (Figure 4.17). While some of the species have rather large error bars resulting from few observations, for others the data would suggest that population densities were genuinely similar and that channel restoration had little impact on those species.

4.3.7.2 Non-HNV birds

The results for non-HNV species show a broadly similar pattern. The vast majority of species did not show a significant preference either way (Figure 4.18). The only exception was the Wood pigeon, which preferred restored channels. However, there is nothing about the ecology of Wood pigeons which makes this result easily explicable so it may simply be random variation which is to be expected given the number of species tested (Svensson *et al.*, 2009). Although in no cases was the effect significant, several species which are associated with clean, flowing water bodies (e.g. Cormorant, Goosander, Kingfisher) were only observed in restored channels, which hints there may have been some impact on the aquatic environment and those species most closely associated with it.

4.3.7.3 All butterflies

The results for butterflies are also very similar, with only one species (the Small skipper) showing a significant preference, in that case for restored channels. However, it is not obvious what features would make restored channels more suitable for that species than non-restored channels (Tolman & Lewington, 2009). No HNV indicator species (Paracchini *et al.*, 2008) were observed.

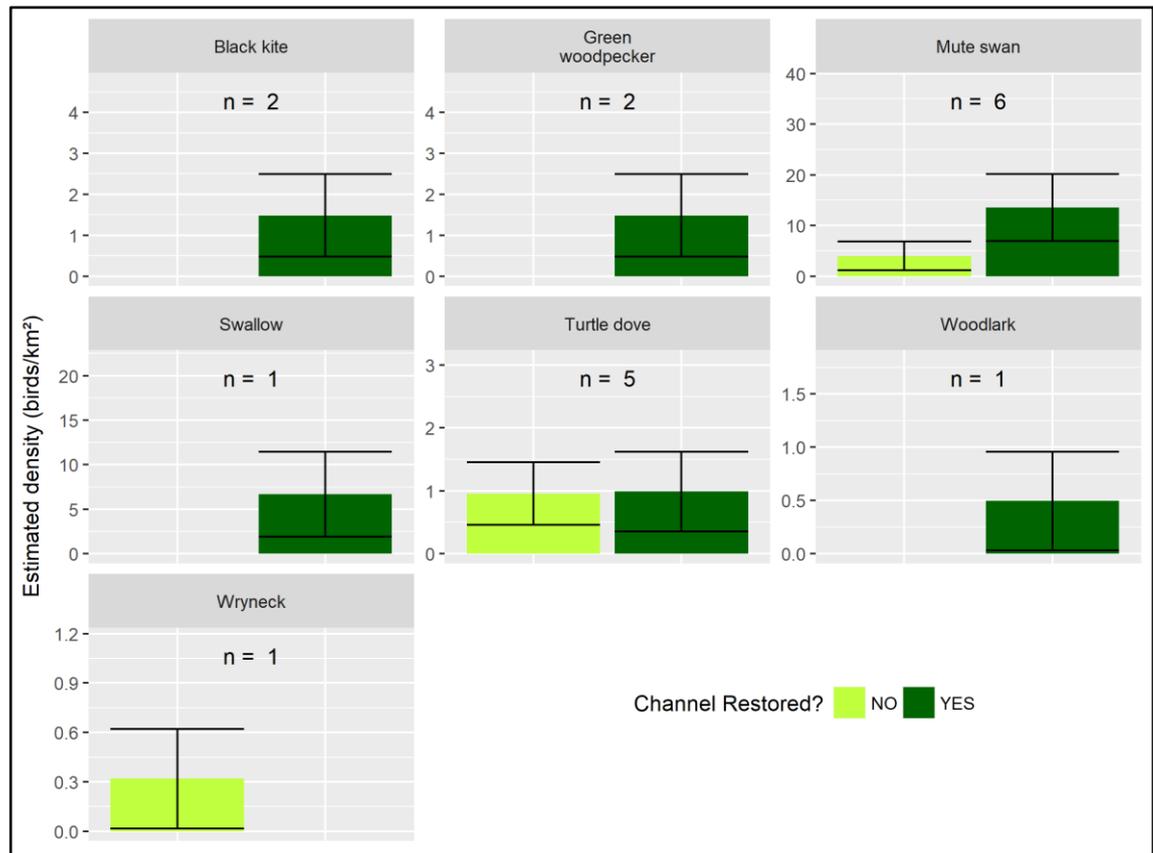


Figure 4.17 – Population density of HNV bird species in non-restored floodplain channels (light green) and restored floodplain channels (dark green), estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. I surveyed birds in 19 restored and 29 non-restored floodplain channels. N values in the figure indicate the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$).

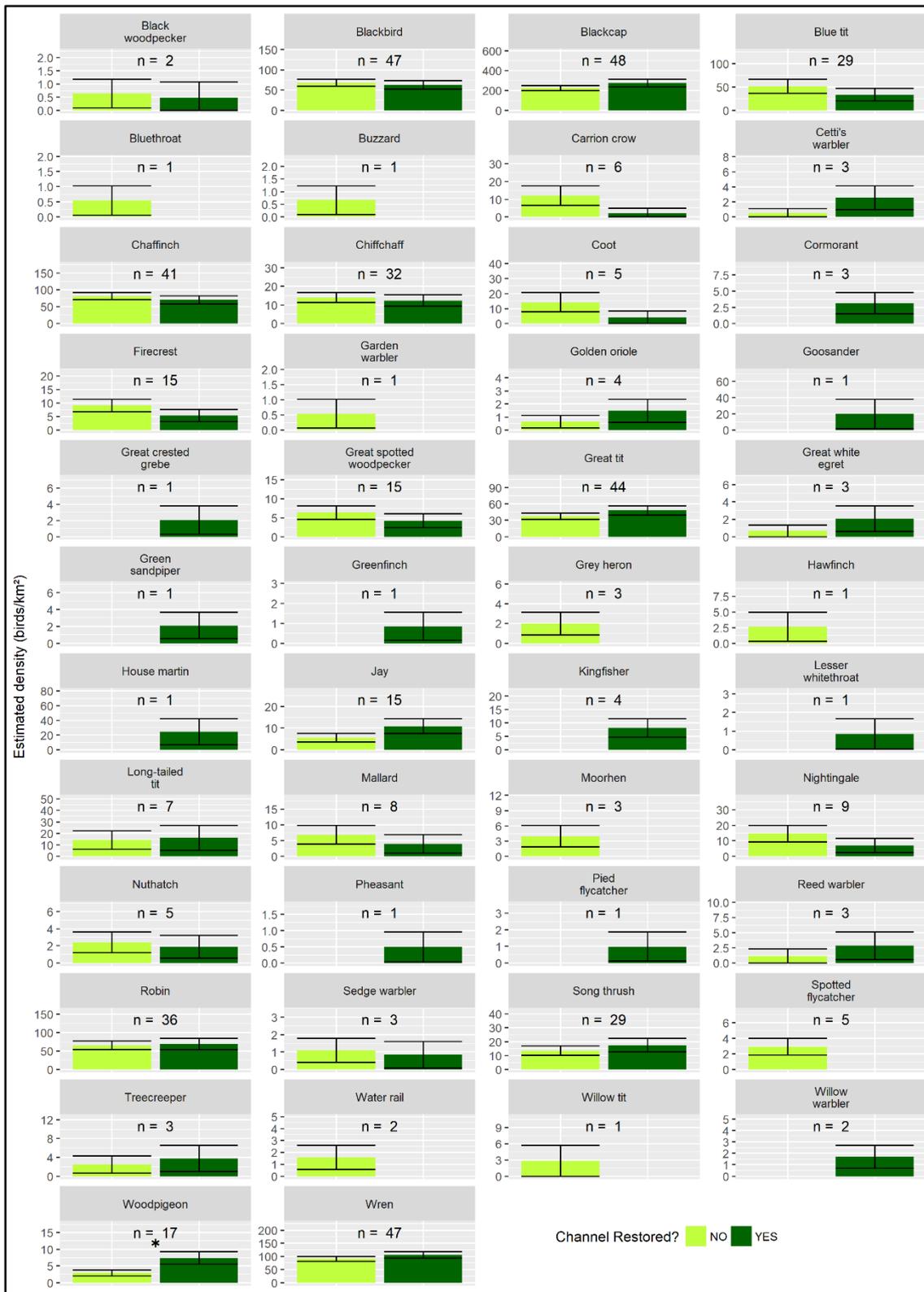


Figure 4.18 – Population density of non-HNV bird species in non-restored floodplain channels (light green) and restored floodplain channels (dark green), estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. I surveyed birds in 19 restored and 29 non-restored floodplain channels. N values in the figure indicate the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

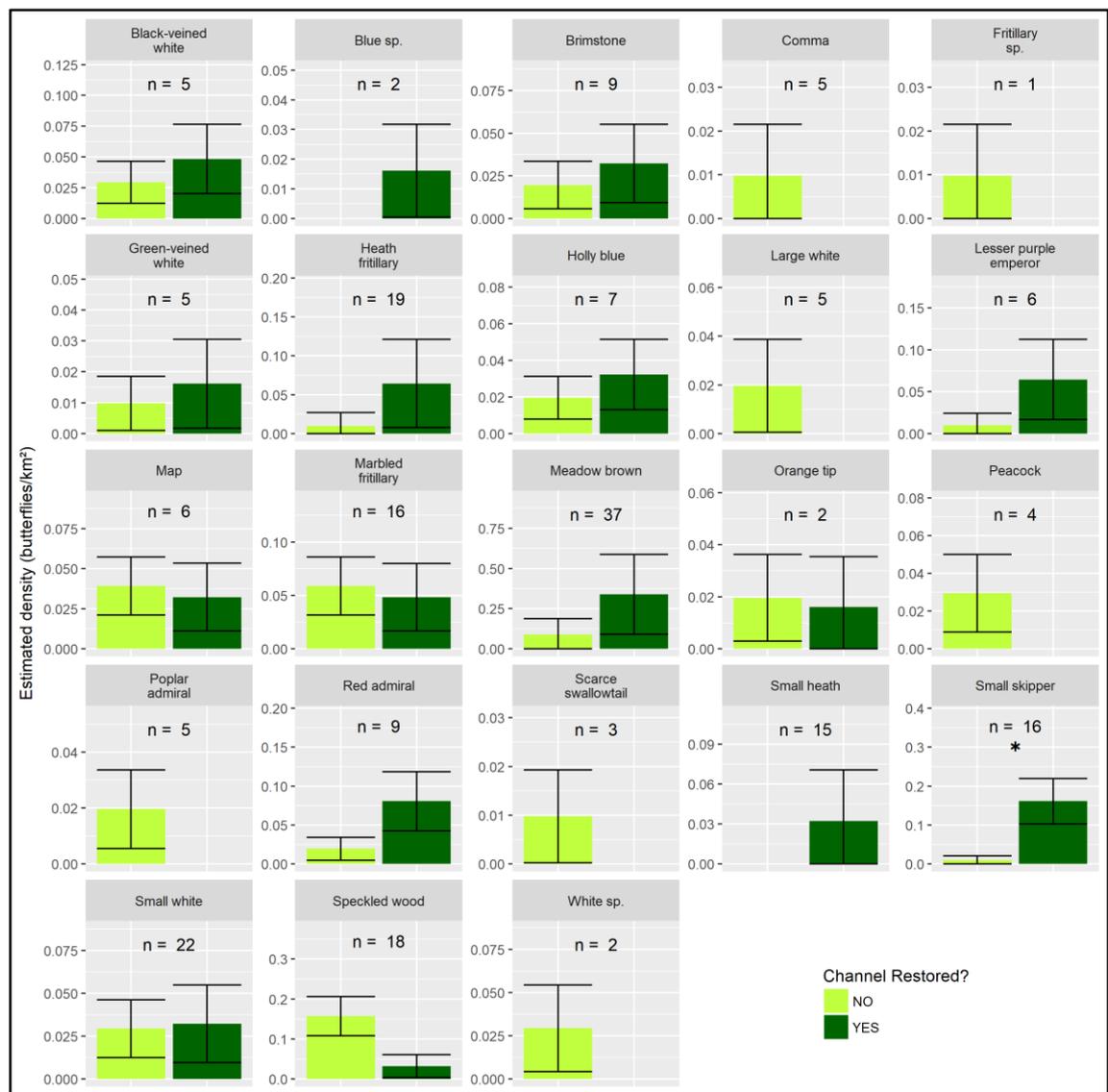


Figure 4.19 – Estimated counts per transect of butterfly species in non-restored floodplain channels (light green) and restored floodplain channels (dark green), estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. I surveyed butterflies in 22 restored and 36 non-restored floodplain channels. N values in the figure indicate the total number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

4.3.8 Comparison of bird densities with Polish results

4.3.8.1 HNV birds

While the restoration project has had only minimal impact on bird species' population densities, many species' population densities did differ between Floodplain Channel sites and Farm sites overall, indicating that, regardless of the restoration project, the floodplains in my study region do differ from the surrounding farmland. To better

understand what is driving these differences, I compared my bird population density estimates to those in low-yielding farmland and natural baseline habitats in the Lubelskie region of Poland (Feniuk, 2015). Although my study region in France and the Lubelskie region in Poland have ecological differences that cannot be completely overlooked, some interesting patterns can be observed and the comparison can help to contextualise my results. Looking at HNV birds, more had significantly higher population densities in low-yielding Polish farmland than in the farmland in my study region in France (Figure 4.20). This fits with the agricultural system in this region of France being more intensive and less wildlife friendly than low-yielding farmland in Poland. Comparing floodplain channels in France to natural baseline habitats in Poland, slightly more species had significantly higher population densities in Poland (four species) than France (two species). However, several of the species which had higher population densities in Polish baseline habitats than French floodplain channels had very low population densities in both (for example Red-backed shrike, Yellow wagtail). In contrast, several of the species which had higher population densities in French floodplains had dramatically higher population densities (for example Mute swan, Turtle dove). This suggests that floodplain habitats, even those which are managed to some extent, can support high densities of some HNV species. However, as in the previous chapter, other HNV species do not fare so well in floodplains (or the other natural habitats studied in Poland), again demonstrating the need to consider additional strategies to conserve all HNV species.

4.3.8.2 Non-HNV birds

Looking at all other (i.e. non-HNV) bird species, a different pattern emerges (Figure 4.21). On farmland, while slightly more species had higher population densities in Poland than France, there is by no means a clear pattern and many species had equal or even higher population densities in French farmland. The species presented here are any which were not defined as HNV species, so this is likely to exclude the species which thrive only in low-yielding farmland. These species therefore are either tolerant of more intensive farmland and have high population densities in both Poland and France (for example Great tit and Starling) or are largely absent from farmland of any intensity (for example Black woodpecker). Looking at natural habitats in Poland versus floodplain channels in France, slightly more species have higher densities in Polish natural habitats than in French floodplain channels (15 species; for example Coal tit; Water rail). However, there are still several species which have higher population densities in French floodplain channels and in some cases those differences are large (11 species; for example

Blackbird, Wren). The data appear to therefore demonstrate that those two sets of study sites are quite different, but there is no strong pattern of one or the other supporting higher bird population densities.

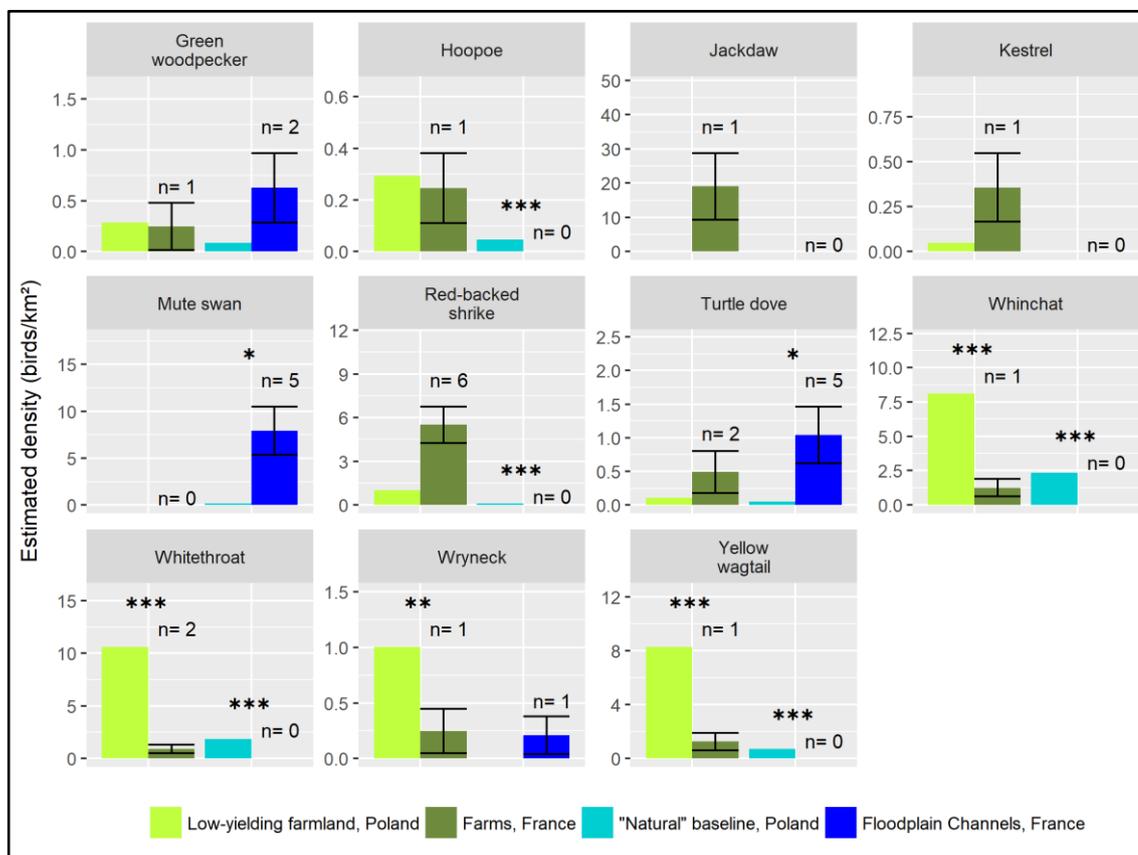


Figure 4.20 – Estimated population density of HNV bird species in farmland (green) and wetlands or natural habitats (blue), in Poland (left) and in France (right). Population densities in Poland were estimated using density-yield functions from (Feniuk, 2015), at $0 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ for natural baseline and at $8 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ for low-yielding farmland. Wetland sites in France are those categorised as “Floodplain Channels”, including both restored and unrestored channels. Population densities in France were estimated using quasi-Poisson models. Black lines on French bars indicate \pm one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus France, and comparing densities in farmland in Poland versus France (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). N values indicate the number of French Farm and Floodplain channel sites (respectively) in which I observed each species at least once.

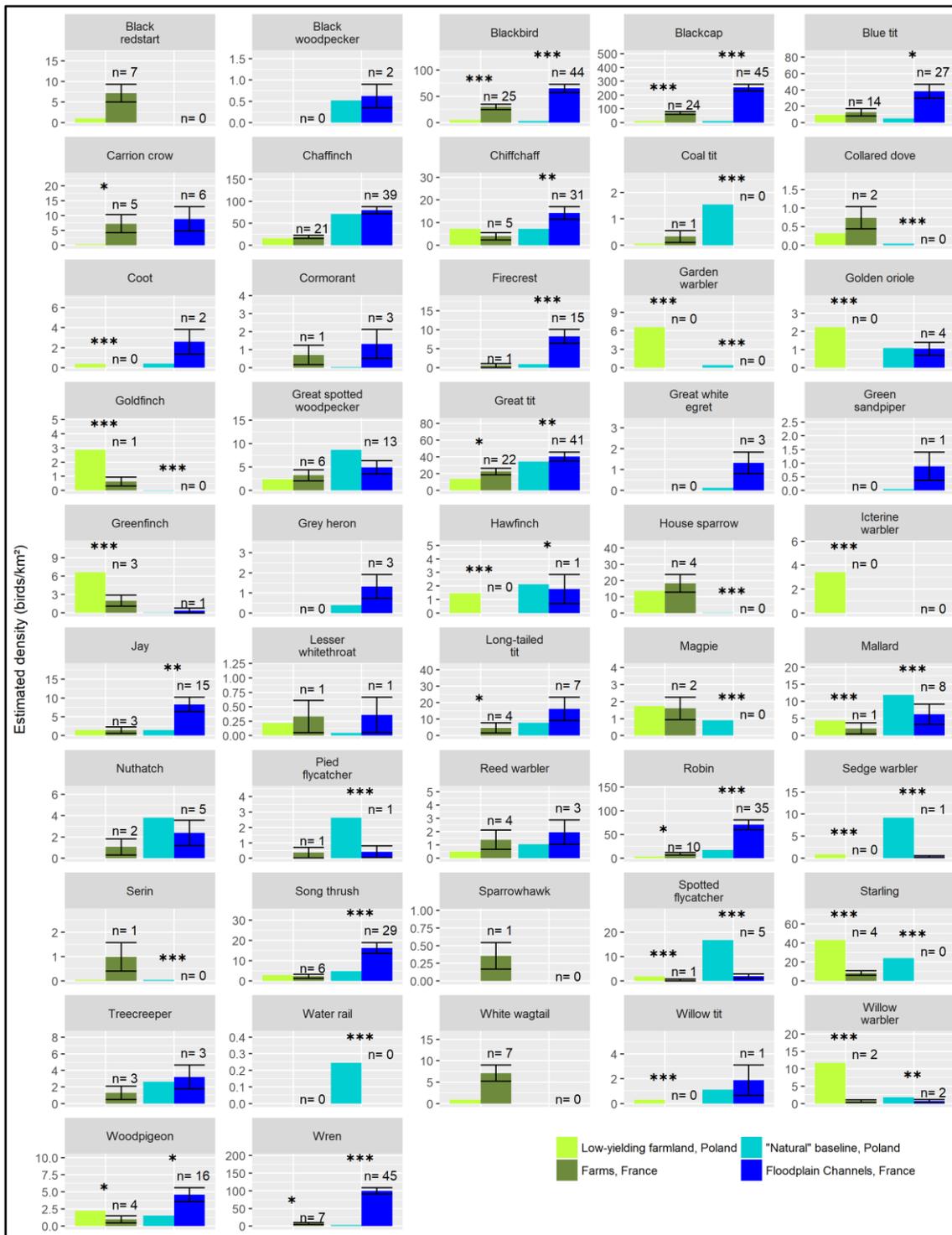


Figure 4.21 – Estimated population density of non-HNV bird species in farmland (green) and wetlands or natural habitats (blue), in Poland (left) and in France (right). Population densities in Poland were estimated using density-yield functions from (Feniuk, 2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland. Wetland sites in France are those categorised as “Floodplain Channels”, including both restored and unrestored floodplain channels. Population densities in France were estimated using quasi-Poisson models. Black lines on French bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus France, and comparing densities in farmland in Poland versus France (* p < 0.05, ** p < 0.01, *** p < 0.001).

4.4 Discussion

This chapter has looked at biodiversity across a range of situations all located within a developed, western country, where very little truly natural habitat remains. The Rhône and its floodplain remain heavily influenced by human activities and management. The flow regime is still regulated (albeit at a slightly more natural level than prior to restoration) and large parts of the floodplain are used for agriculture, forestry, or recreation (Olivier *et al.*, 2009). The Rhône would naturally be a dynamic river (Olivier *et al.*, 2009) but these large scale hydromorphological dynamics (i.e. movements of the main channel) remain absent, and these are important for natural floodplain ecosystems (Bendix & Hupp, 2000; Richards *et al.*, 2002). Even so, my results suggest biodiversity can thrive in the right conditions. I found that there were significant differences across different categories of study site in terms of habitat and vegetation structure, flood disturbance, and population densities of species of bird and butterfly. I found good evidence that bird and butterfly species' population densities were associated with variation in habitat and vegetation structure, and some evidence that habitat and vegetation structure were influenced by flood disturbance. However, my results also demonstrate that the restoration project had very little impact outside the confines of the floodplain channels. Very few bird or butterfly species' population densities differed between restored and non-restored channels. There was no evidence that the restoration affected the habitat and vegetation structure of the surrounding or flood disturbance regime.

I found clear differences in habitat and vegetation structure, and flood disturbance between categories of site, and correlations between metrics of flood disturbance (Flood Risk Score and water depth) and Veg.PC1 suggested that higher flood disturbance may lead to more open habitats. However, human management is important in many of my sites, both in terms of water levels (which are controlled by the barrages) and land management (for example, some sites included timber plantations or were managed for recreation) (Olivier *et al.*, 2009). As such, the effect of natural processes might be masked by anthropogenic influences. Furthermore, human management can change rapidly, as the restoration project demonstrates. However, vegetation responses may be much slower. For example, trees may survive long after the habitat has made them incapable of successfully reproducing, while at the other extreme trees take decades to mature once habitat becomes suitable (Clements, 1916; Veblen, 1992; Richards *et al.*, 2003). This may

result in a disconnect between the prevailing disturbance regime and the current habitat and vegetation structure.

The results of mapping the Flood Risk Score looked sensible for my study sites. Mapped across the study region, the main channel of the Rhône and permanent water bodies are clearly picked out, but outside these the Flood Risk Score drops dramatically. The Flood Risk Score appears to have picked out the tops of mountains too, which suggests a commission error caused by snow or ice. Previous studies into identifying water using remotely sensed data also identified snow and ice as potential sources of error (Ticehurst *et al.*, 2014; Pekel *et al.*, 2016). However, as all my study sites were located in the valley floor, they are unlikely to be affected. The mountains can be >1500m higher than the valley floor and therefore snow is more likely and persists for much longer there than in my study sites.

Looking at species' associations with Veg.PC1 and vegetation mean height, the results confirm widely reported species' preferences for different habitats (Snow *et al.*, 1998; van Swaay *et al.*, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). Both my results and the literature show some species prefer open habitats, for example Red-backed shrikes and Small heath butterflies. Others prefer closed habitats, including Golden orioles (which particularly favour poplar plantations; Milwright, 1998) and the Speckled wood butterfly. This gives me confidence that my biodiversity surveys were effective and accurate in detecting species, and that my measures of habitat and vegetation structure provided biologically relevant data. It made very little difference to the results whether I considered Veg.PC1 as a metric of habitat structure or the more simple metric of mean vegetation height.

By looking at both different categories of study site, and across a gradient of vegetation structure, it is clear that different species thrive in different habitat types, and so heterogenous landscapes are key to biodiversity, whether such heterogeneity is provided by anthropogenic management or by natural processes. The diversity of responses highlights the importance of diverse habitat types for supporting a wide range of species, which has been widely reported before (Benton, Vickery & Wilson, 2003; Sirami, Brotons & Martin, 2011; Patthey *et al.*, 2012; Streitberger & Fartmann, 2016; McGranahan *et al.*, 2018). This underpins the disturbance hypothesis: disturbance events create patches of different sizes in different successional stages (Ward & Stanford, 1983; McIntyre *et al.*, 1999; Wilkinson, 1999; Navarro *et al.*, 2015).

A useful feature of this study region was the ability to directly compare restored channels with non-restored control channels, to investigate the effect of restoration directly. Focusing in solely on the floodplain channels, my results tend to corroborate previous studies that demonstrated a measurable impact on the ecology of the channels themselves (Lamouroux *et al.*, 2015 and refs. therein). Although there were few significant results, I found some suggestion that the restoration carried out has favoured some species associated with lotic waters and piscivorous birds, while species that prefer lentic, weedy water bodies may have lost their preferred habitat. However, I found little evidence to suggest that the restoration had an impact beyond the confines of the channels. Metrics of vegetation structure and flood disturbance did not show a difference between restored and non-restored sites, and most species of both bird and butterfly also showed no significant difference in population density between these sites. It is likely that many species were using the surrounding woodlands and other terrestrial habitats rather than the channels themselves. HNV species tended to fall into this category, and therefore this type of restoration is unlikely to benefit most HNV species. My hypothesis requires that floodplain restoration produces a landscape-scale disturbance effect, which my results indicate this restoration project failed to do.

In comparison to low-yielding farmland Poland (from Feniuk, 2015), the farmland in France supported much lower densities of HNV birds, although non-HNV birds did not differ as much. This suggests that while HNV birds thrive in low-yielding farmland (and that the farmland surveyed in France was thus unsuitable) other species are either tolerant of higher intensities or intolerant of any disturbance. In contrast, floodplain channels in France generally appeared to support similarly high biodiversity as natural habitats in Poland, with many bird species having equal or higher population densities. This suggests that, even when subject to anthropogenic management and surrounded by a hostile matrix, floodplain habitats can support high biodiversity, including some HNV species. These comparisons with results from Poland must come with the caveat that the two systems were quite different in several ways, and so these results and their explanations must be viewed cautiously and not treated as strong evidence. Furthermore, I have only presented results for species observed in both locations, so common and widespread species predominate.

While the restoration project has had a minimal impact on birds or butterflies, doing so was not its objective (Lamouroux *et al.*, 2015). The restoration project did not aim to alter

the surrounding habitats on a large scale, particularly because so much of the surrounding landscape is managed or utilised for the direct benefit of people. If restoration is going to make a noticeable difference, a very different approach is required: it needs to take place at landscape scale over which habitat alterations are relevant to birds and butterflies (Navarro *et al.*, 2015). While some of my study species use river channels directly, the majority do not, and so restoration projects which focus solely on those channels are never going to play a major role in their conservation. However, floodplain restoration projects vary widely in their objectives and methods, so other projects might have different impacts (Buijse *et al.*, 2002; González *et al.*, 2015; Zingraff-Hamed *et al.*, 2017). In the next chapter, I address this by looking at a very different restoration project to that in the Rhône, one which has gone beyond the restoration of channels to instead reconnecting large areas of land to the river and re-establishing a dynamic floodplain.

4.5 Conclusion

In this chapter, I presented results from an area around the River Rhône, where there has been a project to restore some aspects of floodplain ecology, in particular by restoring flows in floodplain channels. Looking across study sites in different land use categories, my results clearly distinguish between these categories, in terms of habitat and vegetation structure, and population densities of bird and butterfly species. Furthermore, there is evidence that sites with more open habitats tended to have higher flood disturbance, which may suggest flood disturbance leads to more open habitats.

However, focusing only on floodplain channels and the restoration itself, there were very few significant differences in bird and butterfly population densities between restored and non-restored channels. Previous studies have shown that the restoration has had significant effects on various biotic and abiotic features within the floodplain channels themselves (Lamouroux *et al.*, 2015 and refs. therein). My results suggest that the restoration has had a minimal impact on the surrounding floodplain.

Given the nature of the restoration project, which focused on increasing flow and connectivity of the floodplain channels (Lamouroux *et al.*, 2015), it is perhaps to be expected that the effects are constrained to the channels themselves and did not spill out into the wider floodplain. However, it is therefore also evident that this type of restoration is insufficient to bring about the benefits to wider biodiversity, and especially HNV species, that I hypothesised in Chapter 1 to occur in restored floodplains.

My next chapter therefore focuses on another restoration project, but a project that differs greatly from that in the Rhône in terms of scale and objectives. This project was carried out in the Peene Valley in north-east Germany, and is part of Rewilding Europe's Oder Delta project region (Schepers & Bosman, 2015). This project reconnected large areas of former floodplain to the river channel, allowing the river to inundate large areas during periods of high flow, and recreating a more natural hydrological regime.

5 GERMANY

5.1 Introduction

The results of the previous chapter indicate that the restoration project carried out on the floodplain channels of the River Rhône had only a limited impact on the surrounding habitats and associated species, suggesting it did not significantly increase flood disturbance. Floodplain restoration projects vary considerably in their scale, scope and methodology and so some types of restoration are more likely to restore flood disturbance to the surrounding landscape than others (Buijse *et al.*, 2002; Roni *et al.*, 2008; Hughes *et al.*, 2012; González *et al.*, 2015; Muhar *et al.*, 2016; Zingraff-Hamed *et al.*, 2017). Over 1,000 river restoration projects across 31 European countries have been reported, including projects in planning, in progress and completed (RESTORE, 2017). However, most of these are relatively small in scale, often restricted to the river itself or a narrow strip of floodplain (Golfieri *et al.*, 2017), and often there is little or no monitoring of impacts (Angelopoulos *et al.*, 2017; Golfieri *et al.*, 2017). Nonetheless, some projects have had significant impacts on birds (for example Raven, 1986; Jonsson *et al.*, 2012), vegetation (for example Timmermann *et al.*, 2006; Göthe *et al.*, 2015), nutrient loading (for example Pedersen *et al.*, 2007) and sedimentation (for example Ahilan *et al.*, 2016).

Landscape-scale restoration projects which increase flood disturbance to a large area are rare, and many questions about their effects remain to be answered (Ockendon *et al.*, 2018). Furthermore, larger projects may not fully rewild the floodplain within the project area, but merely reduce the intensity of human land use (Pedersen *et al.*, 2007). Some of the best examples for large-scale restoration projects come from the Danube. However, these have not focused on reconnecting large areas of floodplain to the river for biodiversity. Instead, projects in the Upper Danube have aimed to reduce flood risk and improve water quality (Brouwer *et al.*, 2016; Stammel *et al.*, 2016), while projects in the Lower Danube focused on restoring aquatic ecosystems within large polders previously used as fish ponds (Schneider, 2014). Other large projects have focused solely on modifying the discharge regime from dams, in most cases to alter the aquatic environment or narrow riparian buffer strips (Olden *et al.*, 2014). One large project on the Kissimmee

river, USA has reflooded the floodplain and led to dramatic vegetation responses, but it is not clear how this has affected wider biodiversity (Toth, 2017).

Given this range of potential project designs, for my third study region I selected a landscape-scale restoration project which aimed to reconnect large areas of floodplain to the river. As such, the nature of the restoration is very different to that carried out on the Rhône, and is likely to have increased flood disturbance to large areas of floodplain. The chosen project took place around the Peene, a small river (mean discharge $30\text{m}^3\text{s}^{-1}$; Waterstraat & Krappe, 1998) in north-east Germany (Figure 5.1) that forms part of the river systems of the Southern Baltic Lowlands (Timmermann *et al.*, 2006). Like most European rivers, the Peene and its natural floodplain have a long history of human influence. The river itself has been used for navigation for centuries, as well as providing water to settlements and industries (*Museum im Steintor*, 2009). For much of its history, the floodplain of the Peene has been used extensively as meadowland or pasture. Under the German Democratic Republic in the 1960s and 1970s the usage became more intensive, with drainage ditches, dykes and pumping stations deployed to increase the agricultural productivity of the floodplain and resulting in water levels 25-100cm below the soil surface (Timmermann *et al.*, 2006; Zak & Gelbrecht, 2007; Zerbe *et al.*, 2013; Herold, 2015). Management practices such as these have meant that, across north-eastern Germany, around 70% of peatland had been converted to agriculture by the start of the 21st Century (Timmermann *et al.*, 2006).

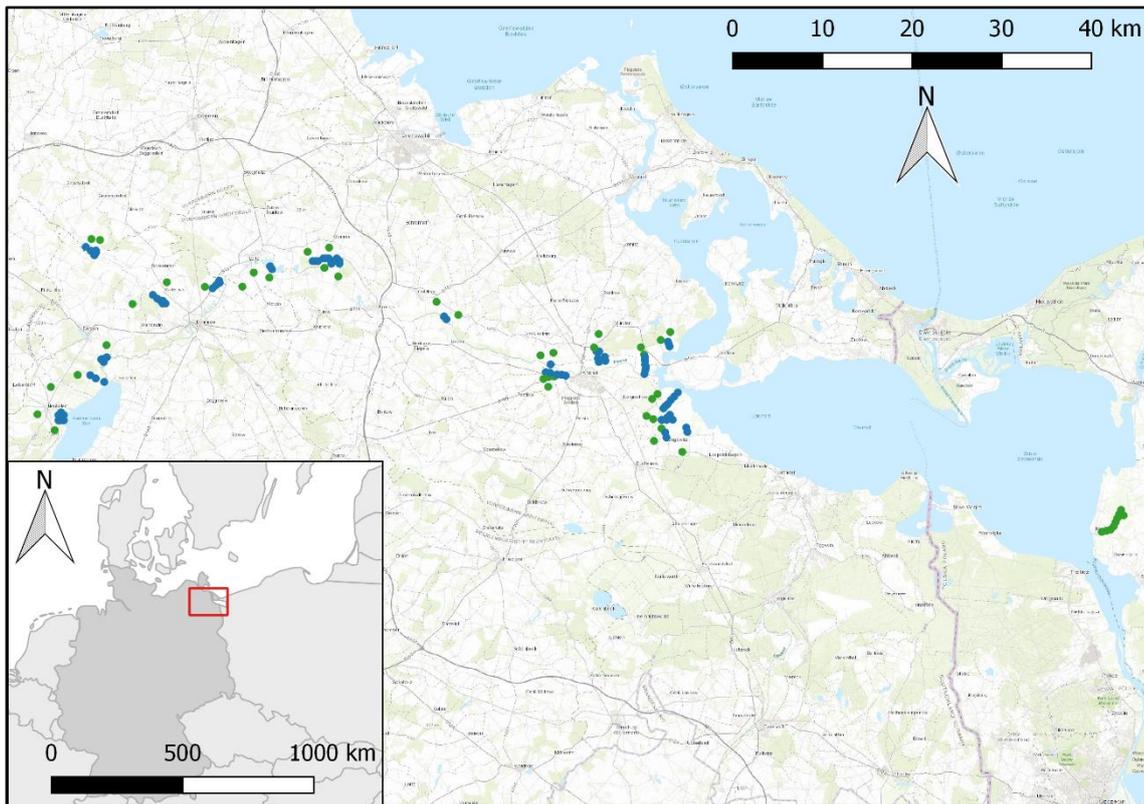


Figure 5.1 – Location of study sites. Main panel shows a topographic map of the study region with positions of individual study sites indicated by coloured dots (blue = restored wetland; green = non-restored farmland; not to scale). Inset panel shows location of study region within Germany (dark shading) and Europe; red box is area detailed in main panel.

However, in the early 1990s, and following the reunification of Germany, approaches to land management changed dramatically. Around the Peene, the decision was made to restore large areas of the former floodplain, primarily for biodiversity benefit but also to make the river more attractive and increase its amenity value (Zweckverband Peenetal-Landschaft, 2018). Another objective was to reverse the carbon emissions resulting from oxidation of peat and restore a carbon sequestration function through peat formation (Zerbe *et al.*, 2013; Beyer & Höper, 2015). Restoration efforts were focused around the lower reaches of the river, so in this case there was little opportunity to alleviate flood risk to urban areas.

Restoration started in 1992 (Zweckverband Peenetal-Landschaft, 2018). The main component of the restoration project was to reconnect the floodplain to the river. As such, dykes were breached or removed and pumping stations were turned off. Water was once again able to flow from the river channel into the surrounding floodplain (Herold, 2015). The characteristics of the surrounding landscape meant that restoration was carried out in a series of isolated polders. Between these restored polders, the previous management

regime continued. The restored polders were given federal protection, in two protected areas (as the project spanned two administrative regions): *NSG Peenetal von Salem bis Jarmen* and *NSG Peenetal von Jarmen bis Anklam*. The total protected area is 10,145ha, in the floodplain of both the Peene itself and its tributary the Trebel (EEA, 2017b). Previous studies in the same region have noted that the rewetted areas differed from pristine fenland, in terms of plants, beetles, hydrological properties and soil processes (Timmermann *et al.*, 2006; Zak & Gelbrecht, 2007; Görn & Fischer, 2015).

The aim of my study was to compare the biodiversity, disturbance regimes and habitats of restored and non-restored areas of floodplain and therefore elucidate the impacts of the restoration that took place. I firstly compared the habitats and disturbance regime in restored and non-restored sites, and I also investigated whether there was evidence that differences in disturbance regimes have led to differences in habitats. I then investigated whether there is evidence that differences in species' population densities were associated with differences in habitat. Finally, I directly compared population densities of bird and butterfly species in restored and non-restored sites. I predicted that the restoration project will have created suitable habitat for many HNV species, potentially even more suitable than the surrounding non-restored farmland, and this will be reflected in species' population densities. I also predicted that the restored wetland will have greater levels of disturbance, especially flood disturbance, than the surrounding non-restored farmland.

The Peene is an example of a much more ambitious, larger scale restoration project than that carried out on the Rhône, with the hydrology being altered over a large area. Furthermore, the Peene situation is broadly similar to that of many lowland rivers in western Europe, with intensive agriculture, high population densities and a range of human use. As such, lessons learned here, both in terms of carrying out such a restoration project and the impacts of that restoration, could be widely applicable.

5.2 Methods

5.2.1 Field methods

I carried out fieldwork in spring 2017. My objective was to compare the restored wetland to non-restored areas, which were comparable areas within the floodplain still disconnected from the river and used as farmland. The nature of the restoration project produced several large, independently restored polders rather than a contiguous area of restored wetland. However, the main river channel offers a corridor of connectivity

between all the polders. I studied 20 such polders of varying size (64 – 1,282 ha; Figure 5.2).



Figure 5.2 – A typical scene from a restored polder of a sedge meadow with areas of scrub. Hard to establish from the photograph is the depth of standing water obscured by the vegetation.

Within 15 of these restored polders, study points were chosen by overlaying a 300m grid of points and excluding points that were within 200m of the edge of the polder (to reduce edge effects) or inaccessible (principally due to deep water). If more than six points remained, I then chose six at random. These points formed the central point of each study site. At each site, I carried out bird counts, butterfly transects, habitat mapping and disturbance transects, as described in Chapter 2. Butterfly transects were mostly 200m; in some cases their length was restricted by inaccessible terrain or deep water. In those cases, I measured the length using GPS points recorded on a hand-held GPS device. I carried out 3-4 bird counts (mean 3.13) at each site, 1-3 butterfly counts (mean 1.97) at each site, and two disturbance transects, on my first and last visit to each site. I carried out habitat mapping once per site, all within a three week period to minimise the variation in vegetation growth between sites.

Five restored polders were almost entirely covered with deep standing water (due to erosion and compaction of soil prior to restoration; Zak & Gelbrecht, 2007) and therefore

it was impossible to carry out any surveys from the interior of those polders. Bird populations in these sites were surveyed using line transects from raised dykes (either at the edge or through the centre of the polder). These raised dykes, combined with little emergent vegetation, meant that there was good visibility out across the polder. This method is similar to that used to survey waterbirds in the UK (Bibby *et al.*, 2000; BTO, 2017). As detectability was much greater in these situations, data were not left-truncated and were right-truncated at 200m rather than 100m, and fitting detection functions was carried out separately from point count data. Neither butterfly surveys nor disturbance transects were carried out in these flooded polders as a transect along the dyke would not have been representative of the restored area. Furthermore, most of the restored area was standing water and therefore unsuitable habitat for butterflies (van Swaay *et al.*, 2006). Habitat mapping was carried out as normal, based on a point halfway along the transect. Where the transect route was at the edge of the polder, the point was offset into the polder such that the surveyed area was entirely contained within the polder. Note that, as such, the habitat maps did include the dyke and emergent vegetation alongside it and so typically overestimate the amount of vegetation and underestimate the amount of open water compared to a random sample of the polder. However, many of the bird species recorded were found exclusively in this narrow band of vegetation and so it made sense to include these habitats. In one polder, I was able to carry out both point counts and a transect, covering different parts of the polder. Overall, this led to the distribution of study sites given in Table 5.1. Note that this variation in the surveys carried out at each site is reflected in variation in n values in my results.

Table 5.1 – Distribution of number of study points per restored polder. For six polders, point counts were not feasible so transects (one per polder) were carried out instead. One polder included both point counts and a transect (covering different parts of the polder); the “number of polders” column therefore sums to 21, one greater than the total number of polders surveyed.

Number of study points per polder	Number of polders
1	1
2	3
3	2
4	3
5	1
6	5
Transect (no butterfly counts)	6
Total: 60 points; 6 transects	

The surrounding landscape was predominantly intensive agriculture, mostly cereals (Figure 5.3). Mean cereal yield in Mecklenburg-Vorpommern NUTS 2 region was 178.8 tonnes per km² in 2012 (EUROSTAT, 2014). I selected two farmland points per polder, located near to each polder (and so spanning the same section of the river; Figure 5.1), although I was unable to complete sampling in two farmland sites. I also surveyed nine sites that were farmed under Higher Level Stewardship (HLS) schemes, in order to include some data on the biodiversity on more wildlife friendly farms in the area. These sites were located ~60km from the bulk of the sample sites, in Goleniów County, NW Poland (for brevity and to avoid confusion, I nonetheless refer to this region as my “German” study region). In total I sampled 47 farmland sites. These farmland sites were assumed to be roughly representative of what would have existed in my restored sites prior to restoration. As such, throughout this chapter, “restored” and “wetland” sites are considered synonymous, as are “non-restored” and “farmland”.



Figure 5.3 – A typical scene within the agricultural landscape of my study region.

5.2.2 Analyses

I first characterised the physical composition and flood exposure of my sites, using (as before) Principal Components Analyses to reduce dimensionality and produce metrics of habitat and vegetation structure. As shown below, the results of these PCAs led me to use one component to describe the vegetation and habitat structure (Veg.PC1) and two components to describe the disturbance regime (Disturbance PC1 and Disturbance PC2). I calculated Flood Risk Score across the entire study region, using the protocol given in Chapter 2. The search was restricted to images taken after the restoration project was completed in 2007. The search was carried out in October 2017. In total, this yielded 492 individual Landsat scenes.

To see what impact the restoration has had on both habitats and disturbance processes, I compared the distribution of habitat types, Veg.PC1, Disturbance PC1, Disturbance PC2, Flood Risk Score and water depth between restored wetland and non-restored farmland sites. For habitat types, I used a MANOVA to test whether there was a significant association between the site type (restored wetland or non-restored farmland) and the distribution of habitat types. For the other comparisons, I used the Shapiro-Wilks test to

test for normality, then carried out the comparison using either Welch's t-test for normal data or the Wilcoxon Rank Sum test for non-normal data. I expected to find that restoration has increased flood disturbance (reflected in an increase in Flood Risk Score and water depth) and that this would have led to more open habitats. I also expected restored areas to support higher population densities of mammals such as deer, wild boar and beaver, which would be reflected in greater levels of biotic disturbance.

I hypothesised that natural disturbance processes influence the habitat and vegetation structure. To test this, I tested for correlations between Disturbance PC1, Disturbance PC2, Flood Risk Score, and water depth and Vegetation PC1 within wetland sites. I only considered wetland sites as vegetation structure in farmland sites is primarily controlled by human activity, and so I would not expect any meaningful associations between those disturbance variables and vegetation structure in farmland sites. While the data collected are insufficient to conclusively identify causal relationships, a correlation may indicate an interesting association.

Different species of bird and butterfly are widely associated with habitats which differ in their vegetation structure (Snow *et al.*, 1998; van Swaay *et al.*, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). I expected this to be reflected in my data. To examine species' associations with habitats, I used GLMs to model bird and butterfly species' responses to the first axis of the vegetation PCA (Veg.PC1) and, separately, to the mean vegetation height at each site. In all cases, the GLM used a quasi-Poisson error structure on the raw count data, a log link function and offset by the log of sampling effort. For birds, sampling effort was the number of visits multiplied by the estimated detection area (as estimated by distance sampling; see Chapter 2). For butterflies, sampling effort was the number of visits multiplied by survey area, based on the length of each transect and a fixed width of 5m.

A key question in this study is how has the restoration project affected biodiversity? In particular, my hypothesis is that many HNV species will have higher population densities in restored wetland than non-restored farmland. To investigate directly the impact restoration has had on bird and butterfly species' population densities, I used a GLM (where possible) for each bird and butterfly species to compare population densities in restored wetland versus non-restored farmland sites. These GLMs followed the same protocol described above, except with restoration state as the explanatory variable. This was not possible for species which I observed either only in restored wetland or only in

unrestored farmland; for those species I used a randomization test to determine the significance of this trend.

Patterns in species' preferences for wetland or farmland sites could be driven by the nature of the wetland or by the nature of the farmland habitats. To further understand this, I again present the results alongside results from natural habitats and low-yielding farmland in Poland (Feniuk, 2015). This German study region is intermediate between my Ukrainian and my French study regions in terms of both physical proximity and ecological similarity to the Lubelskie region of Poland. While this region of Germany and the Lubelskie region of Poland are disparate enough that comparisons should be interpreted as only a rough indicator of patterns, the results from this analysis may suggest whether any observed differences in species population densities between wetland and farmland habitats in my German study region are driven by the characteristics of the farmland or of the wetland being particularly good or bad for certain species. This comparison only includes species observed in both regions, so more specialist species are unlikely to be included. Comparisons were tested using the single-sample t-test.

5.3 Results

5.3.1 Quantifying vegetation structure and disturbance

The first component of the PCA of habitat and vegetation structure explained 26.6% of the variance in the data, while the second component explained 11.2%. All other components explained less than 10% of the variance and so were not considered further. Variable loadings and scores of study sites on the first two axis are shown in Figure 5.4. These suggested that the first principal component has once again picked out a gradient from open habitats (with negative scores) to closed habitats (with positive scores). Variables associated with closed habitats, such as “mean height” and “deciduous wood”, are positively weighted on this axis, while variables associated with open habitats, such as “sedge meadow” and “wet meadow”, are negatively weighted.

The interpretation of the second axis is less clear. There is some suggestion that it has separated wetland habitats from farmland habitats (both of which were frequently open), with variables such as “arable” and “meadow” being negatively weighted while several variables referring to reeds and sedges are positively weighted on this axis. However, given PC2's limited explanatory power and the overlapping of sites in different broad habitat categories, I used Veg.PC1 as my sole metric of vegetation structure.

Signs of disturbance were classified into four categories: Beaver, Boar, Deer and Other animal signs (see Chapter 2 and Appendix 1). The proportion of browsed shrubs (“Browse”) was also then added as a fifth category. Exploratory correlation tests (which were not adjusted for multiple comparisons) found most of the categories were uncorrelated between sites, except for Beaver and Browse, which were significantly positively correlated (Figure 5.5). Given this correlation structure, and to reduce dimensionality, I carried out a PCA.

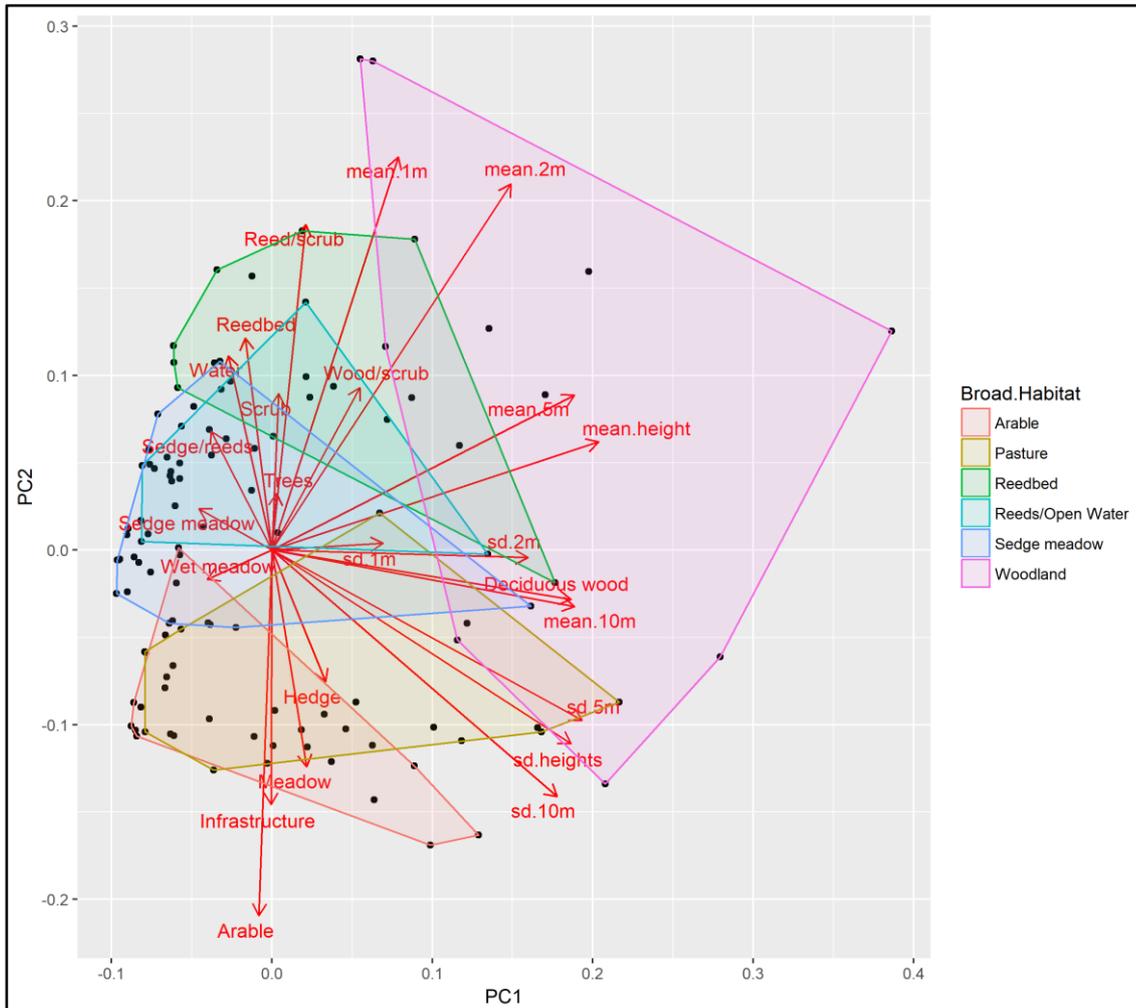


Figure 5.4 – Axes 1 and 2 of Principal Components Analysis on habitat and vegetation data. Length and direction of red arrows indicate the weightings of each habitat variable (see Chapter 2 for details of habitat variables). Black dots indicate scores of individual study sites. Coloured shapes encompass sites within a broad habitat category – note that these broad habitat categories are purely a visual aid and were not used in classification.

In the resulting PCA, the proportion of the variance in the data explained by successive components declined rapidly, with the first two axes explaining 48.8% and 19.2% of the variance in the data, respectively. The loadings of these two axes, and sites’ scores on those axes, are shown in Figure 5.6. There is significant overlap between different major

habitats within this space, which suggests that broad habitat type did not have a strong relationship with the prevailing disturbance regime. Browse is the single most heavily weighted type of disturbance on PC1, whereas Boar is the most heavily weighted variable on PC2. Looking at the distribution of study sites on these two axes, both appear to be important, with sites spread along both axes. Therefore, both Disturbance PC1 and Disturbance PC2 were used for the remaining analyses.

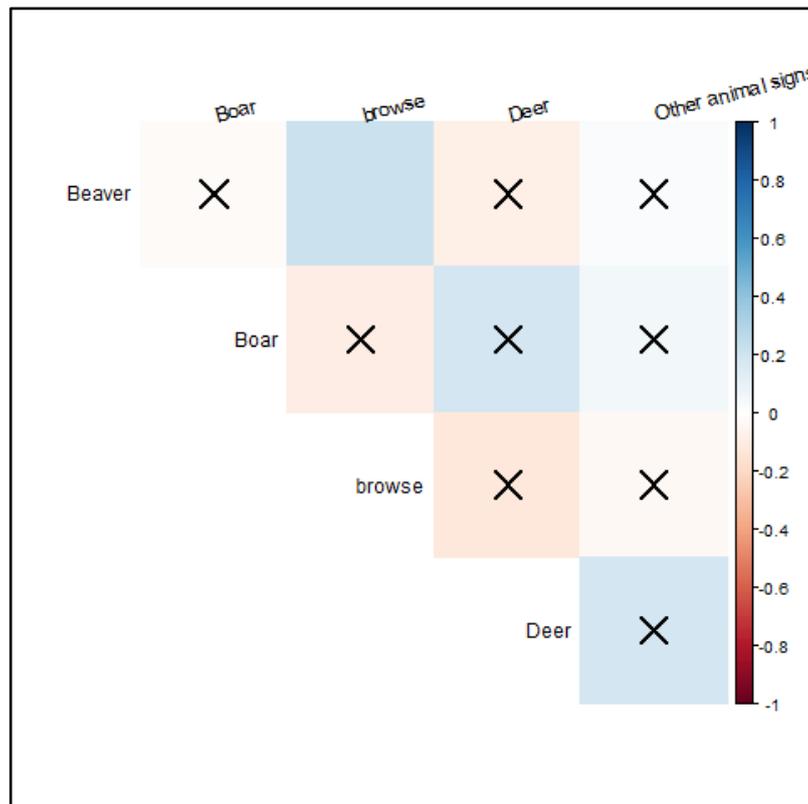


Figure 5.5 – Correlation plot of different categories of disturbance across 107 study sites. The colour of squares indicates the correlation coefficient. X indicates non-significant ($p > 0.05$) correlations.

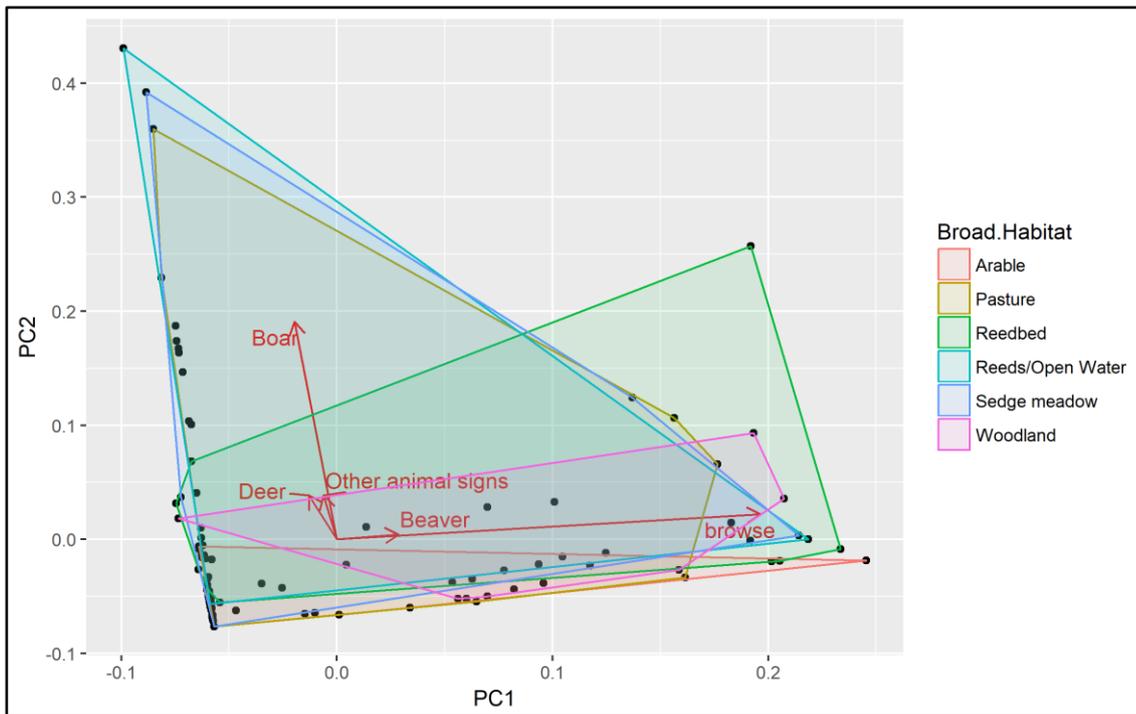


Figure 5.6 – Axes 1 and 2 of Principal Components Analysis on disturbance data. Length and direction of red arrows indicate the weightings of each disturbance variable. Black dots indicate scores of individual study sites. Coloured shapes encompass sites within a broad habitat category – note that these major habitat categories are purely a visual aid and were not used in classification.

5.3.1.1 Flood Risk Score

Figure 5.7 shows Flood Risk Score mapped across the German study region. Permanent water bodies (including the Szczecin Lagoon and part of the Baltic Sea) are well defined, and the Peene and its tributary the Trebel can also be picked out. Along the Peene and Trebel valleys, the Flood Risk Score drops rapidly outside the main channel, with the floodplain not being obviously distinct from the surrounding landscape when viewed at this scale. However, restored sections of floodplain do have significantly higher Flood Risk Scores than non-restored farmland sites (see below). Other areas picked out as having high Flood Risk Scores include the large wetland *Ostoja Wkrzańska* to the south of the Szczecin lagoon.

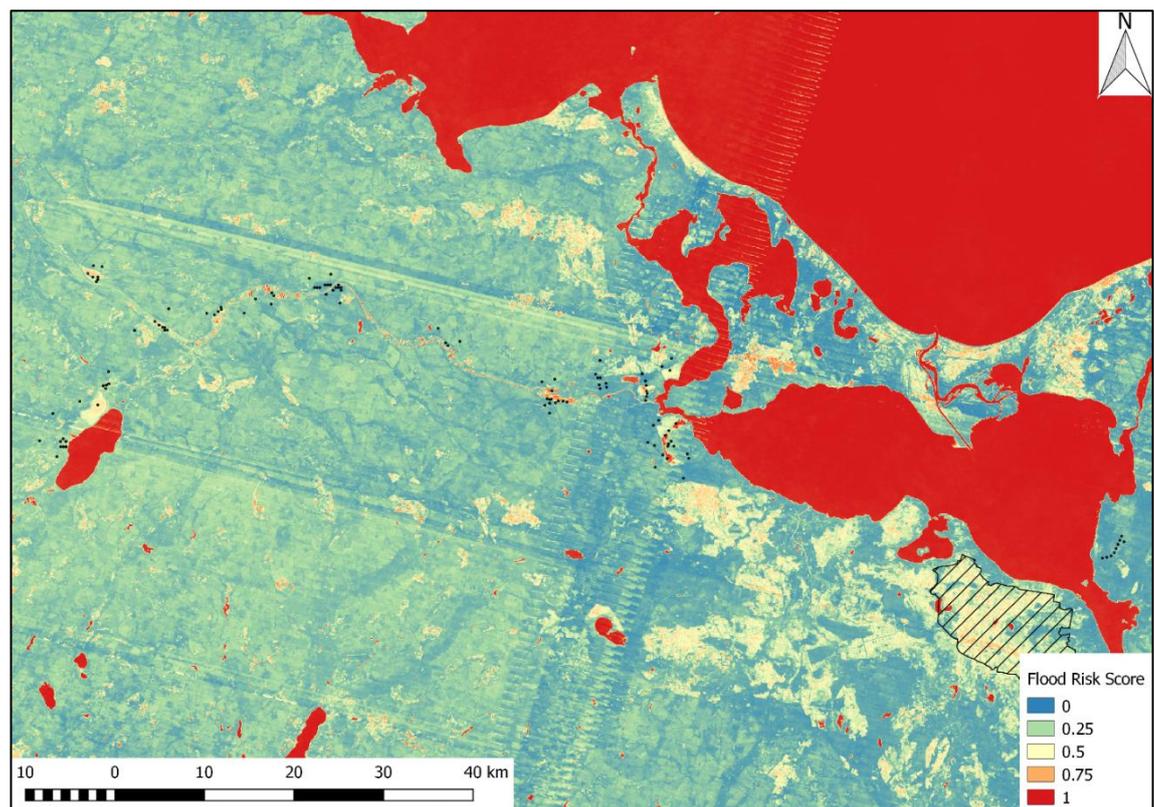


Figure 5.7 – Flood Risk Score mapped across German study region showing individual study sites (black dots). Flood Risk Score was calculated as the mean occurrence of water across 492 Landsat scenes taken between 2007 and 2017. Colour indicates Flood Risk Score from 0 (no water occurrence) to 1 (permanent water occurrence). *Ostoja Wkrzańska* protected area (see text) is indicated by the black striped area (UNEP-WCMC & IUCN, 2018).

5.3.2 Do restored wetland and non-restored farmland sites differ in habitats, vegetation structure and disturbance?

Restored wetland and non-restored farmland differed significantly in their distribution of habitat types (MANOVA residual $df = 112$, $p < 0.001$; Figure 5.8). Non-restored farmland sites were dominated by Arable (covering 53% of the area) and Meadow (covering a further 34% of the area) habitats. By contrast, restored wetland sites were covered with a mixture of reeds, sedge, scrub and open water. In total, habitats classed as Reed/scrub, Reedbed, Scrub, Sedge meadow, Sedge/reeds and Water accounted for 81% of the area of restored wetlands. These results show how restoration has affected the habitats, going from agricultural habitats (arable fields and hay meadows) to natural wetland habitats. Unlike wetlands in my Ukrainian study region, the restored wetlands in this German study region only have a small area of closed habitats such as Deciduous wood. This may be indicative of the recency of restoration; it takes a long time for closed canopy habitats to develop, even in the absence of disturbance processes.

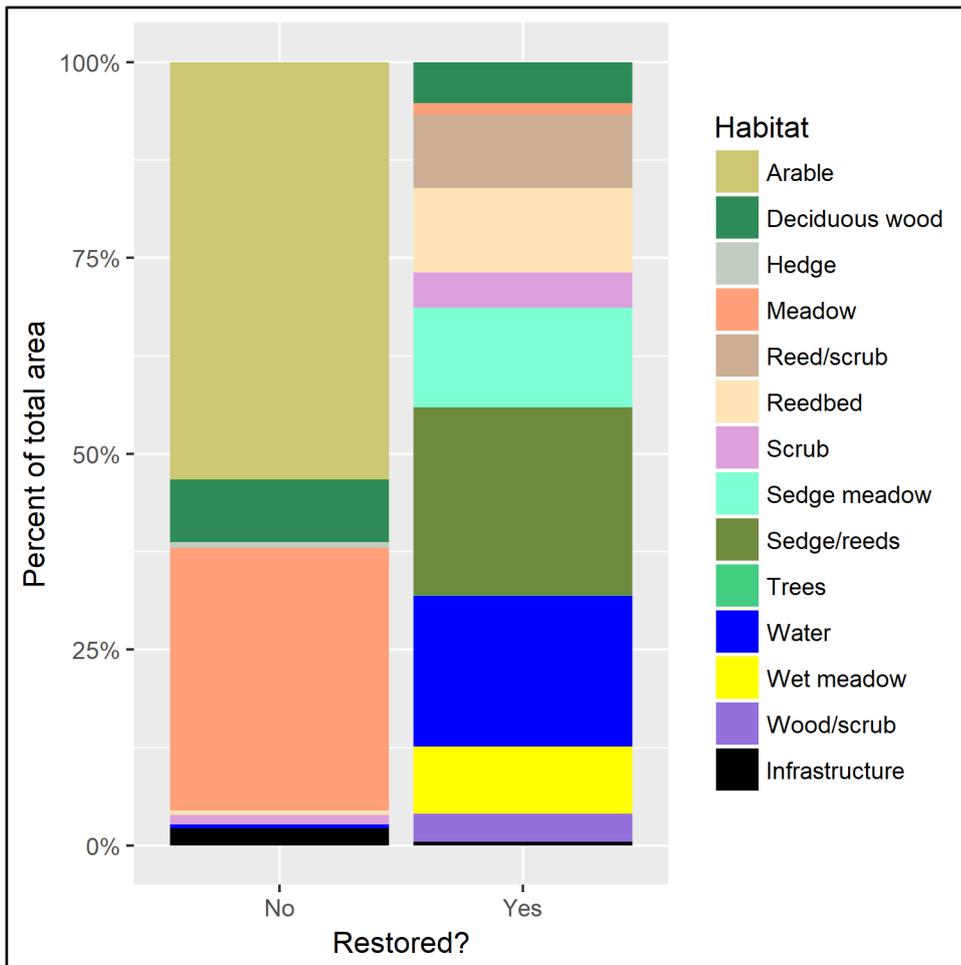


Figure 5.8 – The proportion of area covered by each habitat type in non-restored farmland and restored wetland differs significantly (MANOVA residual df = 112, $p < 0.001$).

There was no significant difference in Veg.PC1 between restored and non-restored sites (Wilcoxon Rank Sum Test $W = 1857$, $n = 114$, N.S.; Figure 5.9). While my impression in the field was that the habitats did differ, Veg.PC1 primarily picked out a gradient between open and closed. Both restored and non-restored sites had a range of habitat structures, even if they are different in other characteristics. For example, restored sites may be open sedge meadows or reedbeds, whereas non-restored sites may be open due to arable land.

Restored wetlands and farmland did not differ significantly in Disturbance PC1 but they did differ in Disturbance PC2, with restored sites having significantly higher Disturbance PC2 scores (Wilcoxon Rank Sum Test $W = 1472$, N.S. and $W = 995$, $p < 0.01$, respectively; both $n = 107$; Figure 5.9). Disturbance PC1 was most strongly weighted with browsing, followed by signs of beaver disturbance; Disturbance PC2 was most strongly weighted by signs of boar and deer. The interpretation of this result is therefore not entirely clear. Possibly the results are confounded to some extent by the fact that very

few farm sites (14 out of 47) had a large enough sample size of shrubs to assign a browse score to those sites.

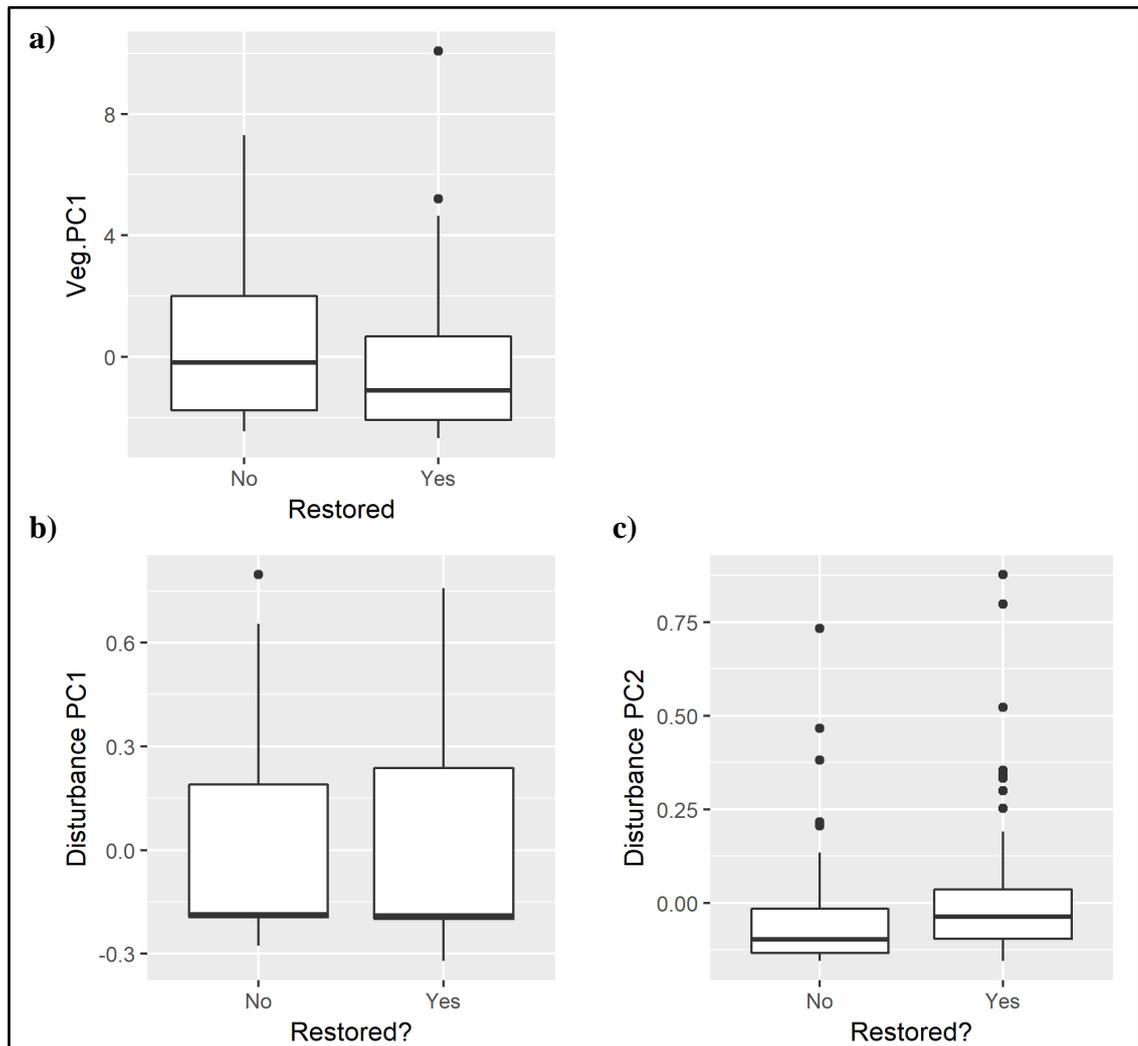


Figure 5.9 – **a)** There was no significant difference in Veg.PC1 between restored and non-restored sites (Wilcoxon Rank Sum Test $W = 1857$, $n = 114$, N.S.). **b)** There was no significant difference in Disturbance PC1 between restored and non-restored sites (Wilcoxon Rank Sum Test $W = 1472$, $n = 107$, N.S.). **c)** Disturbance PC2 was significantly higher in restored than non-restored sites (Wilcoxon Rank Sum Test $W = 995$, $n = 107$, $p < 0.01$). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Disturbance PC1 is positively associated with browsing and beaver disturbance. Disturbance PC2 is positively associated with boar and deer disturbance. See Chapter 2 for details of boxplots.

5.3.2.1 Flood Risk Score and water depth

There was significantly higher Flood Risk Score and significantly greater water depth in restored sites (Wilcoxon Rank Sum Test $W = 688$, $p < 0.001$ and $W = 204$, $p < 0.001$, respectively; both $n = 114$; Figure 5.10). Both these results are as would be expected

given the nature of the restoration that has been carried out: the restored wetland is indeed wetter than non-restored farmland.

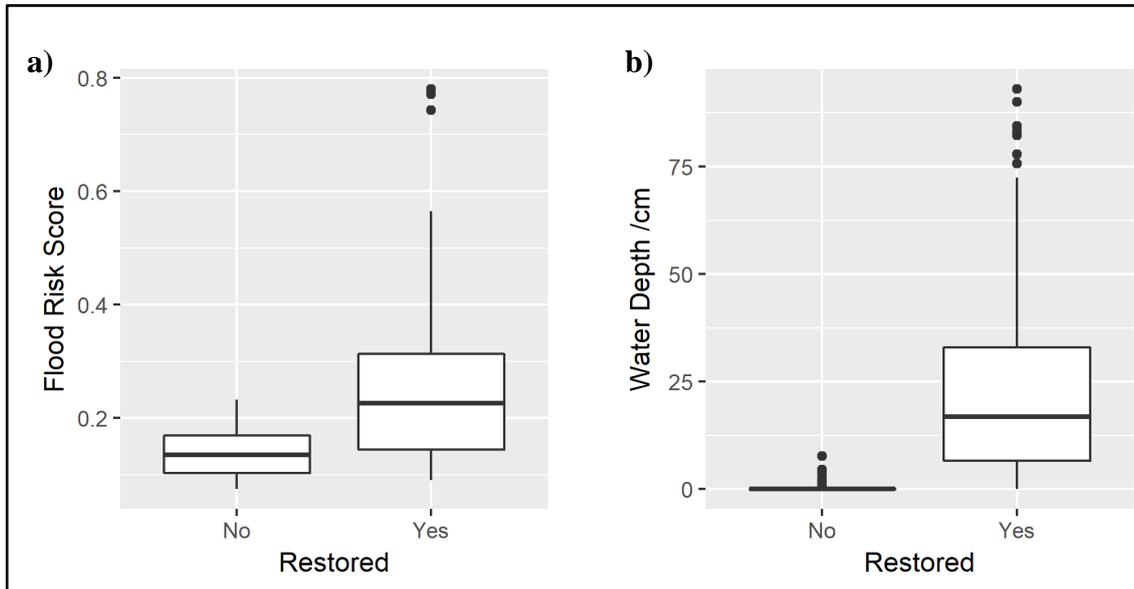


Figure 5.10 – a) Flood Risk Score was significantly higher in restored than non-restored sites (Wilcoxon Rank Sum Test $W = 688$, $n = 114$, $p < 0.001$). and b) Water depth was significantly higher in restored than non-restored sites (Wilcoxon Rank Sum Test $W = 204$, $n = 114$, $p < 0.001$). Flood Risk Score could vary from 0 (never inundated) to 1 (always inundated). See Chapter 2 for details of boxplots.

5.3.3 Are disturbance and flooding regimes associated with vegetation structure?

In all the analyses in this section, I only considered restored wetland sites. Farmland sites were excluded as the habitat structure in those sites is dominated by anthropogenic management rather than natural (biotic or abiotic) disturbance processes. There was a significant positive correlation of Vegetation PC1 with Disturbance PC1 but not with Disturbance PC2 (Pearson's $R = 0.454$, $p < 0.001$ and Pearson's $r = -0.0977$, N.S., respectively; both $n = 58$; Figure 5.11). This suggests higher Disturbance PC1 scores (browsing and beaver disturbance) were associated with more closed habitats. There was no correlation between Veg.PC1 and Flood Risk Score or water depth (Pearson's $R = -0.095$, N.S. and Pearson's $R = -0.061$, N.S., respectively; both $n = 65$; Figure 5.11).

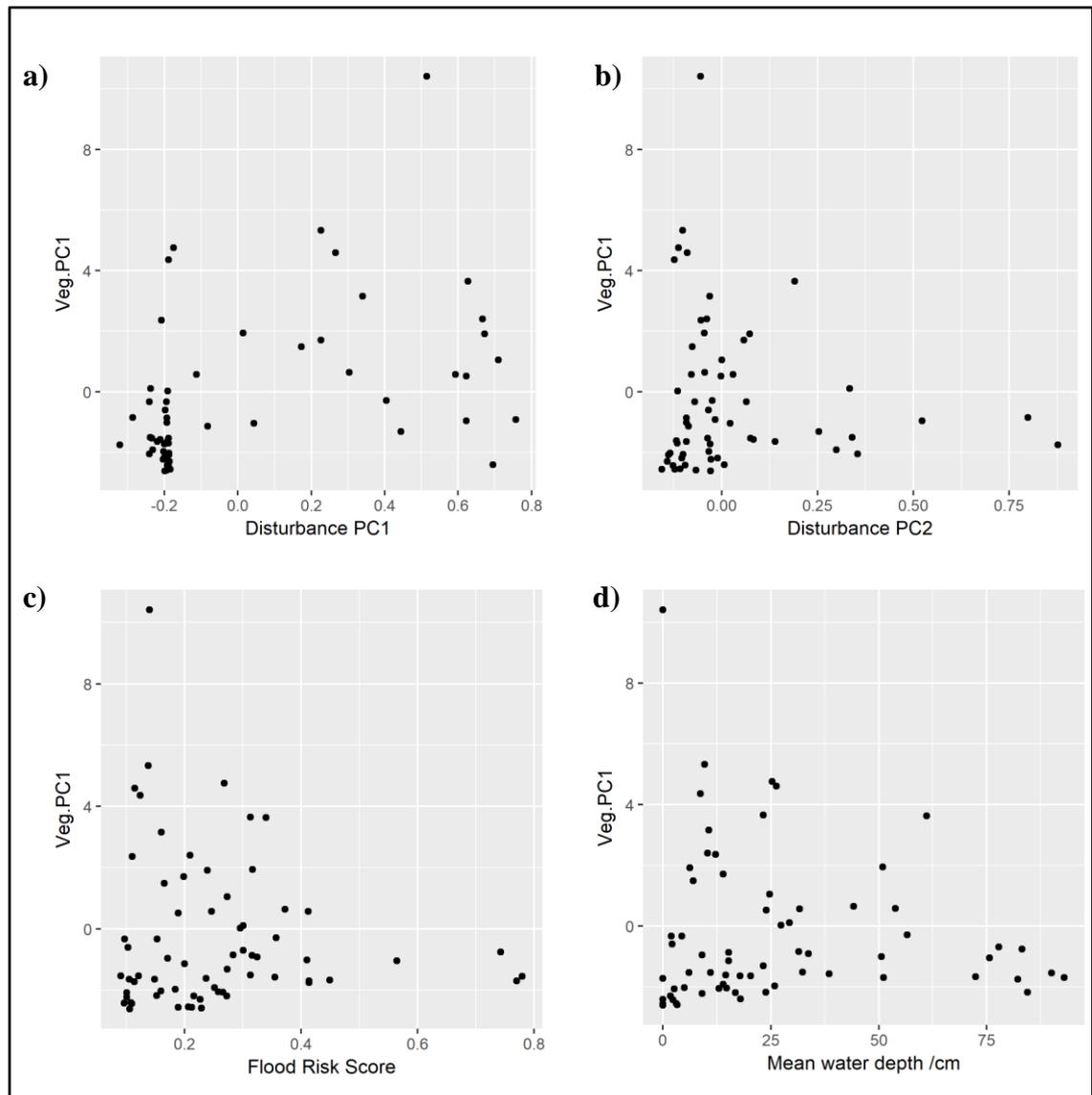


Figure 5.11 –a) Disturbance PC1 was positively correlated with Veg.PC1 (Pearson's $R = 0.454$, $n = 58$, $p < 0.001$). b) Disturbance PC2 was not correlated with Veg.PC1 (Pearson's $r = -0.0977$, $n = 58$, N.S.). c) Flood Risk Score was not correlated with Veg.PC1 (Pearson's $R = -0.095$, $n = 65$, N.S.). d) Water depth was not correlated with Veg.PC1 (Pearson's $R = -0.061$, $n = 65$, N.S.). Veg.PC1 represents a gradient from open habitats (negative scores) to closed habitats (positive scores). Disturbance PC1 is positively associated with browsing and beaver disturbance. Disturbance PC2 is positively associated with boar and deer disturbance. Flood Risk Score varies from 0 (never inundated) to 1 (always inundated). Points are individual restored study sites.

5.3.4 How are species' population densities related to vegetation structure?

Figure 5.12 and Figure 5.13 show the modelled responses of birds and butterflies (respectively) to Veg.PC1, while Figure 5.14 and Figure 5.15 show the modelled responses of birds and butterflies (respectively) to the mean height of the vegetation. These results match well with widely reported species' preferences (Snow *et al.*, 1998; van Swaay *et al.*, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). Some species preferred open habitats with lower vegetation heights (e.g. meadows), such as Montagu's harrier, Corncrake and Small tortoiseshell (positioned further left on the figures). Others preferred more closed habitats with higher vegetation (e.g. woodlands), for example Treecreeper, Nuthatch and Large skipper. That my results are in accordance with the published literature gives me confidence that my biodiversity surveys were accurate, and my habitat and vegetation structure mapping produced biologically relevant data. The results were broadly similar whether the model used Veg.PC1 or vegetation mean height as the explanatory variable.

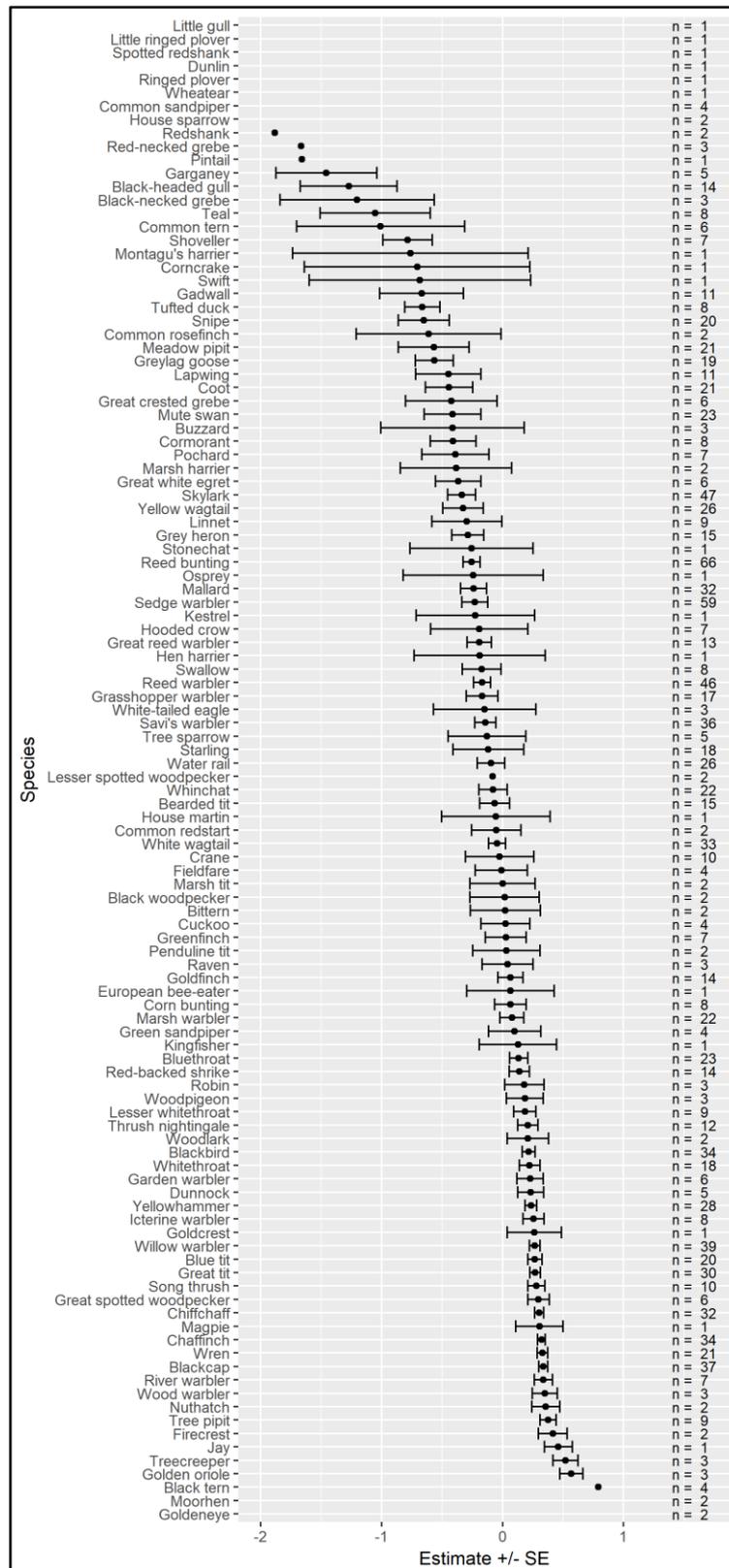


Figure 5.12 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species’ population density and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more positive estimate indicates that species had higher population densities in sites with a higher Veg.PC1 (i.e. prefers more closed habitats). All GLMs used a quasi-Poisson error structure. Models failed to fit for some species. N gives the number of sites in which each species was observed at least once.

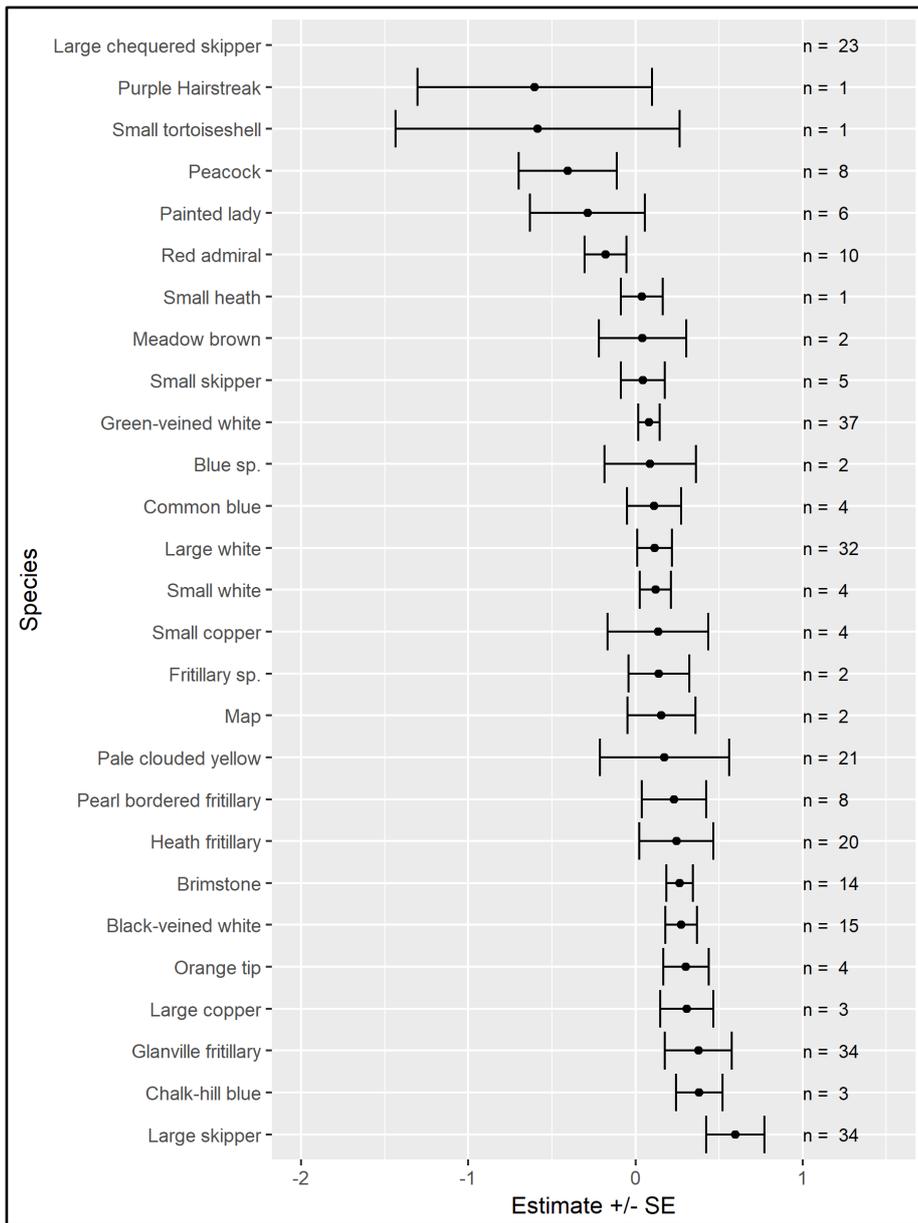


Figure 5.13 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between butterfly counts and habitat as measured by the first Principal Component of vegetation structure and habitat data (Veg.PC1). A more positive estimate indicates that species/groups had higher counts in sites with a higher Veg.PC1 (i.e. prefers more closed habitats). Models failed to fit for one species. N gives the number of sites in which each species was observed at least once.

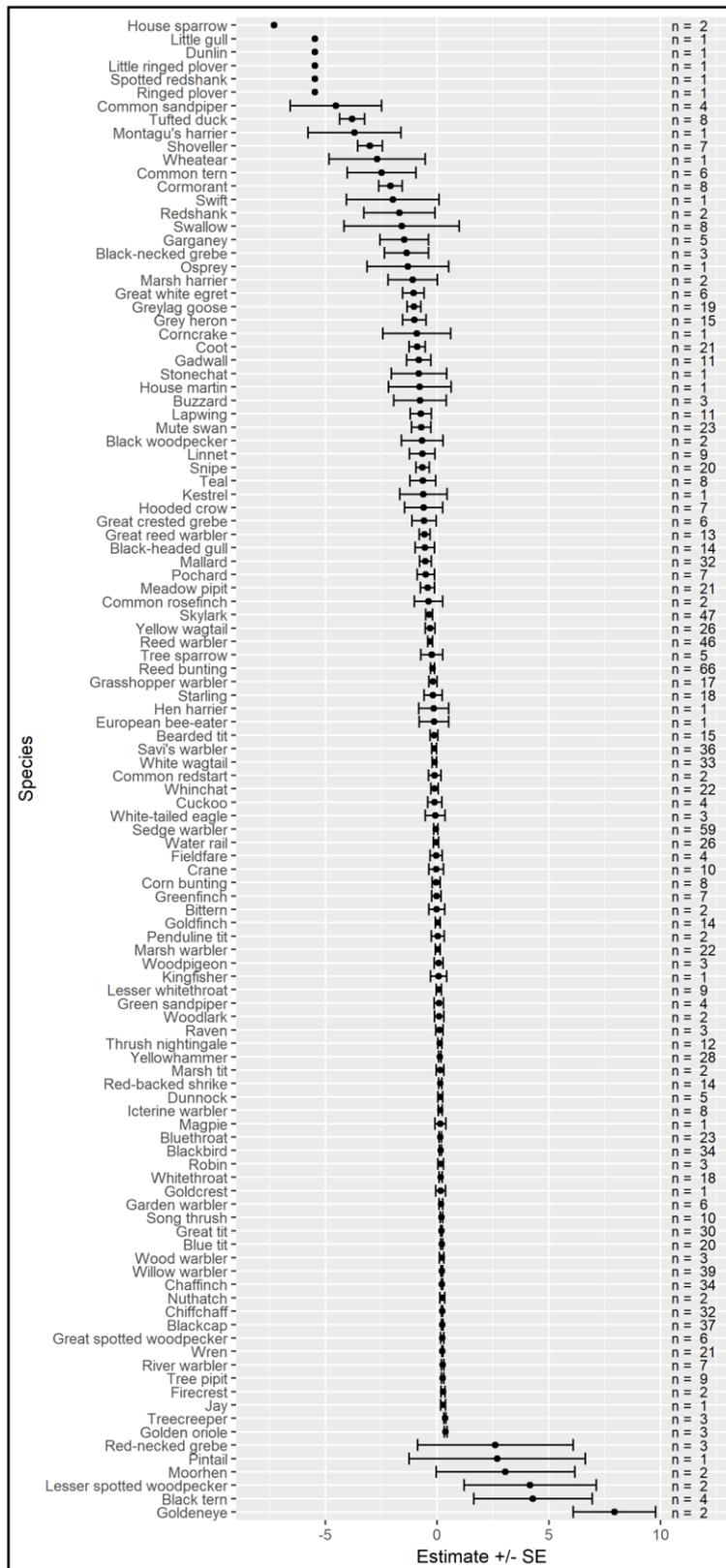


Figure 5.14 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between bird species’ population density and vegetation mean height in each site. A more positive estimate indicates that species had higher population densities in sites with higher vegetation. All GLMs used a quasi-Poisson error structure. Models failed to fit for some species. N gives the number of sites in which each species was observed at least once.

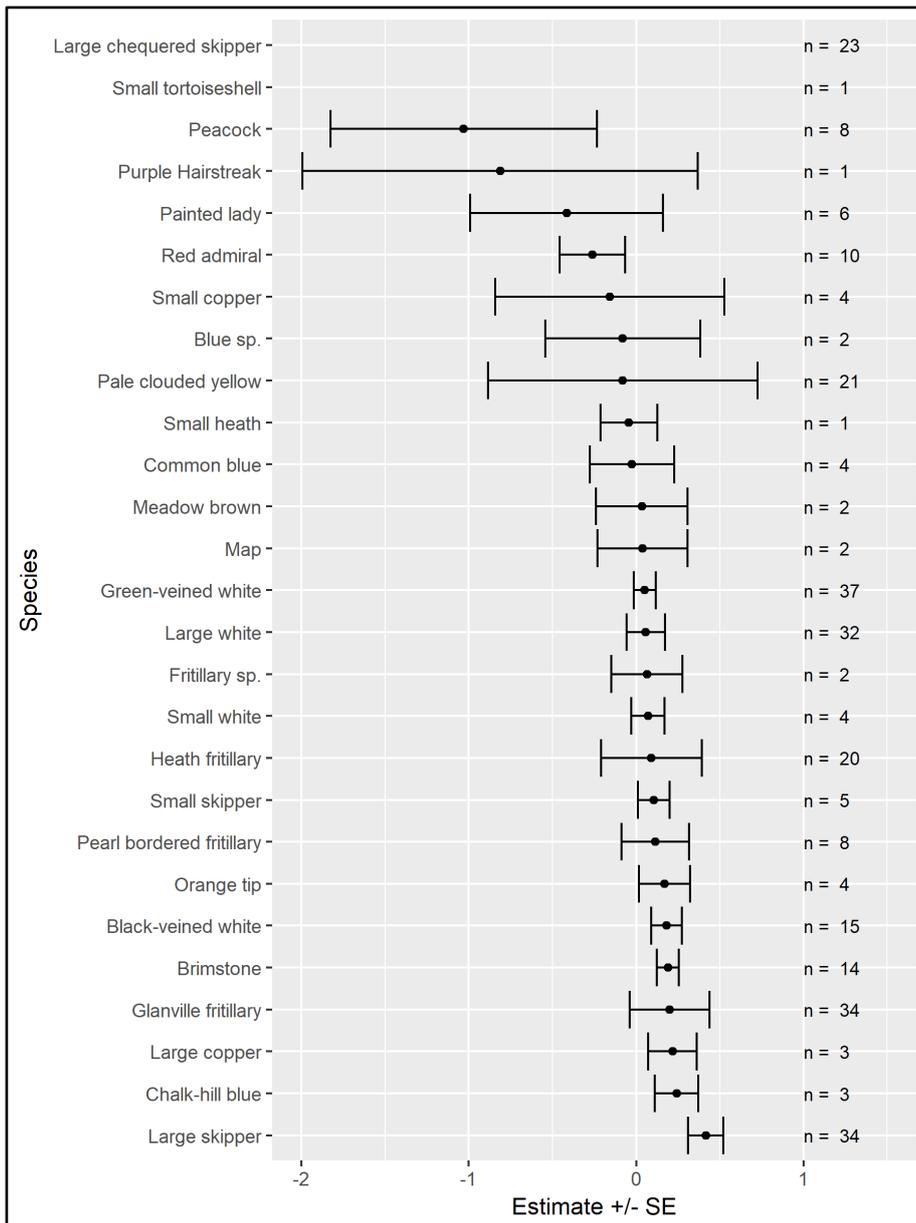


Figure 5.15 – Modelled estimates of the slope \pm 1 Standard Error (SE) of the relationship between butterfly species’ population density and vegetation mean height in each site. A more positive estimate indicates that species had higher population densities in sites with higher vegetation. All GLMs used a quasi-Poisson error structure. Models failed to fit for some species. N gives the number of sites in which each species was observed at least once.

5.3.5 How do species’ population densities compare between restored wetlands and unrestored farmland?

5.3.5.1 HNV birds

Figure 5.16 shows the estimated population densities of HNV bird species in unrestored farmland and restored wetland sites. Five species had significantly higher densities in the restored sites. These species tended to be strongly associated with water (for example Greylag goose, Reed bunting). A further 17 species showed no significant preference,

having approximately equal population densities between restored and unrestored sites. These species are considered HNV species because they are closely associated with HNVf across Europe, and thought to be threatened by the loss of HNV farming systems (Paracchini *et al.*, 2008). Therefore, even showing no preference could suggest that the restored landscape benefits these species, and that they are not dependent on HNV farmland. An alternative explanation, that in Germany these species have low densities in both unrestored farmland and restored wetlands, is addressed below.

On the other hand, five HNV species had significantly higher population densities in the unrestored farmland than the restored wetland. For these species, wetland restoration is unlikely to be a useful conservation intervention, and so other approaches must be considered to address the threat posed by the loss of HNVf across Europe.

5.3.5.2 Non-HNV birds

The remaining 85 species were not classified as HNV species, and so for these species I had no *a priori* expectations of which habitat they would prefer, as non-HNV species includes a range of habitat generalists and specialists associated with other habitats, including more intensive farmland. In total, 20 species preferred restored wetland, six species preferred unrestored farmland and 59 species showed no significant preference (Figure 5.17). Looking at individual species, patterns match what would be expected from their reported ecology (Snow *et al.*, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018). Wetland birds preferred the restored wetland (for example grebe species, ducks); farmland birds prefer the farmland sites (for example Goldfinch) and some species are generalists (for example Chiffchaff, Great tit). Overall, these results tend to suggest that wetlands are a more valuable habitat for birds than farmland, with far more species preferring the wetland than prefer the farmland. Many species showed no significant preference, either because they were common in both habitats or observed too rarely for me to observe a statistically significant pattern.

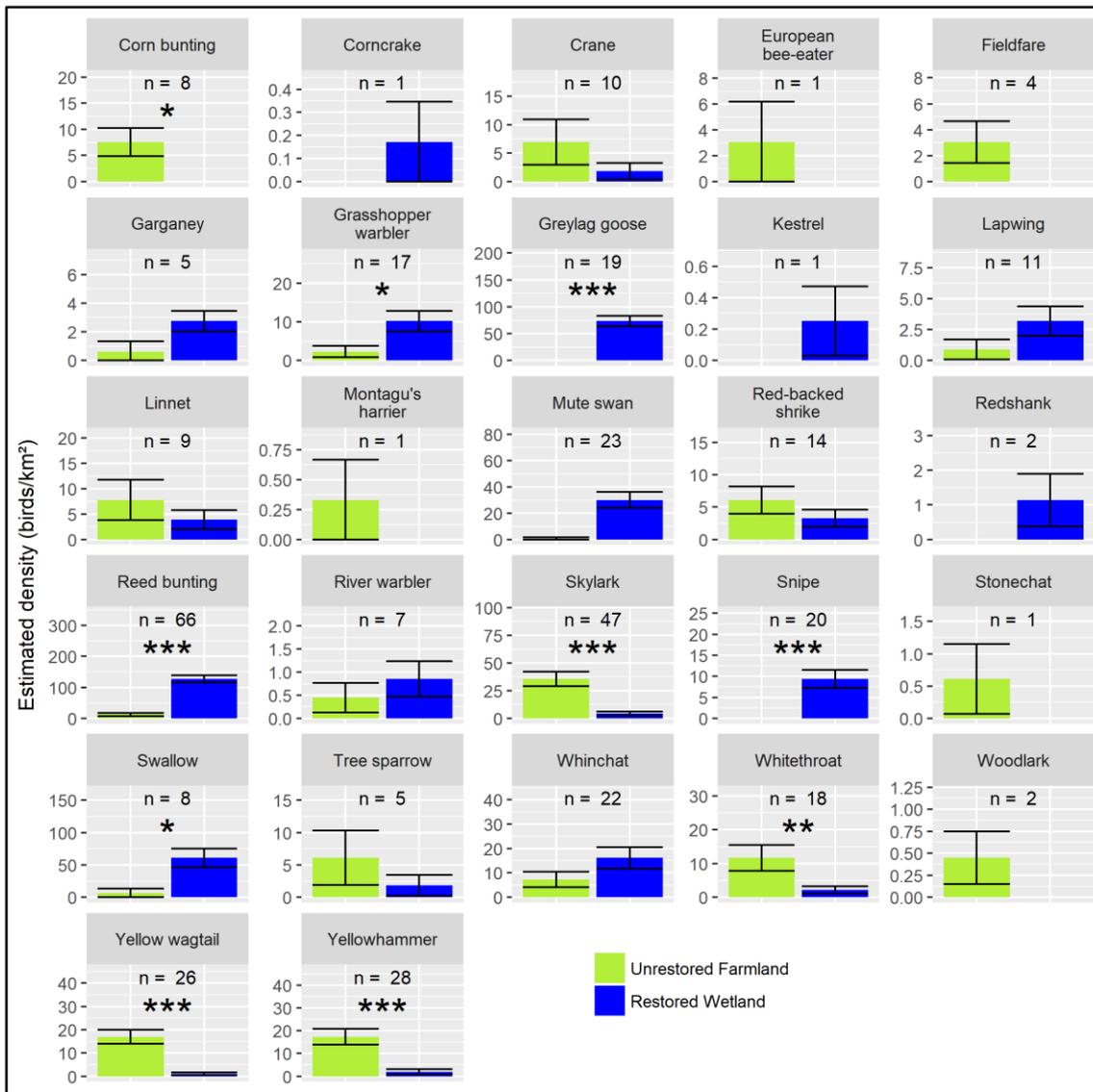


Figure 5.16 – Population density of HNV bird species in unrestored farmland (green) and restored wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. N is the number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).



Figure 5.17 – Population density of non-HNV bird species in unrestored farmland (green) and restored wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. N is the number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

5.3.5.3 Butterflies

Looking at butterflies, only two species showed a significant preference (Small heath and Small white) and both of these preferred unrestored farmland (Figure 5.18). No HNV indicator species were observed (Paracchini *et al.*, 2008). This is the opposite trend to birds. For butterflies as a whole, farmland appears to be the more valuable habitat. This is likely a reflection of their ecology, as butterflies need flowering plants and suitable larval host plants which are uncommon in areas covered in standing water, as was the case for many restored sites. Common wetland plants such as reeds and sedges are wind-pollinated and therefore do not have flowers that butterflies can feed from.

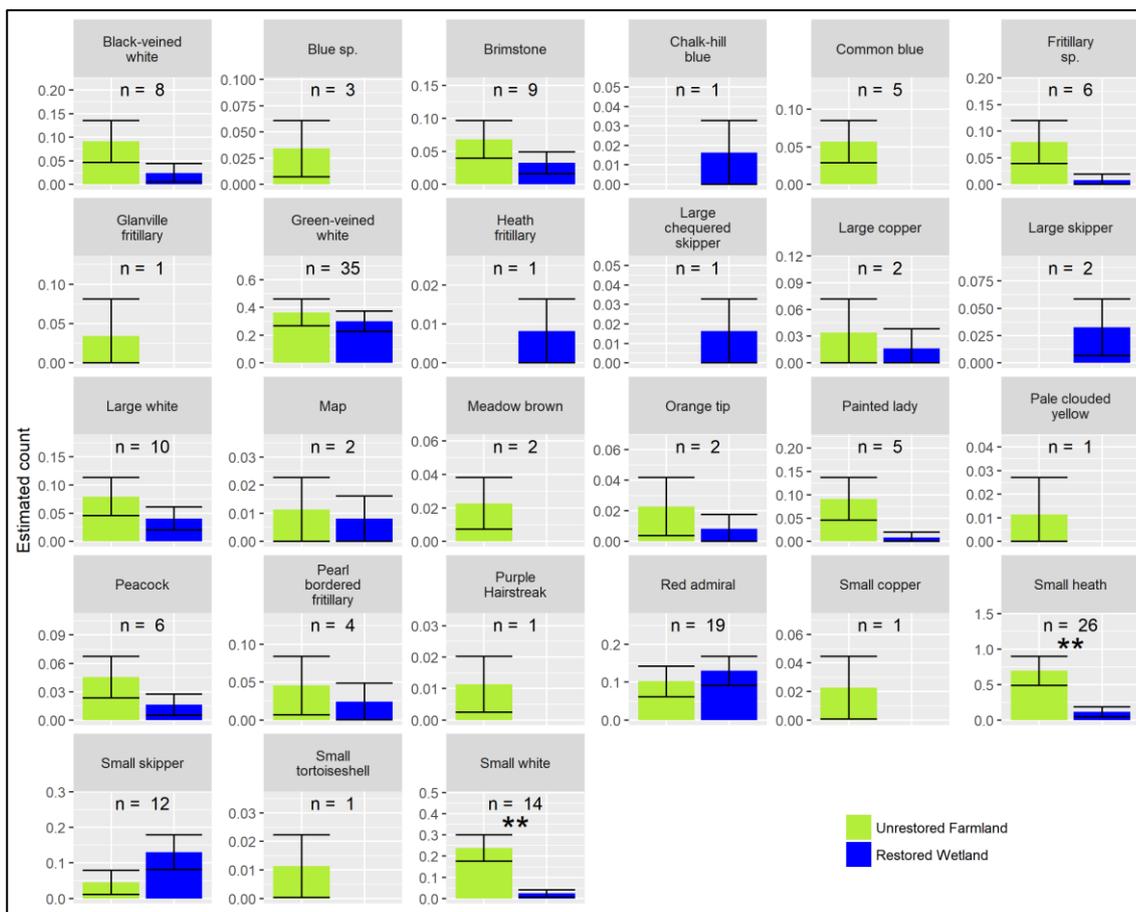


Figure 5.18 – Estimated count per transect of butterflies in unrestored farmland (green) and restored wetland (blue) sites, estimated using quasi-Poisson models. Black lines show \pm one Standard Error in modelled estimations. N is the number of sites with at least one observation of that species. Stars indicate statistically significant results based on quasi-Poisson models or Randomization Tests for species only observed in either restored or non-restored sites (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

5.3.6 Comparison of bird densities with Polish results

5.3.6.1 HNV Birds

Figure 5.19 shows the estimated densities of HNV birds compared between Poland (Feniuk, 2015) and Germany. Looking at farmland in the two countries, two species had higher population densities in Polish than German farmland, while four showed the reverse pattern. Given that these species were all classified according to their association with HNV farmland, and that the German farmland was more intensive than most HNV systems, I did not expect any species to have higher population densities in German farmland. It is therefore surprising that more species preferred German farmland than the less intensive farmland studied in Poland. It is possible that species' habitat preferences vary across the range and they are not always strictly associated with HNV farmland. For example, one species which preferred German to Polish farmland was the Skylark, which may be tolerant of relatively intensive farmland (Wilson *et al.*, 1997; Svensson *et al.*, 2009), and not to be dependent on low-yielding agriculture.

In wetlands, there was an almost ubiquitous trend for HNV bird species to have higher population densities in my study region than in natural habitats in Poland, with five species having significantly higher population densities in German wetland than Polish baseline habitats, and none showing the opposite trend. This suggests that the restored wetland in Germany is a more suitable habitat for many HNV bird species than the natural baseline habitats studied in Poland. Furthermore, in combination with finding inconsistent differences between countries in farmland bird densities, it would indicate that my previous result that many HNV bird species prefer restored wetland to non-restored farmland (Figure 5.16) is best explained by the restored wetland being suitable habitat for those species, rather than the surrounding farmland being particularly unsuitable.

5.3.6.2 Non-HNV Birds

Figure 5.20 shows the results for non-HNV birds. In farmland, there is no obvious pattern, with some species having significantly higher densities in Poland (nine species), others in Germany (seven species), and most showing no preference (15 species). This also suggests that, despite its apparent intensity, farmland in my study region of Germany can support similar population densities of many bird species to low-yielding farmland in Poland. Contrasting German restored wetland and Polish baseline habitats, there was also a mixed pattern, with some species having significantly higher densities in Poland (four species) and others in Germany (four species). These results might be suggesting that

restored sites in Germany are more typical “wetland” sites, favouring species such as Grey heron and Mallard, while natural baseline sites in Poland favour woodland species such as Treecreeper (Snow *et al.*, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018).

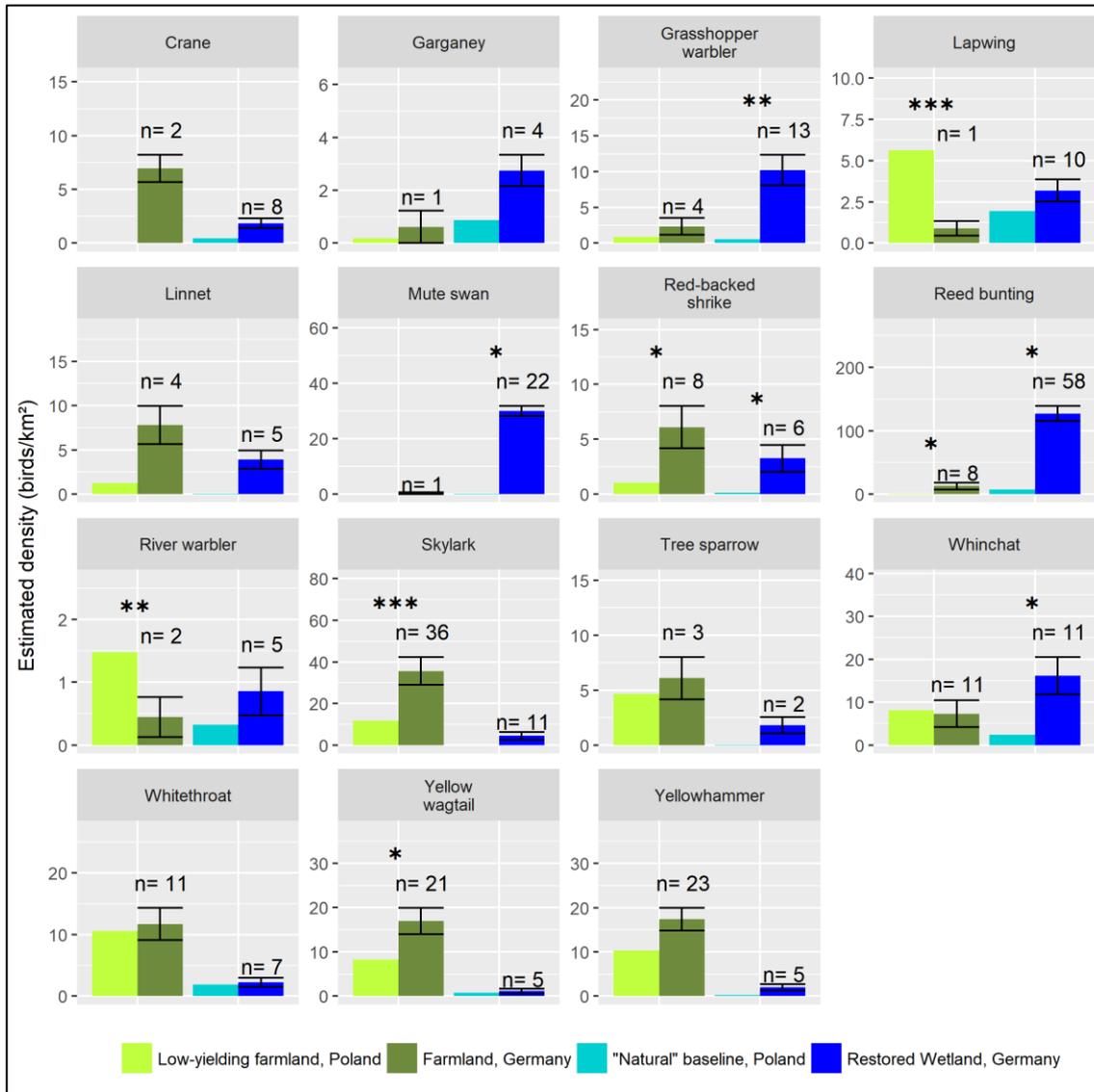


Figure 5.19 – Estimated population density of HNV bird species in farmland (green) and wetlands or natural habitats (blue), in Poland (left) and in Germany (right). Population densities in Poland were estimated using density-yield functions from (Feniuk, 2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland. Population densities in Germany were estimated using quasi-Poisson models. Black lines on German bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus restored wetlands in Germany, and comparing densities in low-yielding farmland in Poland versus farmland in Germany (* p<0.05, ** p<0.01, *** p<0.001).

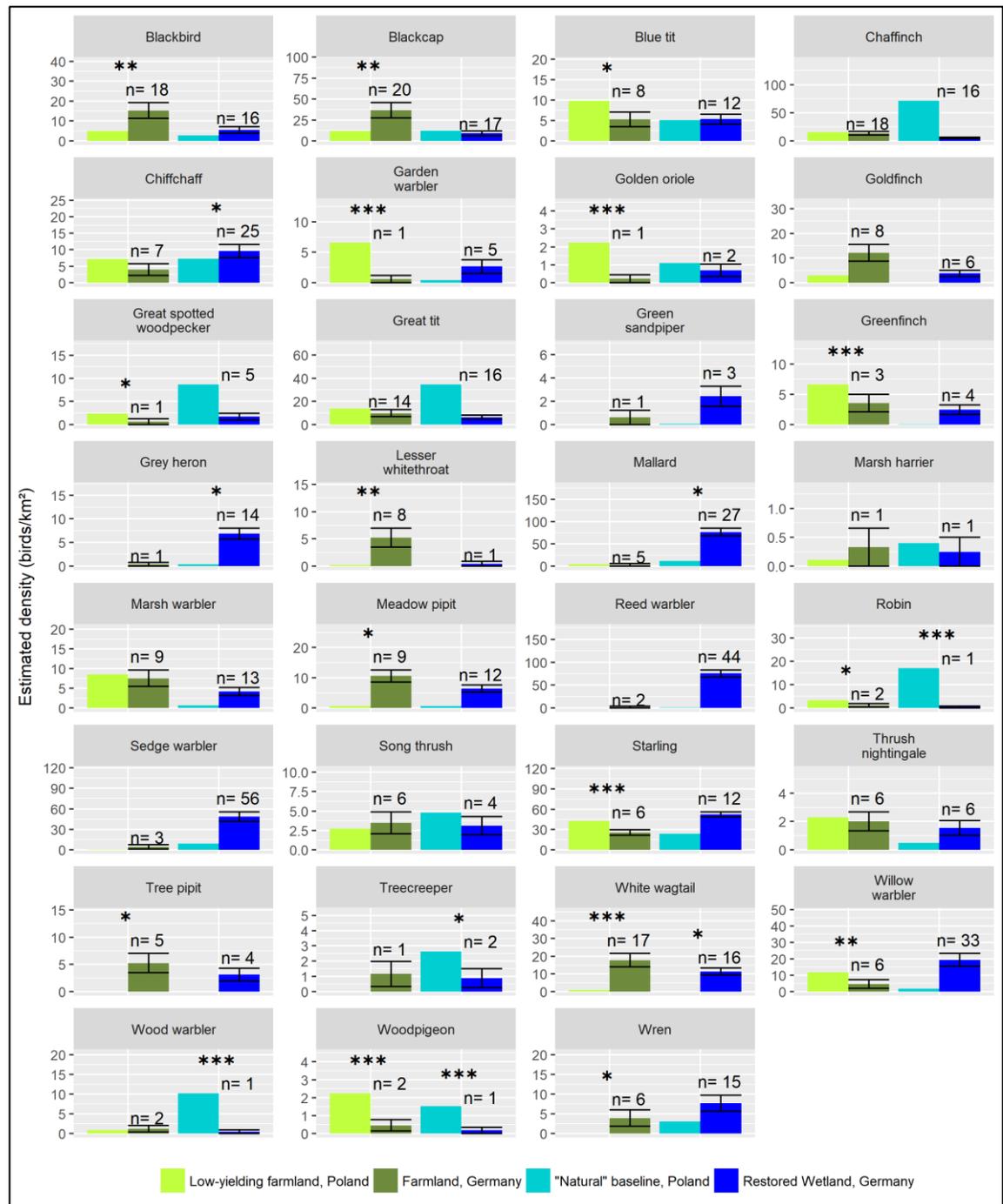


Figure 5.20 – Estimated population density of non-HNV bird species in farmland (green) and wetlands or natural habitats (blue), in Poland (left) and in Germany (right). Population densities in Poland were estimated using density-yield functions from (Feniuk, 2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland. Population densities in Germany were estimated using quasi-Poisson models. Black lines on German bars indicate \pm one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus restored wetlands in Germany, and comparing densities in low-yielding farmland in Poland versus farmland in Germany (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

5.4 Discussion

In this chapter, I looked at a large-scale floodplain restoration project where a large area of floodplain has been rewetted and reconnected to the river. The results suggest that the restoration has been beneficial for bird biodiversity, with many more species having higher population densities in the restored wetland than the surrounding, non-restored farmland. However, it does not seem to have been quite so valuable for butterflies, with more species having higher densities in the surrounding farmland. Despite this, I would view the results as demonstrating that the restoration project has had a net positive impact on biodiversity within the region. Assuming that the surveyed farmland is typical of farmland in the region more generally, those species which preferred farmland still have ample suitable habitat in the region, while the restoration project has created new habitat which is preferred by other species.

I first characterised the habitats and vegetation structure of the sites, along with the disturbance regime. When I compared the disturbance regimes across habitats, there was surprisingly little difference between restored wetland and non-restored farmland sites, with neither Disturbance PC1 nor PC2 being significantly different between them. Veg.PC1 did not differ significantly either, although in some ways this may be positive for farmland species as it indicates the vegetation structure in the restored wetland is very similar to that of farmland. Flood Risk Score and water depth did differ significantly, with restored sites being higher in both. This indicates that, at the very least, the restoration project has been successful in rewetting the restored areas.

Considering just restored sites (where vegetation is expected to be driven by natural processes rather than human management), unlike in my previous two chapters, there is little evidence that biotic or flood disturbance control the habitat structure. There was a significant relationship between Disturbance PC1 and Veg.PC1, but this showed browsing was more common in closed habitats, the opposite of the hypothesised relationship. This may be explained by browsing animals being more abundant or their signs more obvious in closed habitats. Hunting is permitted at certain times of year within the restored area, and this may mean game species (including deer) are more likely to use more densely vegetated habitats (Laundré, Hernández & Ripple, 2010; Lone *et al.*, 2014). Furthermore, browse damage to shrubs is quite obvious, but grazing on sedges or grasses may be less so. There was no relationship between Disturbance PC2 (which was most strongly associated with signs of wild boar) and Veg.PC1, perhaps because signs of boar

rooting are obvious across a range of habitats (Sandom, Hughes & Macdonald, 2013). I expected the flood regime to have been an important determinant of habitat but there was no correlation between Veg.PC1 and either Flood Risk Score or water depth. This may be explained by the relative recency of restoration. The habitats currently present still reflect historic habitats to some extent and have not had time to fully adjust to the new disturbance regime. Successional changes in vegetation act over long timescales (Clements, 1916), and ongoing changes in abiotic conditions (particularly with regards to soil processes) may mean that an equilibrium state is not achieved for decades or even centuries (Pfadenhauer & Klötzli, 1996; Timmermann *et al.*, 2006; Zak & Gelbrecht, 2007). For example, in certain sites where I recorded trees, many of the trees had died following the restoration, unable to cope with the waterlogged conditions (Figure 5.21). These sites might still have had a high Veg.PC1 score because the trees were still standing, but in the long term these habitats are likely to open up as dead trees fall down. Conversely, many currently open habitats may, in time, develop into wet woodlands (Hughes *et al.*, 2012).



Figure 5.21 – Dead trees still standing following restoration.

I once again found clear evidence that species of both bird and butterfly respond to differences in vegetation structure, with some species preferring open habitats and others

closed. These preferences corresponded well to the species' reported habitat preferences, giving me confidence in the reliability and accuracy of my surveys (Snow *et al.*, 1998; van Swaay *et al.*, 2006; Svensson *et al.*, 2009; Tolman & Lewington, 2009; del Hoyo *et al.*, 2018). However, it is also evident that vegetation structure alone is not a complete description of habitat, especially for butterflies which depend on certain flowers for nectar and the presence of suitable larval host plants. While many species of butterfly prefer open habitats with lots of sunlight, this may be negated to some extent by the fact that many of the open habitats surveyed in this region were open water, or reedbeds or sedge meadows which are dominated by wind-pollinated species.

As in previous chapters, it made little difference whether I considered Veg.PC1 or mean vegetation height as the metric of habitat and vegetation structure. The mean height of the vegetation is strongly correlated with Veg.PC1, and so the observed response of species was similar for both metrics. Mean vegetation height has the benefit of being simple to understand and easily measured in the field, where as Veg.PC1 is a derived metric that combines numerous measurements of the habitat and vegetation structure. Some aspects of the habitat type would not be captured by mean vegetation height alone. For example, a wet sedge meadow and a dry hay meadow might have similar vegetation heights but have ecologically important differences. However, both the results of the PCA and the modelled effect on species' population densities demonstrate that mean vegetation height is nonetheless one of the most important explanatory variables.

HNV species are a conservation concern across Europe due to the intensification and abandonment of large areas of HNVf (EEA, 2004). Looking at HNV birds, the results are promising. Most species had equal or higher population densities in the restored wetland than the surrounding farmland. Furthermore, by comparison to Poland, there was little evidence that this was caused by low densities in the farmland in Germany. Instead, the comparison suggested that some HNV species do genuinely thrive in the restored wetland, and exist at higher population densities than in natural baseline habitats in Poland. However, other species did not benefit from the restoration, highlighting again the diversity in species' habitat preferences and the need to consider a range of conservation interventions, such as continued agri-environment schemes to support HNV farming, or perhaps other types of rewilding, such as restoring natural fire or grazing regimes (Navarro *et al.*, 2015).

Overall, these results suggest that the restoration has successfully created a healthy wetland and benefitted a suite of wetland-associated species. Furthermore, the fact that some of those species are classified as HNV species supports my hypothesis that some species traditionally associated with HNVf benefit from naturally disturbed habitats, in this case disturbed by flooding.

However, this particular project may be better viewed as habitat creation than restoration, an argument which has been put forward for other restored wet terrestrial ecosystems in Europe and elsewhere (Pfadenhauer & Klötzli, 1996; Toth, 2017) and is supported by studies of nutrient cycling and soil processes (Schindler, Behrendt & Müller, 2003; Zak & Gelbrecht, 2007), and beetle and plant communities in rewetted areas along the Peene (Görn & Fischer, 2015), all of which demonstrated differences between restored sites and reference conditions for natural floodplains. Decades of agricultural use prior to restoration has led to soil compaction and soil erosion. As such, the land is currently lower than it would have been naturally, leading to deeper standing water (Timmermann *et al.*, 2006; Zak & Gelbrecht, 2007). In time, the soil will be regenerated, although this is a very slow process, potentially taking thousands of years (Belyea & Clymo, 2001; Bent & Tauber, 2008; Bain *et al.*, 2011). The main river channel remains regulated and channelized, and unable to exhibit natural dynamic processes. These factors all highlight that restoration projects can face major challenges in attempting to restore pristine habitats. Furthermore, the restored sites are likely to continue changing, particularly as old trees fall down and new vegetation grows, and also as a result of slow changes in soil structure and nutrients (Timmermann *et al.*, 2006; Zak & Gelbrecht, 2007). As the abiotic environment changes, so too will the biodiversity. However, appropriate species planting and management of the water table could accelerate the restoration of a more natural floodplain system, particularly during the early stages of the project (Zerbe *et al.*, 2013).

Importantly, this project demonstrates what could be accomplished elsewhere in Europe. Nothing about the Peene or its surroundings is particularly unusual: it is a typical lowland river, surrounded by agriculture and small towns. As such, it is a good example of what could be achieved in other places, and how the barriers to carrying out a restoration project are not insurmountable. While I have focused on biodiversity, the restoration project has also brought economic benefits, with eco-tour operators becoming established, offering wildlife watching trips along with other recreational activities on the river (Abenteuer Flusslandschaft, 2018).

5.5 Conclusion

This chapter looked at a large scale and ambitious restoration project, and showed that the restoration has had significant effects on both biodiversity and habitats. Moreover, the effects on biodiversity appear to include supporting high population densities of HNV bird species within the restored floodplain. My work in a natural floodplain in Ukraine (Chapter 3) indicated that natural floodplains can support HNV species; this chapter extends that to demonstrate that restoration of floodplains (and the associated disturbance regime) can be successful in recreating habitats for HNV species.

It is also important to note that this restoration project was carried out in a modern European country, with intensive agriculture and dense human settlement. While the exact political and environmental landscape is unique in each situation, the context of this region is somewhat similar to many lowland rivers in western Europe. This offers hope that similarly ambitious projects could be carried out widely across western Europe, with correspondingly widespread benefits to biodiversity, including HNV species threatened by agricultural abandonment and intensification.

However, the results also show that not all species benefitted from the restoration, including several HNV species. Flood-disturbed landscapes, and floodplain restoration, therefore are not a panacea for conservation of HNV species. Other strategies need to be considered, whether this be other forms of rewilding (such as restoring fire or grazing regimes), or agri-environment schemes to promote the maintenance of HNV farming systems.

One question that remains is why species show such diverse responses. Are there traits which determine how species relate to environmental gradients? In the next chapter, I examine this question by using data from all three of my field studies carrying out an analysis to link species' traits to environmental variables.

6 ASSOCIATIONS BETWEEN FUNCTIONAL TRAITS AND ENVIRONMENTAL VARIABLES

6.1 Introduction

In the previous chapters I have shown that different species have different habitat preferences and respond differently to restoration. This is to be expected, as it is a fundamental principal of ecology that different species have evolved to occupy different niches (Darwin, 1859; Elton, 1927). On the other hand, distantly related species may evolve convergently in order to take advantage of similar opportunities (Owen, 1848).

This leads naturally to the question of whether it is possible to identify traits which are associated with particular niches and hence show similar patterns of response to environmental gradients (McGill *et al.*, 2006). Such a question is of great interest in terms of pure ecology, but also for conservation in the Anthropocene (Corlett, 2015) as ecosystems with novel combinations of species become the norm and where conservation may increasingly involve creating novel ecosystems or the use of species substitution (Donlan *et al.*, 2006; Thomas, 2011; Svenning *et al.*, 2015; Bowman *et al.*, 2017; Hobbs *et al.*, 2018). At least one case study has already demonstrated that functional traits can be useful in guiding restoration projects (Sandel, Corbin & Krupa, 2011).

Functional traits have also been used extensively in risk assessment and identifying which species are most likely to be vulnerable to environmental change, including habitat fragmentation (Barbaro & Halder, 2009; Farneda *et al.*, 2015), disturbance (McIntyre *et al.*, 1999; Williams *et al.*, 2010; Mouillot *et al.*, 2013), and climate and land use change (Aguirre-Gutiérrez *et al.*, 2016). Diversity of functional traits across species may also be important for ecosystem processes (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Cadotte, Carscadden & Mirotnick, 2011; Díaz *et al.*, 2013).

Previous work has identified associations between functional traits and environmental gradients in a range of taxa, including birds (Henry & Cumming, 2017) and butterflies (Aguirre-Gutiérrez *et al.*, 2017). Such analysis may also extend the applicability of this thesis into other regions with broadly similar ecologies but different species pools, by helping to identify which sorts of species might benefit, and which sorts of species might lose out from floodplain restoration. However, it has been suggested that associations found might be context-specific, and not scalable to whole regions or biomes (Hatfield *et al.*, 2018).

In this chapter, I look for associations between functional traits of birds and butterflies and environmental variables across all my study regions. Finding such associations might provide insight into why some species thrived in wetlands (restored or otherwise) while others did not, and identify traits of species which are most likely to benefit from restoration. In the cases of species which had low population densities in wetlands, it might be possible to identify what sort of habitats those species would benefit from, and hence suggest alternative conservation strategies. I have focused on associations between species' traits and habitats rather than disturbance, as I believe species respond primarily to habitat, and respond to disturbance only indirectly via the impact of disturbance on habitats.

6.2 Methods

Trait-based analysis has received renewed attention in recent years (McGill *et al.*, 2006) and is still an advancing field. Two statistical approaches were originally developed: the RLQ method (Dolédec *et al.*, 1996) and the fourth-corner method (Legendre, Galzin & HarmelinVivien, 1997). More recently, methods have been developed which combine both these approaches (Dray *et al.*, 2014). The RLQ method involves an ordination of each of three tables: Table R (environmental characteristics of sites), Table L (species' distribution across sites) and Table Q (species' traits). The combined ordination allows elements from each table to be plotted in the same ordination space, so that elements which tend to be associated with each other are positioned close together within this ordination space.

The fourth-corner method uses the same three tables as matrices to estimate the "fourth-corner" matrix **D**, which contains associations between species' traits and environmental variables (Legendre *et al.*, 1997). Data are first standardised, with

quantitative variables transformed to a mean of zero and variance of one, while categorical variables are expanded into a series of binary variables. Set out as a matrix algebra problem:

$$\begin{bmatrix} \mathbf{L} (k \times m) & \mathbf{Q} (k \times n) \\ \mathbf{R} (p \times m) & \mathbf{D} (p \times n) \end{bmatrix}$$

(with some number k species, each described by n traits and observed across m sites described by p environmental variables), solving for \mathbf{D} is straightforward:

$$\mathbf{D} = \mathbf{RL}'\mathbf{Q}$$

which gives an estimate of the parameters linking species' traits to environmental variables. However, on their own these parameters are uninformative; it is necessary to determine which parameters are significant through appropriate testing. Legendre *et al.* (1997) proposed to test this through a bootstrapping approach. The null hypothesis is that species are distributed at random across locations, or equivalently that where a species was observed was due to chance alone. From the latter formulation, it can be inferred that all permutations of Table L would be equally likely under the null hypothesis. Therefore, a null distribution of the parameters in \mathbf{D} can be estimated by repeatedly taking random within-row permutations of Table L and using them to calculate \mathbf{D} . The parameters estimated from the data can then be compared to this random distribution.

The RLQ and fourth-corner approaches both have advantages and disadvantages. Like other forms of ordination, the RLQ approach can be considered a descriptive statistical approach; that is to say, it aims to make patterns in the data more easily identified and interpreted. However, it cannot be used to estimate the likelihood of those patterns occurring by chance, and therefore cannot be used in hypothesis testing. The fourth-corner method does produce robust probabilities of parameter estimates and therefore can be used to identify statistically significant relationships. However, by only yielding the results of pairwise associations between traits and environmental variables, other patterns in the data are lost. For example, species which have similar traits will tend to be clustered together in the ordination space following the RLQ approach, but this information is not available from the fourth-corner method.

I followed the protocol outlined in Dray *et al.* (2014), carrying out RLQ analysis and fourth-corner analysis separately before combining the results. This allows the data to be visualised in an easily understandable way (as per the standalone RLQ analysis) but with

significant associations highlighted, determined using the fourth-corner method. Analyses were carried out using the *ade4* package (Dray & Dufour, 2007) in R Version 3.4.1 (R Core Team, 2017).

6.2.1 Data collection

For Table L (associations between species and sites) and Table R (environmental variables in each site), I used the combined data collected across all three study regions. Full details on data collection are given in the preceding chapters. The environmental data table combined both habitat type and vegetation structure. To reduce the number of variables, certain habitats which accounted for small proportions of the total area and/or were only recorded in one field season were excluded. These habitats were: Garden, Gravel, Heath, Hedge, Mixed wood, Orchard, Reed/scrub, Sedge/reeds, Trees, Vineyard, Wood/scrub, Wet meadow and Wet wood. In total, these excluded habitats accounted for 12.2% of the surveyed area. Furthermore, Pine plantation and Pine wood were merged into a single category “Pine”. This left 10 habitat classes: Arable, Deciduous plantation, Infrastructure, Water, Deciduous wood, Meadow, Reedbed, Scrub, Sedge meadow and Pine.

Dimensionality of data on vegetation structure was reduced by carrying out a PCA on all vegetation structure variables except mean height (i.e. mean percent cover at each height class, standard deviation in cover at each height class, and standard deviation in height; see Chapter 2 for details). The first axis of this PCA (see below) and mean height were then used in the analysis, along with the habitat variables.

As I did not gather any data on species’ traits (Table Q) in the field, I obtained these data from other sources. For birds, I used the Elton Traits database (Wilman *et al.*, 2014) as the basis of my trait table. This database has complete trait profiles for all 9,993 species of bird recognised at the time (see reference for details of taxonomy used and original data sources). The traits used (and codes displayed in figures) are given in Table 6.1. Species that were entirely aerial feeders according to the Elton Traits database were excluded, as they are unlikely to be strongly influenced by the characteristics of the vegetation beneath them (only the Swift in my data). The taxonomy used in the Elton Traits database does not distinguish Hooded crow *Corvus cornix* from Carrion crow *Corvus corone* (unlike my field records) so for this analysis all records of Hooded crow were treated as Carrion crow. This lumping is consistent with the latest taxonomy (del

Hoyo *et al.*, 2016), and in none of my field regions did I observe both Hooded crow and Carrion crow. In presenting results (below), species names were taken from the database, broadly following the Birdlife V3 Checklist (BirdLife International, 2010). This differs from the names used throughout the rest of this thesis (British common names).

For butterflies I assembled my own trait database (Table 6.2). Wingspan (mm), flight period (weeks), voltinism, diet generality, habitat aridity and habitat closedness were all taken from Tolman & Lewington (2009). Habitat breadth was extracted from van Swaay *et al.* (2006) as the count of the number of Corine biotopes listed as important for each species (so a higher number indicates a generalist species). These traits are frequently used for butterflies, as they are related to key aspects of the butterflies' life histories, such as dispersal, reproduction, habitat use and diet (Díaz *et al.*, 2013; WallisDeVries, 2014; Aguirre-Gutiérrez *et al.*, 2016; Aguirre-Gutiérrez *et al.*, 2017).

Table 6.1 – Bird traits used for analysis, based on Elton Traits database (Wilman et al., 2014). The short code is used in later figures.

Trait Description	Details	Short Code	Justification
Dietary preference classification	Factor with levels <ul style="list-style-type: none"> - Invertebrate - Omnivore - Plant/Seed - Vertebrates/Fish/Scavenging (A fifth category, “Fruit/nectar” was absent from my data)	Diet-5Cat	Different food sources may be more or less abundant in certain habitats
Foraging Strategy	Percent score in each of the following: <ul style="list-style-type: none"> - Water (above and below surf) - Ground/understory - Mid to high levels in trees or high bushes, but below canopy - Canopy - Aerial 	ForStrat.water ForStrat.ground ForStrat-midhigh ForStrat-canopy ForStrat-aerial	Foraging strategy requires appropriate vegetation structure
Body mass	Body mass in grams	BodyMass-Value	Larger species tend to have smaller populations, slower life histories and larger home ranges (Meyer <i>et al.</i> , 2008) and so may be more sensitive to habitat.

Table 6.2 – Butterfly traits used for analysis, extracted from van Swaay *et al.* (2006) and Tolman & Lewington (2009).

Trait	Description	Details	Justification
Wingspan	mm		Related to foraging and/or dispersal
Voltinism		1 = univoltine 2 = bivoltine 3 = trivoltine or polyvoltine	Related to degree of habitat specialisation
Diet generality		1 = single larval host plant (LHP) species 2 = several LHP species within one family 3 = several LHP species across more than one family	Related to degree of habitat specialisation
Habitat aridity		Ranked from 1 = prefers very damp habitats to 4 = prefers very dry habitats	Related to habitat preference
Habitat closedness		Ranked from 1 = prefers very open habitats to 4 = prefers closed habitats	Related to habitat preference
Habitat breadth		Number of Corine biotopes listed as important for each species, extracted from (van Swaay <i>et al.</i> , 2006)	Related to degree of habitat specialisation

6.2.2 Analysis

For the RLQ analysis, I first carried out Correspondence Analysis (CA) of the species-site table (Table L). CA is a form of ordination, similar to PCA, but which can be applied to categorical data (Sourial *et al.*, 2010; Šmilauer & Lepš, 2014). The result is an ordination table indicating the proportion of variance in species-site relationships explained by each species and each site. Next I carried out a PCA of environmental variables in each site (Table R), weighting sites using the site weights from the Correspondence Analysis. As seen in previous chapters, a PCA uses linear combinations of variables to maximise the variation between sites which is explained. The additional step of weighting sites combines this step with the previous step, such that the resulting ordination separates sites by variation in both environmental variables and species' distributions. I then carried out a PCA of the species' trait table (Table Q), weighting species using the species' weights from the CA of Table L. As before, the weighting means that the resulting ordination separates species which both vary most in their traits and simultaneously vary most in their distribution among sites. I then carried out the RLQ

analysis to combine the results from the three previous analyses into a single set of ordination tables. The result is that species, traits and environmental variables can all be plotted within the same ordination space, with axes chosen to maximise the proportion of variance across all three tables explained. Note that, for clarity of presentation, the scale used for displaying results varied across species, traits and environmental variables; the scale of each figure is given so that they can be directly compared.

I then carried out the fourth-corner analysis as described above. Once the data tables were appropriately prepared, all steps of the analysis were carried out using the *fourthcorner* function within the *ade4* package (Dray & Dufour, 2007). As significance is estimated using a bootstrap-type approach, a high number of random permutations is needed to ensure accurate estimation of probabilities; I used 49,999.

Finally, I combined the results from both the RLQ and fourth-corner analyses, which allows traits and environmental variables to be shown on a biplot with significant associations highlighted.

6.3 Results

6.3.1 Vegetation structure PCA

Figure 6.1 shows the results of the PCA on vegetation structure variables (excluding mean height). The first component explained 61.0% of the variance in the data, while the second only explained 28.1%, and further components less still. The first axis is clearly a gradient in vegetation height, with mean percentage cover in each of the four height classes being positively weighted on this axis. This therefore indicates a gradient from open to closed habitats. The second axis may pick out degree of variability, as standard deviation in percentage cover in each of the four height classes are all negatively weighted on PC2. This axis therefore distinguishes, to some extent, sites which have a uniform but intermediate height from sites with a mixture of patches of high and low vegetation, giving an intermediate mean but high standard deviation. However, looking at the spread of study sites, the majority lie along a downwards-pointing arc, such that most sites which are intermediate on PC1 have negative PC2 scores. As such, and given the much lower explanatory power of PC2 compared to PC1, PC2 was not been used for further analysis.

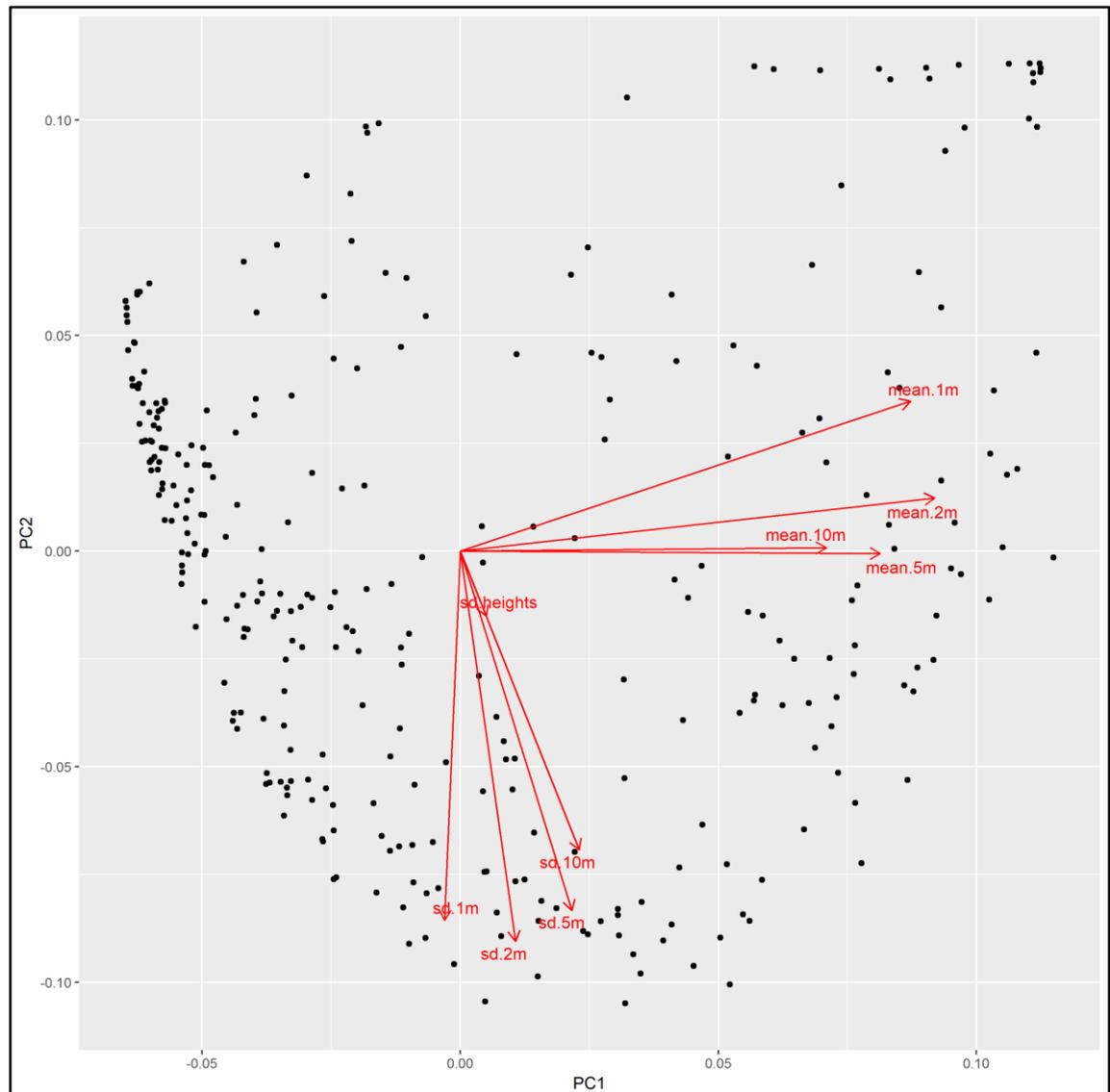


Figure 6.1 – Axes 1 and 2 of Principal Components Analysis on habitat and vegetation data. Length and direction of red arrows indicate the weightings of each habitat variable. Black dots indicate scores of study site.

6.3.2 Birds

The RLQ analysis allowed patterns to be observed by carrying out an ordination across all three data tables (species by site, environmental variables by site and traits by species). The following three figures (Figure 6.2, Figure 6.3 and Figure 6.4) plot bird species, environmental variables and bird species' traits on the same axes.

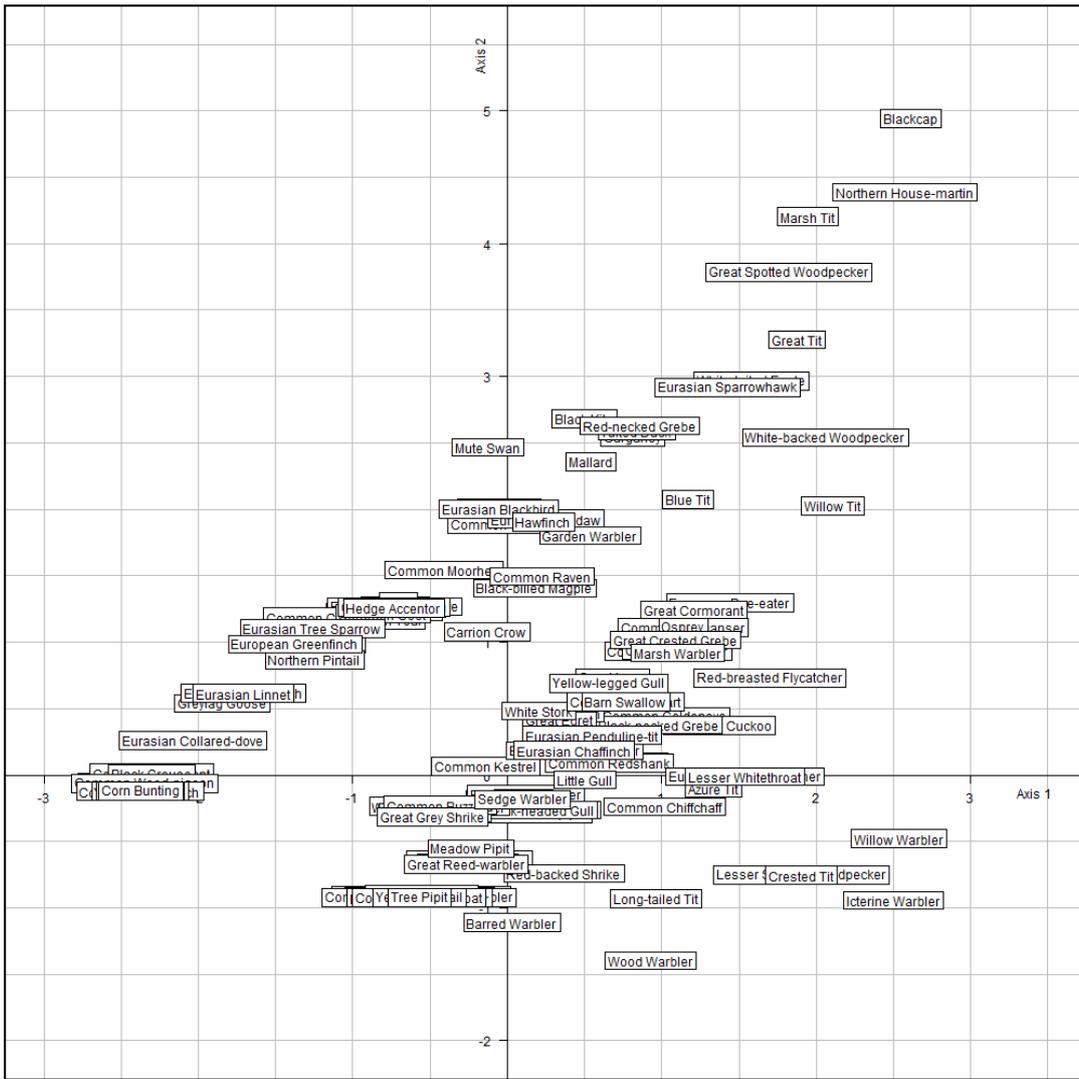


Figure 6.2 – Bird species plotted on the first two axes resulting from RLQ analysis.

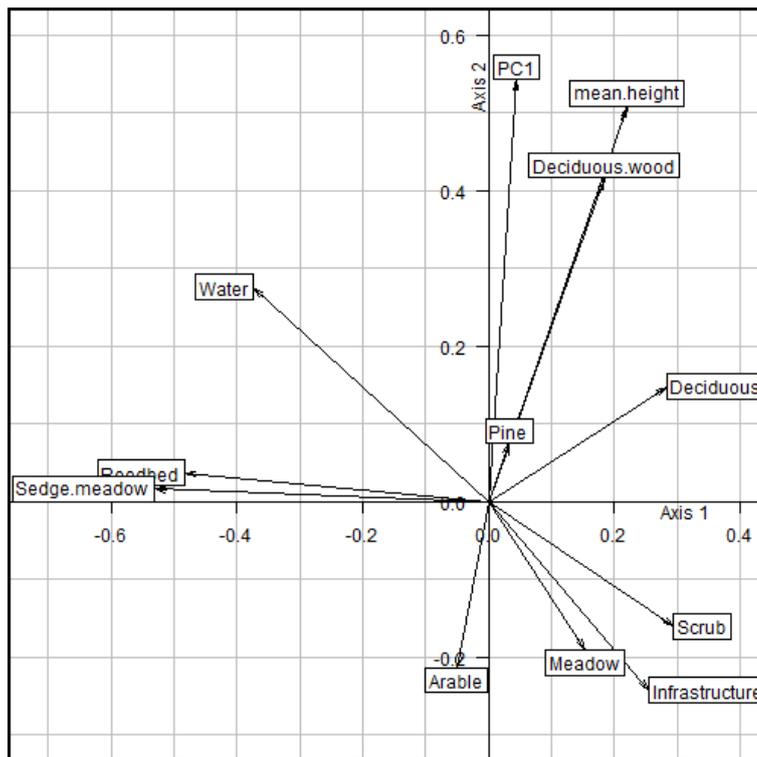


Figure 6.3 – Environmental variables plotted on the first two axes resulting from RLQ analysis.

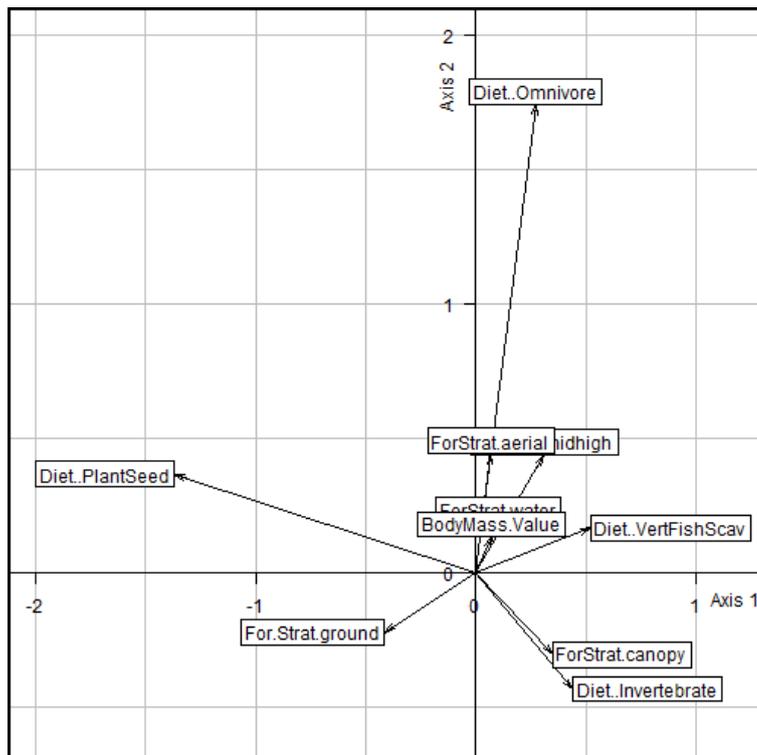


Figure 6.4 – Bird traits plotted on the first two axes resulting from RLQ analysis.

Species, environmental variables and species traits which have similar scores on the two axes shown (i.e. appear in similar positions across the three figures) tended to be associated with each other. To illustrate this, the top-right corner shows several bird species (for example Blackcap, Great spotted woodpecker and Great tit) were associated

with high deciduous woodland and mean height scores (and negatively associated with high arable scores). These species were also positively associated with the trait *For.Strat.midhigh* (i.e. foraging in mid to high levels in trees or high bushes (2m upward), but below the canopy) and negatively with *For.Strat.ground* (i.e. ground foraging strategy). The centre-bottom of the figure contains several farmland birds, such as Meadow Pipit and Red-backed shrike, and shows them to be positively associated with arable and meadow habitats, and negatively associated with PC1 (which, as described above, ascribed more positive scores to more closed vegetation structures, so this indicates that those species prefer open habitats). Furthermore, these species (and habitats) are strongly negatively associated with an omnivorous diet, and slightly positively associated with a ground foraging strategy and an insectivorous diet.

Table 6.3 shows the parameter values estimated by the fourth-corner method, showing associations between species' traits and environmental variables. Overall, one significant relationship was found – the trait “*For.Strat.ground*” (ground foraging strategy) was negatively associated with the habitat variable “Deciduous plantation”.

The combined approach plots species' traits and environmental variables in the same ordination space, with significant associations highlighted. This is shown for birds in Figure 6.5.

Table 6.3 – Parameter estimates of strength of association between butterfly species' traits and environmental variables. Significant terms ($p < 0.05$) are shown in **bold** and cells shaded to indicate the direction of the association. Red shaded cells indicate a positive association, while blue indicates a negative association.

		Species' Traits									
		Diet Category				Foraging: water	Foraging: ground	Foraging: mid-height	Foraging: canopy	Foraging: aerial	Body mass
		Invertebrate	Omnivore	Plant/ seed	Vertebrate/ Fish/ Scavenger						
Environmental Variables	Mean height	0.555	0.134	0.194	0.094	0.047	-0.1	0.167	-0.041	0.13	0.02
	Arable	0.512	0.085	0.323	0.075	0.007	0.013	-0.07	0.032	-0.078	0.02
	Deciduous plantation	0.551	0.188	0.143	0.108	0.051	-0.104	0.069	0.051	0.031	0.02
	Infrastructure	0.613	0.065	0.191	0.099	-0.021	-0.019	0.008	0.068	-0.025	0.02
	Water	0.201	0.081	0.634	0.04	-0.006	0.068	-0.002	-0.124	0.058	0.02
	Deciduous wood	0.571	0.116	0.215	0.08	0.051	-0.092	0.117	-0.017	0.095	0.02
	Meadow	0.545	0.085	0.279	0.08	-0.033	-0.013	-0.011	0.089	-0.031	0.02
	Reedbed	0.055	0.048	0.825	0.025	-0.025	0.114	-0.079	-0.108	-0.007	0.02
	Scrub	0.688	0.057	0.101	0.12	-0.007	-0.037	0.031	0.057	-0.006	0.02
	Sedge meadow	0.057	0.029	0.839	0.019	-0.039	0.131	-0.084	-0.112	-0.012	0.02
	Pine	0.216	0.474	0.042	0.268	0.021	-0.021	0.01	-0.005	0.015	0.02
	PC1	0.555	0.13	0.195	0.092	0.058	-0.073	0.128	-0.076	0.12	0.02

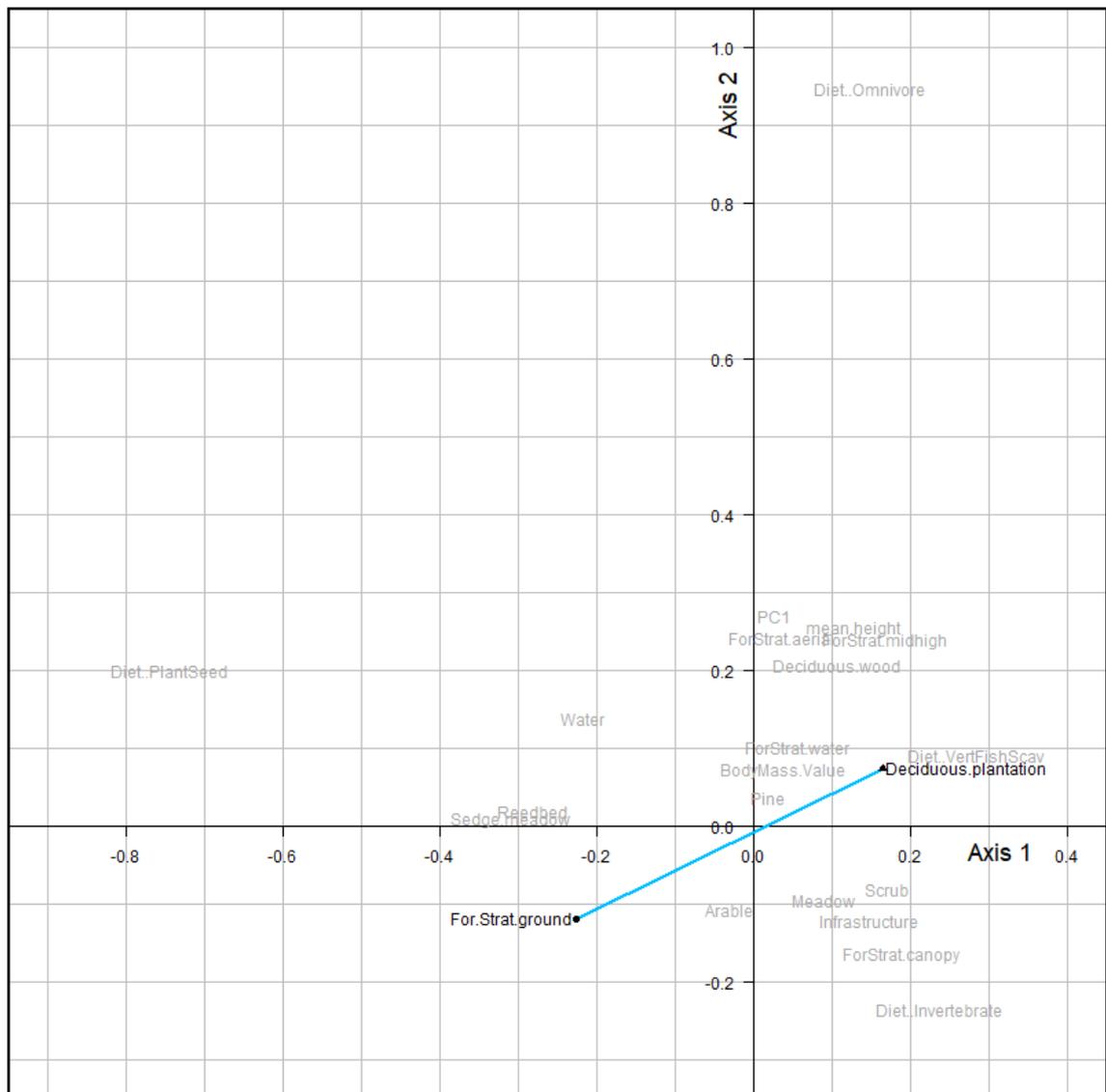


Figure 6.5 – Combined RLQ and Fourth Corner analysis. Species' traits and habitat variables are plotted in the same ordination space, as calculated using the RLQ method. Significant associations, determined using the Fourth Corner method, are highlighted. Variables connected with a blue line indicate a significantly negative association. Variables not significantly associated with any other are shown in grey.

6.3.3 Butterflies

As with birds, the RLQ analysis allowed me to plot species, habitat variables and species' traits on the same ordination axes (Figure 6.6, Figure 6.7 and Figure 6.8 respectively). The RLQ analysis shows some clear patterns. For example, species in the top-right quadrant (such as Lesser purple emperor and Poplar admiral) are associated with deciduous woodland and scrubby habitats, and have a high habitat closedness score (indicating a preference for closed habitats). The Small heath, to the left on those axis, is strongly associated with meadow habitats and has high voltinism.

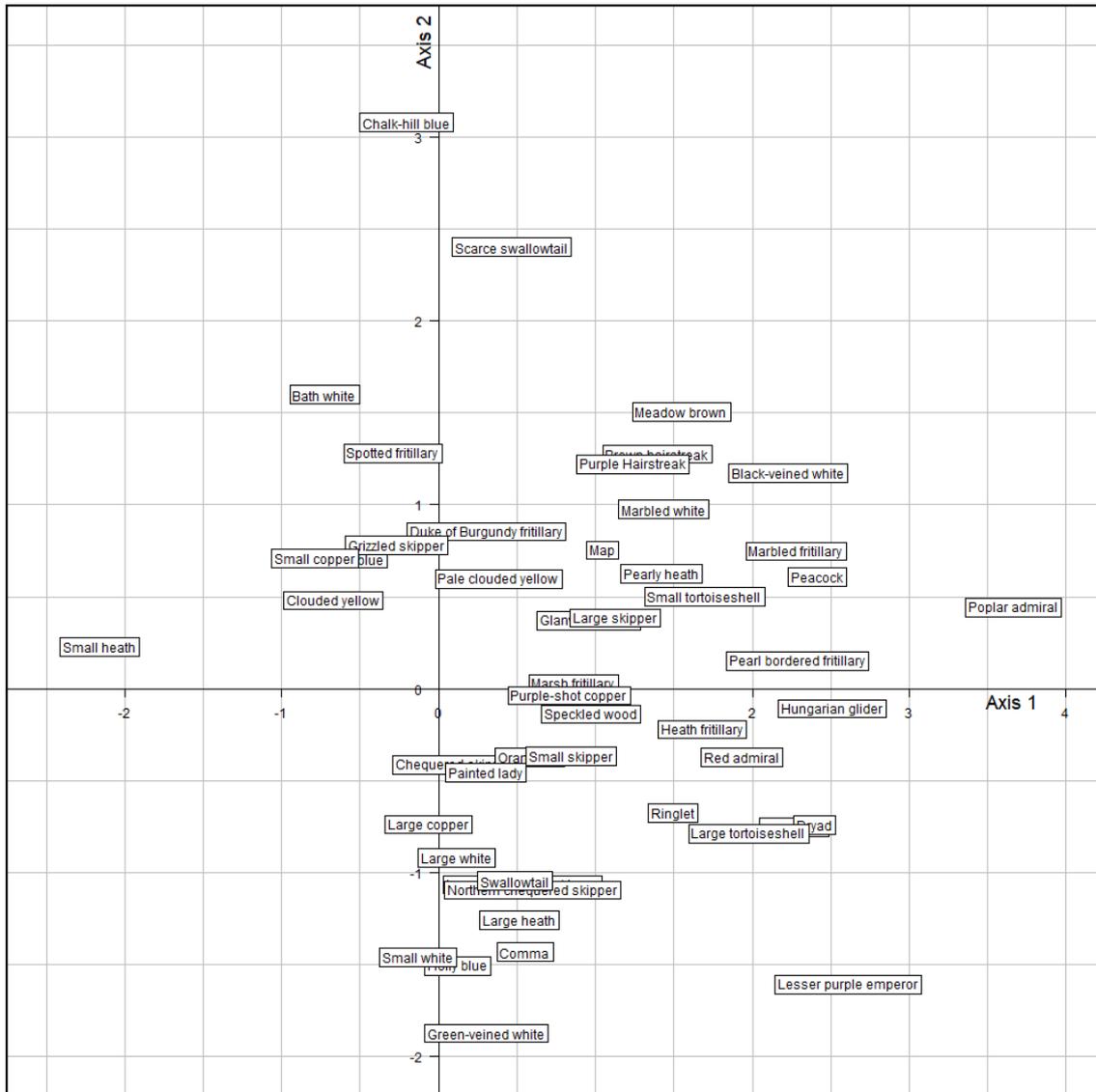


Figure 6.6 – Butterfly species plotted on the first two axes resulting from RLQ analysis.

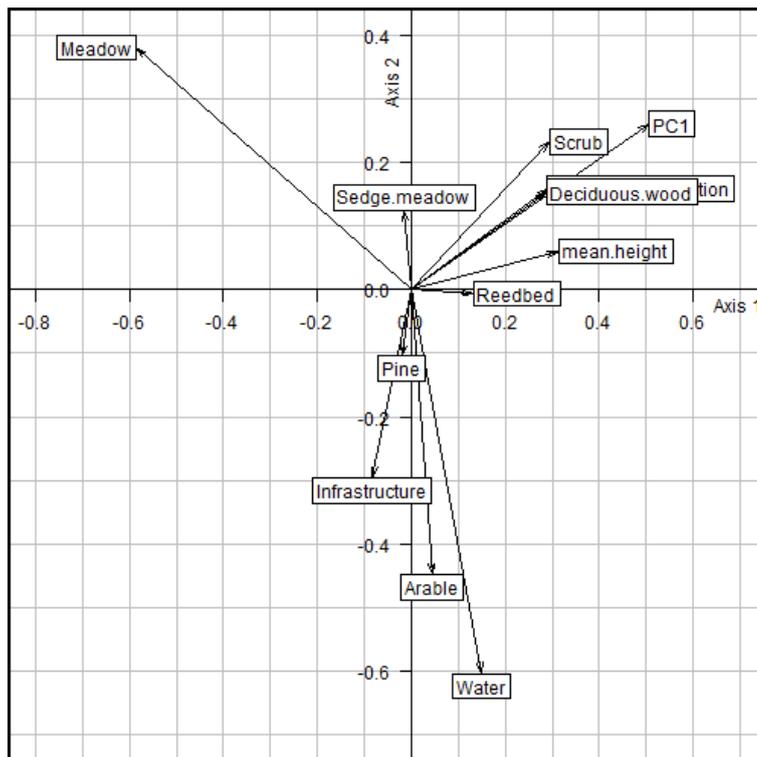


Figure 6.7 – Environmental variables plotted on the first two axes resulting from RLQ analysis.

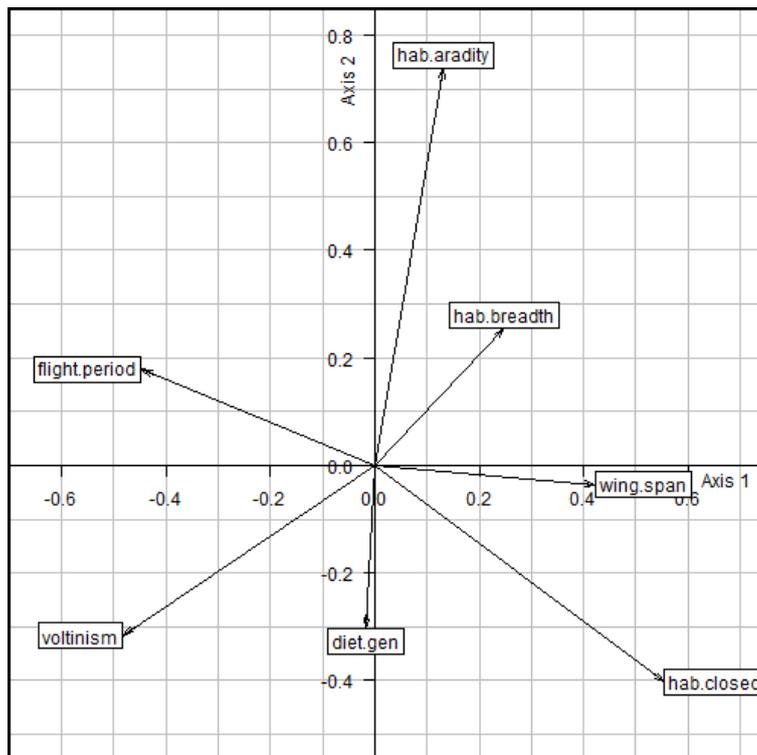


Figure 6.8 – Butterfly species' traits plotted on the first two axes resulting from RLQ analysis.

Table 6.4 shows the parameter values for trait-environment associations as estimated using the fourth-corner approach. There were nine significant relationships. The trait “Habitat closedness” was positively associated with “Mean height”, “Water”, “Deciduous wood” and “PC1” and negatively associated with “Meadow”. With the exception of the

positive association with water, these all make intuitive sense. Species which prefer closed habitats prefer habitats with higher vegetation, which tend to be woodlands not meadows, and PC1 was also correlated with vegetation closedness. The trait “Voltinism” was positively associated with “Meadow” but negatively associated with “Deciduous wood” and “PC1”. This suggests species with greater voltinism (i.e. more generations per year) prefer open habitats such as meadows. Finally, trait “Flight period” was positively associated with “Meadow”, meaning species with a longer flight period prefer meadow habitats. Note that flight period was measured as the total flight period summed across all generations in a year, so there is a positive correlation between voltinism and flight period.

Combining the two approaches, Figure 6.9 shows traits and habitat variables plotted in the same ordination space, with significant associations picked out. From this figure, it is clear that traits and habitat variables which are positively associated tend to appear close together in the ordination space, while negatively associated traits and habitat variables tend to be in the opposite quadrant.

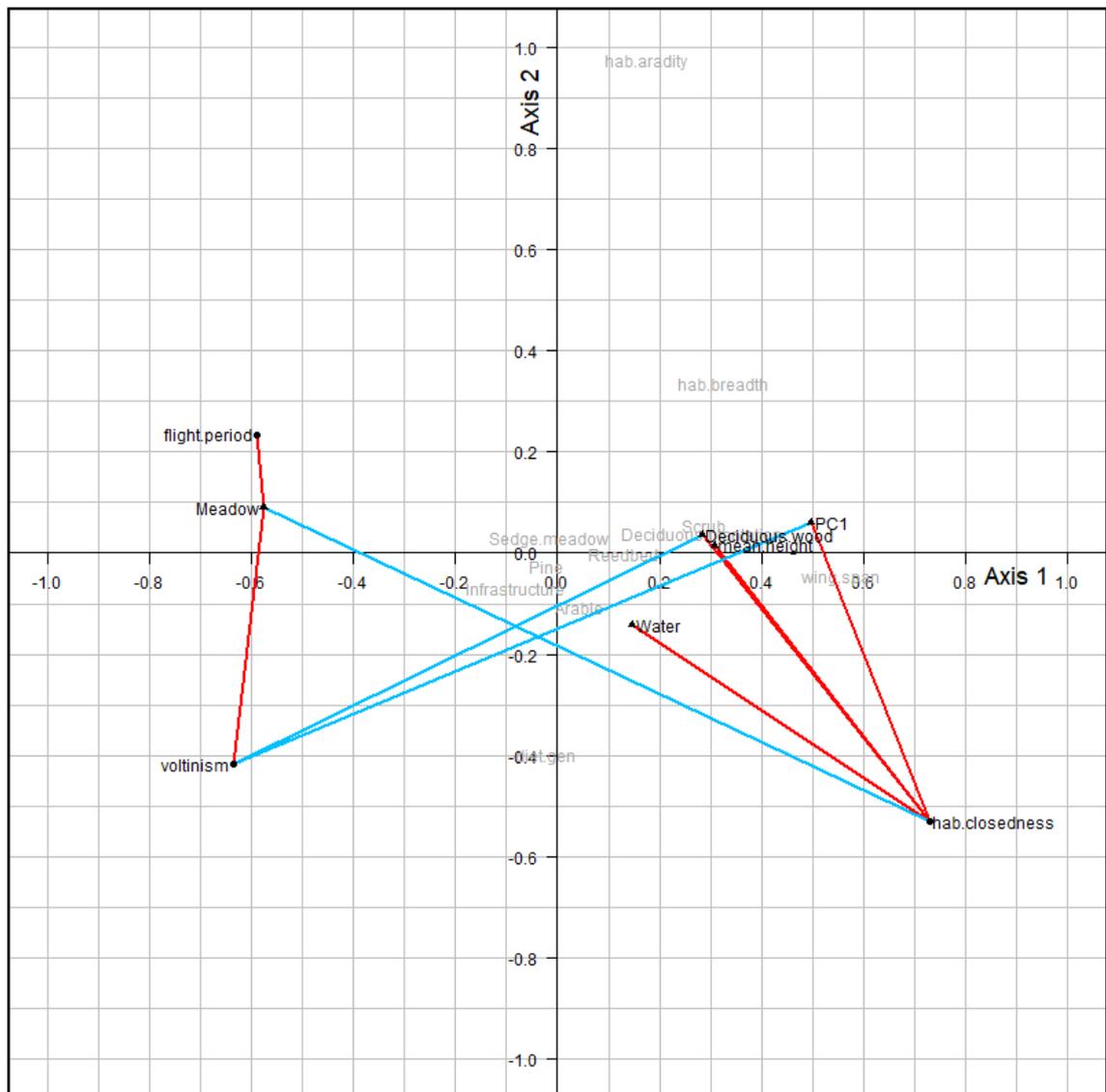


Figure 6.9 – Combined RLQ and Fourth Corner Analysis. Species’ traits and habitat variables are plotted in the same ordination space (as determined using the RLQ method), and statistically significant associations (as determined by the Fourth Corner Analysis) are picked out. Significantly associated traits and habitat variables are linked by a coloured line. Blue lines indicate negative associations. Red lines indicate positive associations. Traits and habitat variables which were not part of a significant association are shown in grey.

Table 6.4 – Parameter estimates of strength of association between butterfly species’ traits and environmental variables. Significant ($p < 0.05$) parameters are shown in **bold** and cells shaded to indicated the direction of the association. Red shaded cells indicate a positive association, while blue indicates a negative association.

		Species' Traits						
		Wing span	Flight period	Voltinism	Diet generality	Habitat breadth	Habitat aridity	Habitat closedness
Environmental Variables	Mean height	0.147	-0.092	-0.128	0.007	0.118	0.059	0.190
	Arable	0.021	-0.052	-0.011	0.045	-0.014	-0.089	0.039
	Deciduous plantation	0.128	-0.126	-0.138	0.012	0.065	0.089	0.144
	Infrastructure	-0.029	0.029	0.075	0.019	-0.016	-0.064	-0.013
	Water	0.069	-0.084	-0.011	0.032	-0.017	-0.068	0.159
	Deciduous wood	0.130	-0.107	-0.159	-0.050	0.015	0.075	0.162
	Meadow	-0.234	0.285	0.262	-0.018	-0.129	0.002	-0.345
	Reedbed	0.068	-0.080	-0.049	-0.035	0.048	-0.003	0.053
	Scrub	0.096	-0.161	-0.177	-0.005	0.122	0.050	0.097
	Sedge meadow	-0.024	0.026	-0.002	0.034	0.073	0.008	-0.024
	Pine	0.004	0.044	0.029	0.094	0.046	-0.005	0.006
	PC1	0.213	-0.199	-0.253	-0.029	0.137	0.117	0.263

6.4 Discussion

The results for both birds and butterflies show similar patterns. The RLQ analyses both showed patterns of associations between species, environmental variables, and species’ traits, which all made intuitive sense given what is known about species’ ecologies (Svensson *et al.*, 2009; Tolman & Lewington, 2009). The Fourth Corner analysis revealed that some of these associations were statistically significant. For birds, only one association was found to be significant, although a higher number of significant associations were found for butterflies. The fact that only one association was found to be significant for birds suggests there may have been limitations in my methods.

There have been several previous studies carrying out trait-based analyses on birds and on butterflies, and using similar traits to those I used (for example Barbaro & Halder, 2009; Aguirre-Gutiérrez *et al.*, 2017; Henry & Cumming, 2017; Hatfield *et al.*, 2018). These published studies often found significant associations, although the environmental variables studies were different in each case. This suggests that, in line with expectations, such relationships are common in nature. However, it is also possible that such relationships are hard to identify, and a lack of published studies which failed to find

significant results may be the result of a publication bias against negative results (Jennions & Møller, 2002).

It is possible that species' responses to habitat varies across their ranges, which would confound my results. I therefore repeated the analyses separately for each study region. To reduce the number of zeros in the data, I then also repeated the analyses across all my study regions but this time only including species observed in all three. In both cases, I found broadly similar results (presented in Appendix 5). Both the RLQ analyses and Fourth Corner analyses found associations between species' traits and environmental variables.

Overall, the clearest pattern emerging from the results presented both here and in Appendix 5 is for a spectrum in species' preferences for open versus closed habitats which is reflected in the species' traits. For example, the only significant result for birds overall was a negative association between a ground foraging strategy and deciduous plantation habitats. In butterflies, a preference for closed habitats was consistently positively associated with the presence of habitats such as deciduous woodland, and negatively associated with the presence of habitats such as meadows.

There are some results which are harder to explain. For butterflies, voltinism was positively associated with meadows and negatively associated with deciduous woodland and PC1, which suggests species with higher levels of voltinism prefer more open habitats. From my data, that result is not readily explicable. Possibly open habitats change more rapidly in response to seasonal weather patterns and therefore there are shorter windows of suitability, favouring species with more rapid generations. In Appendix 5, some of the results seem to oppose what I would expect. For example, looking just at birds in Ukraine there was a positive association between species which forage at mid-height and meadow habitats, despite meadow habitat being inherently unsuitable for these species. This may reflect that, in my field sites, meadows and mid-height vegetation such as scrub tended to be found close together, but it is nonetheless unexpected that the association was statistically significant. Again, this may highlight limitations in my approach.

While overall both the RLQ and Fourth Corner analysis both tended to produce plausible results, that there were relatively few significant results, including a small number of inexplicable results, suggests that there are limitations in my study design for carrying out this type of analysis. Some general limitations are discussed in the next chapter, but

certain limitations may be particularly relevant here. One potential issue is that most species were not observed in most sites, so Table L has many zeros. Such a high number of zeros, across sites with a range of environmental characteristics, may limit the statistical power of the methods used. While methods exist to overcome this for certain types of analysis (Ridout, Hinde & DeméAtrio, 2001; Zuur *et al.*, 2009), to the best of my knowledge none of these can be readily applied here. As with other forms of ordination, RLQ analysis is mathematically designed to maximise the variance explained by the resulting axes and hence any patterns are amplified to the greatest possible extent (Kessell & Whittaker, 1976). As such, RLQ analysis is best used as an exploratory analysis, and further analyses are needed to rigorously test hypotheses (Clarke, Somerfield & Gorley, 2008). However, study design should then be optimised for those subsequent analyses. My studies, being primarily designed to answer other questions, were not optimised for assessing trait-environment interactions.

Another possible limitation is that my habitat and vegetation structure measurements and the subsequent PCA may fail to distinguish sufficiently between habitats which have ecologically important differences. For example, a wet sedge meadow and a dry hay meadow would score similarly across a number of my environmental variables, but sedges are wind pollinated and therefore far less attractive to many species of butterfly than a flower-rich meadow (van Swaay *et al.*, 2006).

However, it is also possible that low number of significant results I found reflects a genuine lack of association between the traits and the environmental variables considered. This lack of association would indicate that any given habitat supports a range of species which differ in their traits. This could reflect a high level of functional diversity, which is an important aspect of biodiversity (Cadotte *et al.*, 2011). Strong associations between traits and habitats may indicate that certain guilds are absent from certain habitats, indicative of low functional diversity and reduced resilience (Cadotte *et al.*, 2011).

6.5 Conclusion

In this chapter, I have looked for associations between species' traits and environmental variables. I found that such associations existed. Overall, the results suggested that certain traits and environmental variables tend to be associated (such as ground foraging birds being associated with arable habitats). Most of the associations found fit within the same

general pattern that species' traits and their habitat preferences fall along a spectrum from open habitat specialists to closed habitat specialists.

However, relatively few associations were significant and some of the results are hard to interpret. This may reflect limitations in the design of my study to detect such associations, or it may reflect functionally diverse ecosystems in which species differ widely in their traits even within individual sites.

7 DISCUSSION AND CONCLUSIONS

7.1 Summary

In this thesis, I have investigated flood-disturbed ecosystems and examined whether such ecosystems are capable of supporting HNV species, and also whether other species benefit from them. Figure 7.1 shows the numbers of species showing a preference for farmland, wetland or neither, across all three of my study regions. For birds, all three regions showed similar patterns. A similar number of HNV bird species preferred the wetland as preferred the farmland; in all regions most species showed no significant preference. Given that these species were all defined by their association with HNV farmland (Paracchini *et al.*, 2008), even showing no significant preference suggests that floodplains are more suitable habitat for those species than previously thought. Looking next at all other bird species, consistently more species preferred the wetland to farmland, across all three study regions. There were also many species showing no preference. For butterflies, however, the results were more mixed across the three study regions. In Ukraine, most species preferred the wetland. However, in both France and Germany, no species preferred the wetland, while some species preferred the farmland (although most species showed no significant preference). This may reflect the wetland in Ukraine being the only truly natural wetland, with a long history of flood disturbance and a wide range of natural habitats. Neither restoration project has completely restored such an ecosystem, although over time, as natural dynamics play out, both restored regions may become closer to this reference state.

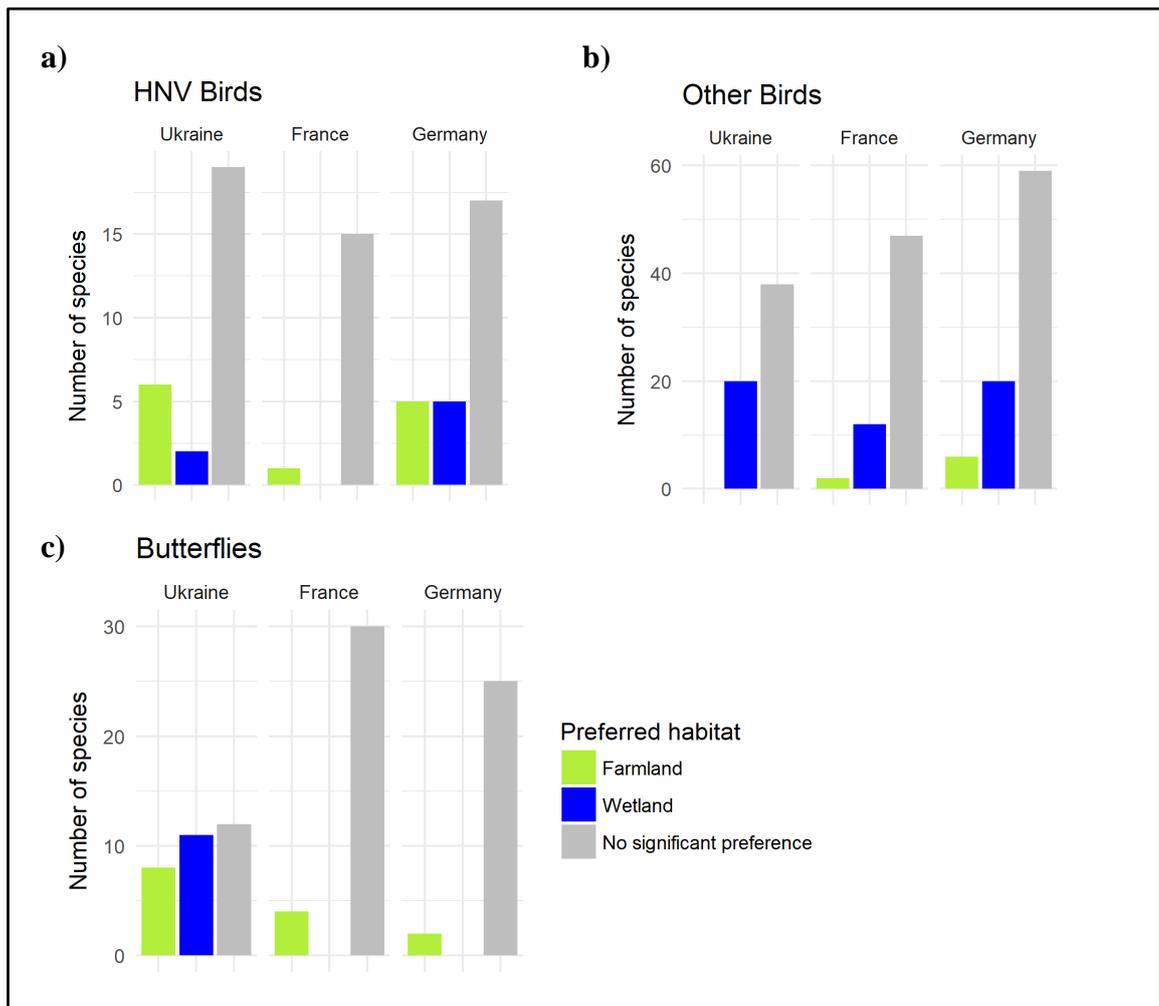


Figure 7.1 – Numbers of species showing significant preferences for farmland and wetland, by country. Panels **a)** HNV birds; **b)** Other birds; **c)** Butterflies.

Across all three regions studied, I think there are some patterns that can be drawn out. I modelled population densities of all the species which I had observed in all three study regions, as a function of region, habitat (agricultural or wetland) and the interaction between region and habitat. In total, there were 38 bird species and 15 butterfly species or species groups which I observed in all my study regions. I was particularly interested in the interaction term, as a significant interaction between region and wetland would indicate that the strength of species' preferences for agricultural or wetland habitats varied across my study regions. For most bird species (32 out of 38) and some butterfly species (6 out of 15), this interaction was significant. Of particular interest are HNV bird species whose preference for wetland differed between the three regions (Figure 7.2). No bird species had particularly high population densities in French wetland; where as several species had high populations in German wetlands (Swallow, Whinchat) or Ukrainian wetlands (Red-backed shrike, Whitethroat). This suggests that both large-scale natural floodplains (such as my Ukrainian study region) and similarly large-scale floodplain

restoration projects (such as my German study region) can both support high population densities of HNV species, but where large-scale flood disturbance is absent (such as my French study region) few HNV species are likely to subsist.

There were also some patterns which were broadly consistent across species (Figure 7.2, Figure 7.3 and Figure 7.4). Looking at farmland in the three regions, more species of both bird and butterfly had particularly high population densities in Ukrainian farmland than in French or German farmland, which supports the conclusion that the farmland in Ukraine was more wildlife friendly and could be considered an example of HNV farmland. The pattern in the wetland sites is less clear. There is some evidence that both Ukraine and France tended to have denser populations of woodland-associated species within the floodplain, such as the Great spotted woodpecker, Nuthatch and Peacock butterfly. German wetland sites tend to support species more closely associated with reed- and sedge-dominated habitats, such as Reed warbler and Water rail. Possibly for the same reason (reeds and sedges are wind-pollinated and thus largely unsuitable for butterflies), German wetlands supported the lowest population densities of several of the butterfly species common to all three regions.

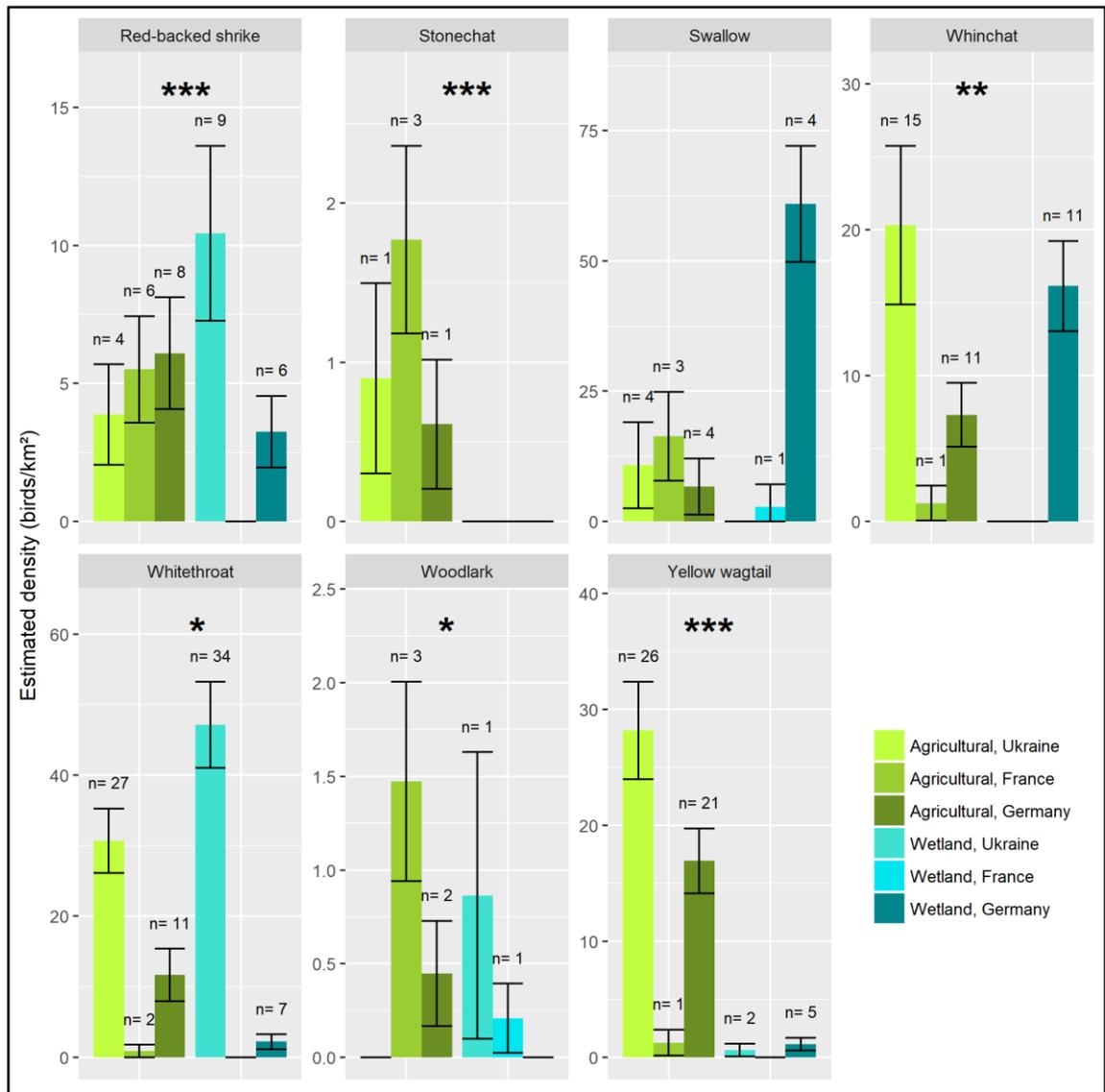


Figure 7.2 – Estimated population densities of all seven HNV bird species that were observed in all three of my study regions, by region and habitat. Population densities were estimated using species-specific GLMs to model total count with a quasi-Poisson error structure, a log link function, region, habitat (agricultural or wetland) and the interaction of region and habitat as explanatory variables, and offset by sampling effort. N values in the figure indicate the number of sites within each region/habitat in which each species was observed at least once. The total numbers of sites surveyed for birds were: Ukraine, wetland = 48; Ukraine, agriculture = 44; France, wetland = 45; France, agriculture = 34; Germany, wetland = 68; Germany, agriculture = 47. Stars indicate significance of the modelled interaction between region and habitat (* p < 0.05, ** p < 0.01, *** p < 0.001).

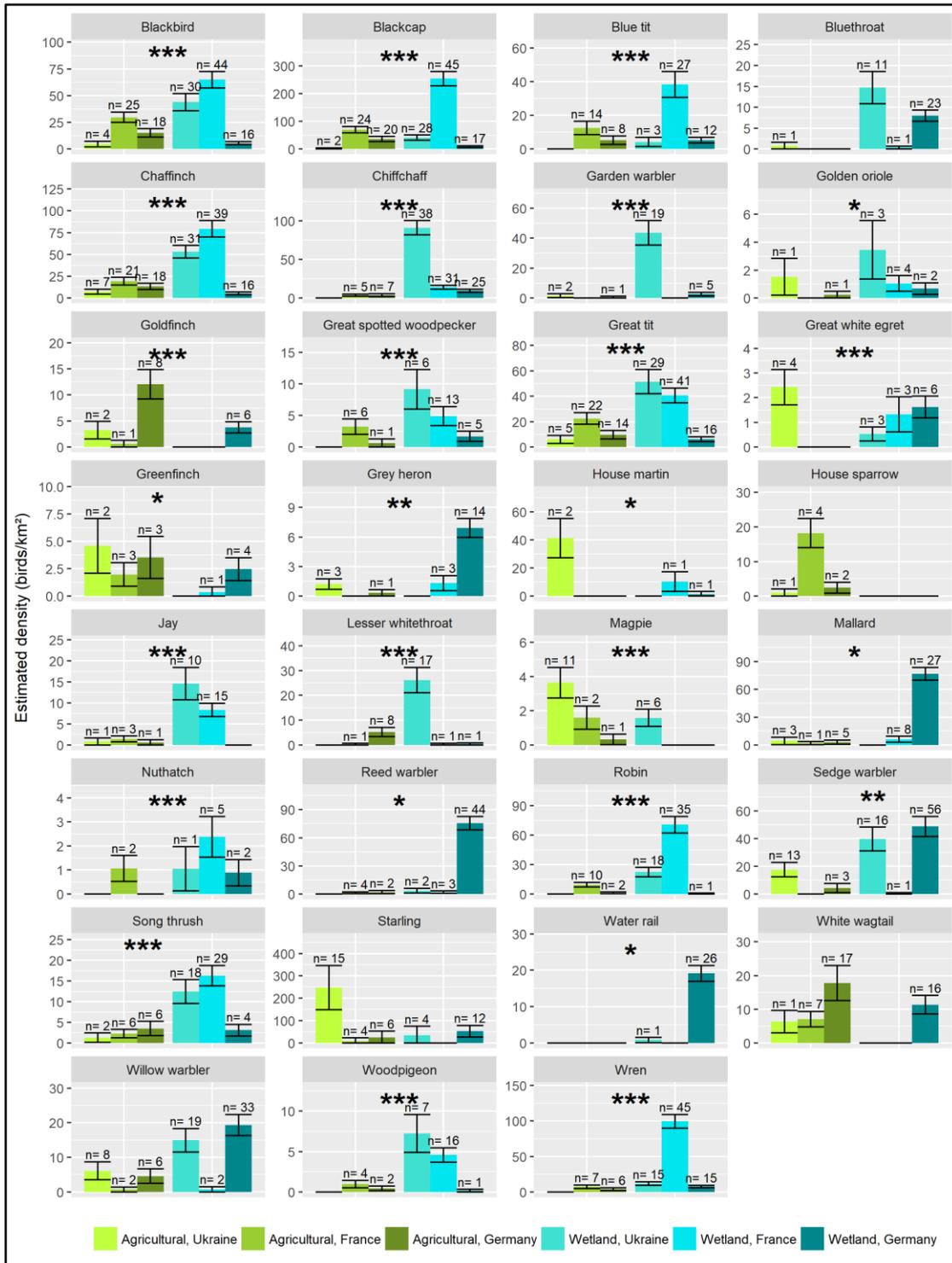


Figure 7.3 – Estimated population densities of all 31 non-HNV bird species that were observed in all three of my study regions, by region and habitat. Population densities were estimated using species-specific GLMs to model total count with a quasi-Poisson error structure, a log link function, region, habitat (agricultural or wetland) and the interaction of region and habitat as explanatory variables, and offset by sampling effort. N values in the figure indicate the number of sites within each region/habitat in which each species was observed at least once. The total numbers of sites surveyed for birds were: Ukraine, wetland = 48; Ukraine, agriculture = 44; France, wetland = 45; France, agriculture = 34; Germany, wetland = 68; Germany, agriculture = 47. Stars indicate significance of the modelled interaction between region and habitat (* p < 0.05, ** p < 0.01, *** p < 0.001).

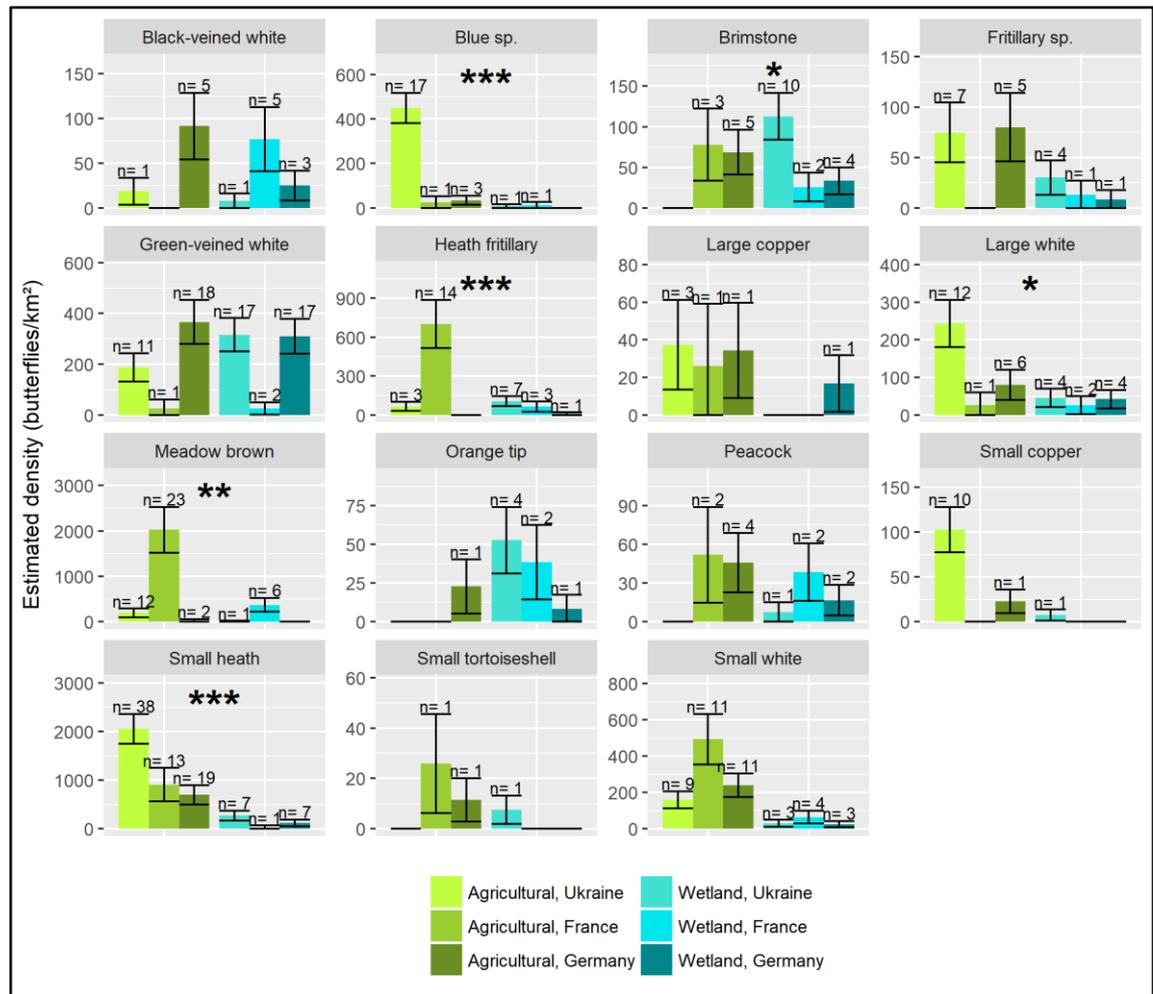


Figure 7.4 – Estimated population densities of all 15 butterfly species that were observed in all three of my study regions, by region and habitat. Population densities were estimated using species-specific GLMs to model total count with a quasi-Poisson error structure, a log link function, region, habitat (agricultural or wetland) and the interaction of region and habitat as explanatory variables, and offset by sampling effort. N values in the figure indicate the number of sites within each region/habitat in which each species was observed at least once. The total numbers of sites surveyed for butterflies were: Ukraine, wetland = 48; Ukraine, agriculture = 44; France, wetland = 55; France, agriculture = 34; Germany, wetland = 60; Germany, agriculture = 47. Stars indicate significance of the modelled interaction between region and habitat (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

As argued in the preceding chapters, I believe this demonstrates that neither floodplain restoration project has truly recreated a natural floodplain, and therefore neither closely mimics the floodplain in Ukraine. In France, the restoration has failed to bring about a sufficiently high level of flood disturbance, and the habitats surrounding the channels remain largely terrestrial. In contrast, the restored area in Germany shows a legacy from its agricultural history, with a very open landscape, high water levels and a lack of late-successional habitats. Perhaps, however, natural processes will return the area to a more natural state, as succession occurs and the soil bank is re-established.

Comparing Flood Risk Score across wetland sites in my three study regions, Ukraine differed significantly from both France and Germany (Figure 7.5). However, I found the opposite trend to that predicted, with Ukrainian sites having a lower mean Flood Risk Score. Looking at water depth, my other metric of flood disturbance, Ukraine and France both had a lower mean than Germany (Figure 7.5). These results indicate that my regions did differ in terms of their flood disturbance. With regards to my German study region, as described in Chapter 5 the restored sites have a higher water level than would have been natural prior to drainage, and this is reflected in both Flood Risk Score and water depth. In France, the presence of the channels themselves in every Floodplain Channel site may have also elevated both Flood Risk Score and water depth above typical values for the floodplain as a whole. These raise some questions about the use of Flood Risk Score and water depth as metrics of flood disturbance, which are discussed further below.

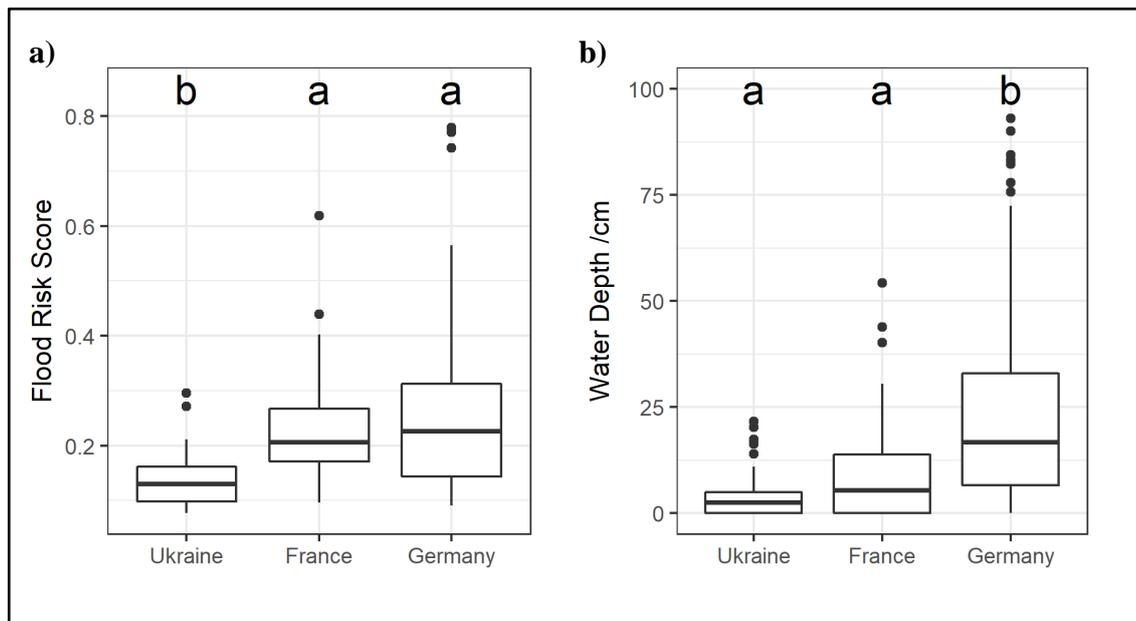


Figure 7.5 – Boxplots of **a)** Flood Risk Score and **b)** water depth across my three study regions. Plotted are Wetland sites in Ukraine ($n = 48$), Floodplain Channel sites in France ($n = 55$) and Restored Wetland sites in Germany ($n = 68$). Countries with different letters have significantly different means (Tukey HSD $p < 0.05$).

7.2 Context and scope

In many ways, the scope of this study was intended to be pan-European. The conservation issues and potential solutions, and the political and social contexts are broadly similar across Europe, especially within the EU. However, any field-based study necessarily restricts itself geographically. I carried out fieldwork in three regions, which represent quite different ecosystems. My study region in Ukraine, Pripyat-Stokhid National Nature

Park, is a low-lying, continental mire, fed by rain. In France, I worked on the River Rhône, a glacial river system on the edge of a mountainous region. Finally, in my German region, I studied the lower reaches of the Peene, a low-lying, rain fed river. Each study region also included agricultural land. In Ukraine, this was low-yielding, small scale subsistence farming, typical of High Nature Value farmland. In France and Germany, farms were larger and more intensively managed. In France, the floodplain was alluvial, where as in Germany it was drained peatland. Carrying out a study in such diverse regions has benefits and drawbacks. On the one hand, patterns that are consistent across all three sites are well supported, and conclusions could therefore be applied to similar regions across much of Europe. On the other hand, comparisons between sites cannot be made directly, and where results differ between regions it is impossible to attribute this to any single characteristic.

Despite their differences, all my study regions fall within the same biome (“Temperate Broadleaf and Mixed Forests”), out of six present in Europe (Olson *et al.*, 2001). Other biomes are also important for biodiversity. In particular, uplands and Mediterranean systems are both associated with High Nature Value farming systems, but are also both hotspots of agricultural abandonment (MacDonald *et al.*, 2000; Andersen *et al.*, 2003; Ribeiro *et al.*, 2014; Lomba *et al.*, 2015; Pereira & Navarro, 2015; O’Rourke, Charbonneau & Poinot, 2016; Brambilla *et al.*, 2017). Those systems are therefore a priority for the conservation concerns this thesis addresses, but nonetheless beyond the scope of this thesis. Rewilding with fire and herbivores may be more appropriate in those contexts (Pons *et al.*, 2003; Fuhlendorf *et al.*, 2009; Menz, Brotons & Arlettaz, 2009; Rost *et al.*, 2012; Navarro *et al.*, 2015).

This study is framed around HNV species and disturbance, but this means I have focused on a specific subset of species and habitats. Many species may prefer habitats such as ancient woodland, and such species are unlikely to have been observed during my fieldwork and hence received little discussion thus far (BirdLife International, 2013; Burns *et al.*, 2013; Gross, 2016; del Hoyo *et al.*, 2018). It is not my intention to dismiss the importance of those species, or the habitats they live in. Nor is it to suggest they are not threatened and of conservation concern. It is simply that the threats facing them, and the solutions to those threats, are very different and beyond the scope of this study (Smith, 2018). In the same vein, I have also only considered two species groups: birds and butterflies. While these were selected for good reasons, as described in Chapter 2, having

only two indicator taxa does limit the generality of my findings. Other groups remain unstudied and may differ in their response; however, my results provide a good indication of patterns which may be found more generally by other studies.

7.3 Limitations of this study

While I believe the approach taken has been rigorous enough to justify the conclusions, there are limitations to this study, which necessarily result from the practicalities and limitations of carrying out this research.

I only carried out a single field season in each region. Thus, the results represent a single moment in time. There is therefore a risk that conditions during the field season were unusual, and do not reflect typical conditions. Speaking with locals, there were suggestions that my field season in Ukraine fell in a particularly dry year, while the early part of my German field season was unusually cold. I do not think that the conditions were so extreme as to have impacted the results hugely or affect the general conclusion, but equally it cannot be assumed that my results would be exactly replicated if the study were to be repeated.

In addition, ecosystems are dynamic processes, and following a restoration project the ecosystem is likely to take time to adjust. Ecosystems also take time to adjust following disturbance events, creating a cyclical pattern of disturbance and regeneration. The limited temporal scope of this study therefore means I cannot consider these processes, and I am restricted to considering the current state, which will not remain constant over time. In Ukraine, the number of sample sites within the region overcomes this limitation to some extent, as they capture a range of different habitats which represent different successional stages. In France and Germany, the restoration was carried out relatively recently (on an ecological timescale) and therefore it would be expected that the sites will continue to change over the coming decades.

Quantifying flood disturbance was important to test my hypothesis, and throughout this thesis I have used Flood Risk Score and water depth to measure this. Flood Risk Score uses a time series of remotely-sensed images to estimate the frequency of water inundation to each parcel of land. This is a broadly similar approach as has been taken by numerous other studies (for example Van Dijk *et al.*, 2011; Dong *et al.*, 2014; Ticehurst *et al.*, 2014; Zhang, Zhu & Liu, 2014; Pekel *et al.*, 2016) and many of the same limitations apply. There is a technical challenge in distinguishing between surfaces with similar

reflectance profiles, and I noted in my French study region (see Chapter 4) that ice or snow in mountainous regions appear to have been incorrectly classified as water. This may have affected other regions too, as Landsat scenes were not seasonally restricted and could have included snow in winter. Remotely sensed data relies on reflectance towards the satellites, and therefore where standing water is covered by vegetation this will inhibit the detection of the water below. There are also conceptual limitations in the use of Flood Risk Score as a metric of flood disturbance. Frequency of inundation is not a complete description of flood disturbance; flood events which are infrequent or brief but highly energetic can be a major source of flood disturbance (Richards *et al.*, 2002; Shafroth, Stromberg & Patten, 2002; Lite, Bagstad & Stromberg, 2005; Parajka *et al.*, 2010). At the other extreme, ground water availability and hydrological connectivity can influence biotic communities even in the absence of any inundation (Richter *et al.*, 1998; Lite *et al.*, 2005; Powell *et al.*, 2014; Hester *et al.*, 2016). Using water depth measured in the field suffers some of the same limitations as a metric of flood disturbance: I did not sample during any extreme flood events, and by measuring water level above the ground I ignore any ground water processes. My measures of water depth are also limited to a single moment in time, which may not reflect typical values.

In both France and Germany, I used a space-for-time substitution, assuming that non-restored areas can be used as controls for the impact of restoration on the restored areas. Space-for-time studies have been criticised (De Palma *et al.*, 2018) but were the best available options given that the restoration work had already been undertaken, and given the constraints on the duration of fieldwork. In France, it was planned into the design of the restoration project that comparable sections of floodplain channel would remain unrestored and therefore can be considered reliable control sites (Lamouroux *et al.*, 2015). This was not the case in Germany, where the restoration was carried out opportunistically across the project area. Nonetheless, I think that the farmland sites surveyed were sufficiently similar to the farmland that would have been present prior to restoration that their use as controls is not problematic.

Whilst the timing of my field seasons and sampling were designed to maximise observations, sampling was not exhaustive. I covered the main breeding season for birds, but my field season is likely to have missed most wintering birds. For butterflies, my field season only covered the start of the summer, and will have missed the flight period for some species (Tolman & Lewington, 2009). By conducting bird surveys around dawn I

am likely to have missed nocturnal species such as most owls (Svensson *et al.*, 2009). However, there is no reason to think that these issues are likely to have biased the results in such a way as to influence the conclusions.

All study regions included patches of natural habitat (of varying size) surrounded by an agricultural matrix. I left a buffer between the edges of the habitats and sampling sites (where possible) to minimise the impact of edge effects (Ries *et al.*, 2004), but it is still possible that the study sites within the natural habitat were influenced by the surrounding agricultural land, and *vice versa*, as some edge effects can extend many hundreds of metres (Laurance, 2000). Wetlands in particular are susceptible to the effects of land use in their catchment, as chemical fertilisers and pesticides are washed into downstream water bodies (Paillex *et al.*, 2017).

In each of the three chapters summarising my regional studies, I have compared my bird results to those obtained in the Lubelskie region of Poland in a previous study (Feniuk, 2015). My Ukrainian region is the closest and ecologically most similar of all my field seasons, and therefore I have conducted the most extensive comparisons between my Ukrainian results and the results from Poland (see Chapter 3). The comparisons between Poland and my other two field seasons must be viewed as less rigorous and more as indicators of potential patterns and trends rather than clear evidence of differences. That said, the vast majority of birds observed are widespread across temperate Europe, and neither my field regions nor the Lubelskie region of Poland represent extremes of their ranges or zones of climatic suitability (Snow *et al.*, 1998; Svensson *et al.*, 2009; del Hoyo *et al.*, 2018). I also used slightly different methods both in the field and for analysis than Feniuk (2015); however, in both cases the objective was to estimate absolute population densities by species and so estimates should be directly comparable. With the exception of a sensitivity analysis carried out in Chapter 3, in all cases I compared my estimates from floodplain/wetland habitats to Feniuk's central estimate for natural baseline habitats. This central estimate is based on a 3:1 weighting in favour of sites with forest soils over sites with wetland soils, determined by the relative abundance of those soils in the study region (Feniuk, 2015). I believe that this is a more relevant comparison than extracting the results just from sites with wetland soils. Habitats, soils and hydrological regimes are all intimately linked (Richards *et al.*, 2003; Begon *et al.*, 2006; Ward & Stanford, 2006; Sutfin *et al.*, 2015; Wohl, 2015; D'Elia *et al.*, 2017) and as such weightings of baseline habitats in Poland can be interpreted as typical of natural habitats in Europe in the absence

of large scale flood disturbance. Restoring floodplains would change the habitats and the soils, as I have demonstrated to some extent in this thesis, and has been demonstrated repeatedly elsewhere (Bendix & Hupp, 2000; Schindler *et al.*, 2003; Timmermann *et al.*, 2006; González *et al.*, 2015; Krzywicka *et al.*, 2017; Morimoto *et al.*, 2017; Ahilan *et al.*, 2018).

7.4 Concluding remarks

Rewilding is a new paradigm in conservation, and in this thesis I have focused on one aspect of it: restoring the natural disturbance caused by flooding. This has been framed around another conservation issue which is currently topical in Europe: the decline of High Nature Value farmland (HNVf). In some places, HNVf is being intensified, and becomes less wildlife friendly as a result, while in others, HNVf is being abandoned (MacDonald *et al.*, 2000; Andersen *et al.*, 2003; EEA, 2004; Navarro & Pereira, 2012). In some respects, this is likely to be good for biodiversity overall as it creates a “land sparing” landscape across Europe, and it has been repeatedly shown that land sparing is better than “land sharing” for biodiversity (Phalan *et al.*, 2011; Edwards *et al.*, 2014; Dotta *et al.*, 2015; Edwards *et al.*, 2015; Feniuk, 2015; Phalan *et al.*, 2016; Williams *et al.*, 2017) as well as other ecosystem services (Lamb *et al.*, 2016; Williams *et al.*, 2017).

However, there are still many species which are associated with HNVf, live at considerably lower density in natural habitats and high-yield farmland, and hence are losers under land sparing (Feniuk, 2015). Traditionally, it has been assumed that these species need agriculture, and so efforts to conserve them have focused on trying to encourage wildlife friendly farming through agri-environment schemes or similar projects. In this thesis, I hypothesise that these species don't need agriculture *per se*, but rather need disturbance. Agriculture can be considered anthropogenic disturbance, affecting habitats and biodiversity in a similar way to natural disturbance processes such as fire, flooding and herbivory. Humans have suppressed natural disturbance processes across Europe, and as anthropogenic landscapes (in particular farmland) have become the dominant form of disturbed habitats they have emerged as the most suitable areas for such species.

If this hypothesis is correct, then an alternative to trying to maintain HNV agriculture in the face of both land abandonment and intensification would be to restore natural disturbance processes and their associated disturbance-dependent habitats. Advocates for

rewilding often use this line of reasoning (for example Navarro *et al.*, 2015), but to date there has been very little empirical evidence to support it. If rewilding is to become a valuable part of conservation, then it needs to be properly supported by evidence, and not merely an ideological approach. I therefore felt that it was important to start to build the evidence base for (or against) this hypothesis.

I collected empirical data by conducting fieldwork in three regions around Europe. The first region (in Ukraine) contains a natural floodplain, where the landscape is dominated by flood disturbance. If the hypothesis is correct, then species typically associated with HNV farmland should also be found in the floodplain. The second and third study regions (in France and Germany, respectively) were both areas where floodplain restoration has been carried out. I used these regions to look at whether restoration can recreate suitable habitat by reinstating flood disturbance, and whether the scale and scope of the restoration project influences its success.

Overall, I have shown that many HNV species do thrive in both natural and restored floodplains. This suggests that restoring floodplains more widely across Europe could help many of the species threatened by intensification or abandonment of HNV farmland. Across the three study regions, the species recorded and their responses differed to some extent. However, there were species that showed consistent patterns. For example, Reed bunting and Snipe are two species that are considered to be associated with High Nature Value farmland (Paracchini *et al.*, 2008). However, I found both species to have significantly higher population densities in floodplains in both my Ukrainian and German study regions than in the surrounding farmland (neither was observed in my French study region). By comparing density estimates with those from Poland, I was able to demonstrate that, for most HNV species which preferred floodplains, these differences were driven by high population densities in those floodplains rather than low population densities in farmland. On the other hand, species such as Stonechat and Yellow wagtail, both also considered HNV species, consistently preferred the farmland (even in the relatively intense agricultural landscapes of France and Germany).

Floodplain restoration would not just benefit HNV species. Overall, I found more species had higher population densities in wetland sites than surrounding farmland, and so floodplain restoration could help increase regional biodiversity in general. Furthermore, farmland is abundant in Europe (covering 48% of EU territory; EUROSTAT, 2014) whereas natural floodplains have been largely lost (Tockner & Stanford, 2002). This

suggests that restoring farmland to natural floodplains would benefit many species without markedly reducing the area of farmland habitat available for those species which require it. However, it is important to consider where such restoration occurs and how this impacts food supply; if the restoration of wetlands in Europe leads to an increase in tropical deforestation via demand for food, this could lead to a net loss of biodiversity on a global scale. This could be mitigated to some extent by restoring only agriculturally marginal land, and meeting food demand through sustainable intensification of existing farmland (Merckx & Pereira, 2015; Phalan *et al.*, 2016).

Although beyond the scope of this study, it has been shown elsewhere that floodplain restoration can have substantial impacts beyond biodiversity. It can reduce flood risk (POST, 2011; Acreman & Holden, 2013; Nilsson *et al.*, 2018); studies suggest peak flows following upstream restoration can be reduced by 19-25% in some cases (Dixon *et al.*, 2016; Ahilan *et al.*, 2018), although there can be a risk of adverse effects in certain situations (Skublics, Blöschl & Rutschmann, 2016). It can improve water quality, as has been demonstrated in several rivers both in Europe (Raith, 1999; Dubgaard *et al.*, 2002; Brouwer *et al.*, 2016; McVittie *et al.*, 2017) and elsewhere (Baron *et al.*, 2002; Hanrahan *et al.*, 2018). Restoration can also increase recreational value and offer new economic opportunities (Dubgaard *et al.*, 2002; Bernhardt *et al.*, 2005; Zingraff-Hamed *et al.*, 2017).

However, not all species benefitted from floodplains or floodplain restoration. Other strategies need to be considered for conserving biodiversity, both HNV species and more generally. This might include continuing to use AES to promote wildlife friendly farming. It could also include other forms of rewilding. I have focused on landscapes created by flood disturbance, but other natural processes such as fire and herbivory also have the potential to create disturbed landscapes which might be important for different sets of species (Fuhlendorf *et al.*, 2009; Müller *et al.*, 2013; Navarro *et al.*, 2015).

I also looked at metrics of habitat, vegetation structure and disturbance (including flood disturbance) to try to understand some of the mechanisms potentially underlying these results. It is a central pillar of my hypothesis that disturbance processes influence the structure of the vegetation and the habitats present. As well as measurements in the field, I developed an indicator of long-term inundation frequency, which I have called Flood Risk Score, using a time series of remotely-sensed data from Landsat satellites. In all three study regions, I showed that population densities of both birds and butterflies

respond to habitat and vegetation structure. Furthermore, vegetation structure and metrics of disturbance differ between wetland sites and agricultural sites. This suggests that the differences observed in biodiversity may be driven by differences in habitat. However, the results were less clear about the mechanisms driving those differences, with relationships between disturbance and vegetation structure being oftentimes weak and noisy. This study was not designed to elucidate those relationships fully, particularly given the constraints of fieldwork. Therefore, further studies are needed if they are to be better understood. There remains much to be fully discovered about the relationships between natural processes and biodiversity. However, I believe this thesis has made a valuable contribution to our understanding of those relationships, and how we can use them to conserve biodiversity.

I am excited by the opportunities that rewilding brings. Much of conservation science focuses on documenting the decline of nature or trying to stem the flood of losses. Rewilding, on the other hand, offers hope and the opportunity to leave biodiversity in a better state than we found it. However, it is vital that, to achieve the best outcomes for biodiversity, we consider rewilding from a scientific perspective, provide evidence for (or against) its effectiveness, and acknowledge its limitations. I hope this thesis contributes towards our understanding of rewilding and can be used for the benefit of both nature and mankind.

REFERENCES

- Abenteuer Flusslandschaft. (2018). Kanureisen und Kanutouren in Vorpommern [WWW Document]. URL <https://www.abenteuer-flusslandschaft.de/>
- Acreman, M. & Holden, J. (2013). How wetlands affect floods. *Wetlands* **33**, 773–786.
- Aguirre-Gutiérrez, J., Kissling, W.D., Carvalheiro, L.G., WallisDeVries, M.F., Franzén, M. & Biesmeijer, J.C. (2016). Functional traits help to explain half-century long shifts in pollinator distributions. *Sci. Rep.* **6**, 24451.
- Aguirre-Gutiérrez, J., WallisDeVries, M.F., Marshall, L., van't Zelfde, M., Villalobos-Arámbula, A.R., Boekelo, B., Bartholomeus, H., Franzén, M. & Biesmeijer, J.C. (2017). Butterflies show different functional and species diversity in relationship to vegetation structure and land use. *Glob. Ecol. Biogeogr.* **26**, 1126–1137.
- Ahilan, S., Guan, M., Sleigh, A., Wright, N. & Chang, H. (2018). The influence of floodplain restoration on flow and sediment dynamics in an urban river: Floodplain influences on flow and sediment dynamics in an urban river. *J. Flood Risk Manag.* **11**, S986–S1001.
- Alfieri, L., Feyen, L. & Di Baldassarre, G. (2016). Increasing flood risk under climate change: a pan-European assessment of the benefits of four adaptation strategies. *Clim. Change* **136**, 507–521.
- Allen, M. & Gardiner, J. (2009). If you go down to the woods today: a re-evaluation of the chalkland postglacial woodland: implications for prehistoric communities. In *Land and People: papers in memory of John G. Evans*, Prehistoric Society Research Paper: 49–66. Oxford, UK: The Prehistoric Society and Oxbow Books.
- Andersen, E., Baldock, D., Bennett, H., Beaufoy, G., Bignal, E., Brouwer, F., Elbersen, B., Eiden, G., Godeschalk, F., Jones, G., McCracken, D., Nieuwenhuizen, W., Eupen, M. van, Hennekens, S. & Zervas, G. (2003). *Developing a High Nature Value Farming area indicator*. Internal report for the European Environment Agency.
- Angelopoulos, N.V., Cowx, I.G. & Buijse, A.D. (2017). Integrated planning framework for successful river restoration projects: Upscaling lessons learnt from European case studies. *Environ. Sci. Policy* **76**, 12–22.
- Archibald, S., Lehmann, C.E., Gómez-Dans, J.L. & Bradstock, R.A. (2013). Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci.* **110**, 6442–6447.
- Attiwill, P.M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manag.* **63**, 247–300.

- Austin, M.P. (1985). Continuum Concept, Ordination Methods, and Niche Theory. *Annu. Rev. Ecol. Syst.* **16**, 39–61.
- Bakker, E.S., Gill, J.L., Johnson, C.N., Vera, F.W.M., Sandom, C.J., Asner, G.P. & Svenning, J.-C. (2016). Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl. Acad. Sci.* **113**, 847–855.
- Balanoff, A.M., Bever, G.S., Rowe, T.B. & Norell, M.A. (2013). Evolutionary origins of the avian brain. *Nature* **501**, 93–96.
- Balmford, A., Green, R. & Phalan, B. (2012). What conservationists need to know about farming. *Proc. R. Soc. B Biol. Sci.* **279**, 2714–2724.
- Barbaro, L. & Halder, I.V. (2009). Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* **32**, 321–333.
- Baron, J.S., Poff, N.L., Angermeier, P.L., Dahm, C.N., Gleick, P.H., Hairston, N.G., Jackson, R.B., Johnston, C.A., Richter, B.D. & Steinman, A.D. (2002). Meeting ecological and societal needs for freshwater. *Ecol. Appl.* **12**, 1247–1260.
- Barral, M.P., Rey Benayas, J.M., Meli, P. & Maceira, N.O. (2015). Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: A global meta-analysis. *Agric. Ecosyst. Environ.* **202**, 223–231.
- Barthélémy, C. & Armani, G. (2015). A comparison of social processes at three sites of the French Rhône River subjected to ecological restoration. *Freshw. Biol.* **60**, 1208–1220.
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* **29**, 1006–1016.
- Begon, M., Townsend, C.R. & Harper, J.L. (2006). *Ecology: from individuals to ecosystems*. 4th ed. Malden, MA: Blackwell Pub.
- Bendix, J. & Hupp, C.R. (2000). Hydrological and geomorphological impacts on riparian plant communities. *Hydrol. Process.* **14**, 2977–2990.
- Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* **57**, 289–300.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188.
- Berga, L., Buil, J.M., Bofill, E., Cea, J.C.D., Perez, J.A.G., Mañueco, G., Polimon, J., Soriano, A. & Yagüe, J. (2006). *Dams and reservoirs, societies and environment in the 21st Century, two volume set: Proceedings of the International Symposium on Dams in the Societies of the 21st Century, 22nd International Congress on Large Dams (ICOLD), Barcelona, Spain, 18 June 2006*. CRC Press.

- Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B. & Sudduth, E. (2005). Synthesizing U.S. river restoration efforts. *Science* **308**, 636–637.
- Beyer, C. & Höper, H. (2015). Greenhouse gas exchange of rewetted bog peat extraction sites and a Sphagnum cultivation site in northwest Germany. *Biogeosciences* **12**, 2101–2117.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000). *Bird census techniques*. 2nd ed. London; San Diego: Academic Press.
- Bibby, C.J. & Etheridge, B. (1993). Status of the Hen Harrier *Circus cyaneus* in Scotland in 1988–89. *Bird Study* **40**, 1–11.
- BirdLife International. (2010). *The BirdLife checklist of the birds of the world, with conservation status and taxonomic sources. Version 3*. Downloaded from http://www.birdlife.org/datazone/species/downloads/BirdLife_Checklist_Version_3.zip.
- BirdLife International. (2013). *State of the world's birds: indicators for our changing world*. Cambridge, UK: BirdLife International.
- BirdLife International. (2015). *European Red List of Birds*. Office for Official Publications of the European Communities, Luxembourg.
- Birnie-Gauvin, K., Tummers, J.S., Lucas, M.C. & Aarestrup, K. (2017). Adaptive management in the context of barriers in European freshwater ecosystems. *J. Environ. Manage.* **204**, 436–441.
- Boitani, L., Ciucci, P. & Raganella-Pelliccioni, E. (2010). Ex-post compensation payments for wolf predation on livestock in Italy: a tool for conservation? *Wildl. Res.* **37**, 722–730.
- Bond, N., Costelloe, J., King, A., Warfe, D., Reich, P. & Balcombe, S. (2014). Ecological risks and opportunities from engineered artificial flooding as a means of achieving environmental flow objectives. *Front. Ecol. Environ.* **12**, 386–394.
- Bond, W.J. & Keeley, J.E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **20**, 387–394.
- Bormann, F.H. & Likens, G.E. (1979). Catastrophic Disturbance and the Steady State in Northern Hardwood Forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *Am. Sci.* **67**, 660–669.
- Bowman, D.M.J.S., Garnett, S.T., Barlow, S., Bekessy, S.A., Bellairs, S.M., Bishop, M.J., Bradstock, R.A., Jones, D.N., Maxwell, S.L., Pittock, J., Toral-Granda, M.V., Watson, J.E.M., Wilson, T., Zander, K.K. & Hughes, L. (2017). Renewal ecology: conservation for the Anthropocene. *Restor. Ecol.* **25**, 674–680.

- Brambilla, M., Gustin, M., Vitulano, S., Falco, R., Bergero, V., Negri, I., Bogliani, G. & Celada, C. (2017). Sixty years of habitat decline: impact of land-cover changes in northern Italy on the decreasing ortolan bunting *Emberiza hortulana*. *Reg. Environ. Change* **17**, 323–333.
- Bridgewater, P. & Aricò, S. (2016). Turbo-charging the Ecohydrology paradigm for the Anthropocene. *Ecohydrol. Hydrobiol.* **16**, 74–82.
- Brinson, M.M. & Malvárez, A.I. (2002). Temperate freshwater wetlands: types, status, and threats. *Environ. Conserv.* **29**.
- Brouwer, R., Bliem, M., Getzner, M., Kerekes, S., Milton, S., Palarie, T., Szerényi, Z., Vadineanu, A. & Wagtendonk, A. (2016). Valuation and transferability of the non-market benefits of river restoration in the Danube river basin using a choice experiment. *Ecol. Eng.* **87**, 20–29.
- BTO. (2017). *WeBS Core Counts: Methodology and counting techniques*. British Trust for Ornithology, Thetford.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001). *Introduction to distance sampling: estimating abundance of biological populations*. Oxford: Oxford University Press.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (Eds.). (2007). *Advanced distance sampling: estimating abundance of biological populations*. Oxford; New York: Oxford University Press.
- Buckland, S.T., Magurran, A.E., Green, R.E. & Fewster, R.M. (2005). Monitoring change in biodiversity through composite indices. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 243–254.
- Buijse, A.D., Coops, H., Staras, M., Jans, L.H., Van Geest, G.J., Grift, R.E., Ibelings, B.W., Oosterberg, W. & Roozen, F.C.J.M. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshw. Biol.* **47**, 889–907.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.
- Burns, F., Eaton, M., Gregory, R., Al Fulaij, N., August, T., Biggs, J., Bladwell, S., Brereton, T., Brooks, D., Clubbe, C., Dawson, J., Dunn, E., Edwards, B., Falk, S., Gent, T., Gibbons, D., Gurney, M., Haysom, K., Henshaw, S., Hodgetts, N., Isaac, N., McLaughlin, M., Musgrove, A., Noble, D., O’Mahony, E., Pacheco, M., Roy, D., Sears, J., Shardlow, M., Stringer, C., Taylor, A., Thompson, P., Walker, K., Walton, P., Willing, M., Wilson, J. & Wynde, R. (2013). *State of nature report*. The State of Nature Partnership.
- Cadotte, M.W., Carscadden, K. & Mirotnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* **48**, 1079–1087.
- Caro, T. (2007). The Pleistocene re-wilding gambit. *Trends Ecol. Evol.* **22**, 281–283.

- Castella, E., Béguin, O., Besacier-Monbertrand, A.-L., Hug Peter, D., Lamouroux, N., Mayor Siméant, H., McCrae, D., Olivier, J.-M. & Paillex, A. (2015). Realised and predicted changes in the invertebrate benthos after restoration of connectivity to the floodplain of a large river. *Freshw. Biol.* **60**, 1131–1146.
- Cerqueira, Y., Navarro, L.M., Maes, J., Marta-Pedroso, C., Honrado, J.P. & Pereira, H.M. (2015). Ecosystem services: The opportunities of rewilding in Europe. In *Rewilding European Landscapes: 47–64*. Springer, Cham.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., Arx, M. von, Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbínšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519.
- Čížková, H., Květ, J., Comín, F.A., Laiho, R., Pokorný, J. & Pithart, D. (2013). Actual state of European wetlands and their possible future in the context of global climate change. *Aquat. Sci.* **75**, 3–26.
- Clarke, K.R., Somerfield, P.J. & Gorley, R.N. (2008). Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J. Exp. Mar. Biol. Ecol.*, Marine ecology: A tribute to the life and work of John S. Gray **366**, 56–69.
- Clements, F.E. (1916). *Plant Succession. An analysis of the development of vegetation*. Washington: Carnegie Institution of Washington.
- ClimateWire. (2012). How the Dutch make “room for the river” by redesigning cities [WWW Document]. *Sci. Am.* URL <https://www.scientificamerican.com/article/how-the-dutch-make-room-for-the-river/>
- Coles, J.M. & Orme, B.J. (1983). Home sapiens or Castor fiber? *Antiquity* **57**, 95–102.
- Corlett, R.T. (2015). The Anthropocene concept in ecology and conservation. *Trends Ecol. Evol.* **30**, 36–41.
- Corlett, R.T. (2016). Restoration, reintroduction, and rewilding in a changing world. *Trends Ecol. Evol.* **31**, 453–462.
- Crawley, M.J. (2013). *The R book*. Second edition. Chichester, West Sussex, United Kingdom: Wiley.

- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Michael Wotton, B. (2001). Climate change and forest disturbances. *BioScience* **51**, 723–734.
- Darwin, C. (1859). *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. London: J. Murray.
- Daufresne, M., Veslot, J., Capra, H., Carrel, G., Poirel, A., Olivier, J.-M. & Lamouroux, N. (2015). Fish community dynamics (1985–2010) in multiple reaches of a large river subjected to flow restoration and other environmental changes. *Freshw. Biol.* **60**, 1176–1191.
- Davidson, N.C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Mar. Freshw. Res.* **65**, 934–941.
- Davidson, N.C., Fluet-Chouinard, E. & Finlayson, C.M. (2018). Global extent and distribution of wetlands: trends and issues. *Mar. Freshw. Res.* **69**, 620–627.
- De Palma, A., Sanchez-Ortiz, K., Martin, P.A., Chadwick, A., Gilbert, G., Bates, A.E., Börger, L., Contu, S., Hill, S.L.L. & Purvis, A. (2018). Challenges with inferring how land-use affects terrestrial biodiversity: Study design, time, space and synthesis. In *Advances in Ecological Research*, Next Generation Biomonitoring: Part 1: 163–199. Bohan, D.A., Dumbrell, A.J., Woodward, G. & Jackson, M. (Eds.). Academic Press.
- Decker, S.E., Bath, A.J., Simms, A., Lindner, U. & Reisinger, E. (2010). The return of the king or bringing snails to the garden? The human dimensions of a proposed restoration of European bison (*Bison bonasus*) in Germany. *Restor. Ecol.* **18**, 41–51.
- DEFRA. (2016). *Agriculture in the United Kingdom*. Department for Environment, Food and Rural Affairs.
- Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B. & Böhm, M. (2013). *Wildlife comeback in Europe: The recovery of selected mammal and bird species*. Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council, London, UK: ZSL.
- D’Elia, A.H., Liles, G.C., Viers, J.H. & Smart, D.R. (2017). Deep carbon storage potential of buried floodplain soils. *Sci. Rep.* **7**.
- Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers Robert M., Jordano Pedro & Pearse William D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* **3**, 2958–2975.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science* **345**, 401–406.
- Dixon, S.J., Sear, D.A., Odoni, N.A., Sykes, T. & Lane, S.N. (2016). The effects of river restoration on catchment scale flood risk and flood hydrology. *Earth Surf. Process. Landf.* **41**, 997–1008.

- Dolédec, S., Castella, E., Forcellini, M., Olivier, J.-M., Paillex, A. & Sagnes, P. (2015). The generality of changes in the trait composition of fish and invertebrate communities after flow restoration in a large river (French Rhône). *Freshw. Biol.* **60**, 1147–1161.
- Dolédec, S., Chessel, D., Braak, C.J.F. ter & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* **3**, 143–166.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. B Biol. Sci.* **268**, 25–29.
- Dong, Z., Wang, Z., Liu, D., Song, K., Li, L., Jia, M. & Ding, Z. (2014). Mapping wetland areas Using Landsat-derived NDVI and LSWI: A case study of West Songnen Plain, Northeast China. *J. Indian Soc. Remote Sens.* **42**, 569–576.
- Donlan, J.C., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soulé, M.E. & Greene, H.W. (2006). Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *Am. Nat.* **168**, 660–681.
- Dotta, G., Phalan, B., Silva, T.W., Green, R. & Balmford, A. (2015). Assessing strategies to reconcile agriculture and bird conservation in the temperate grasslands of South America. *Conserv. Biol.* **30**, 618–627.
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S. & ter Braak, C.J.F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* **95**, 14–21.
- Dray, S. & Dufour, A.-B. (2007). The **ade4** package: Implementing the duality diagram for ecologists. *J. Stat. Softw.* **22**.
- Dubgaard, A., Kallesøe, M.F., Petersen, M.L. & Ladenburg, J. (2002). Cost-benefit analysis of the Skjern River restoration project. *Dep. Econ. Nat. Resour. R. Vet. Agric. Univ. Cph.*
- Edwards, D.P., Gilroy, J.J., Thomas, G.H., Uribe, C.A.M. & Hugaasen, T. (2015). Land-sparing agriculture best protects avian phylogenetic diversity. *Curr. Biol.* **25**, 2384–2391.
- Edwards, D.P., Gilroy, J.J., Woodcock, P., Edwards, F.A., Larsen, T.H., Andrews, D.J.R., Derhé, M.A., Docherty, T.D.S., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C. & Wilcove, D.S. (2014). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Glob. Change Biol.* **20**, 183–191.
- EEA. (2004). *High nature value farmland - Characteristics, trends and policy challenges* (Publication No. 1/2004). European Environment Agency, Copenhagen.
- EEA. (2007). *Reservoirs and dams*. European Environment Agency, Copenhagen.

- EEA. (2017a). *Green infrastructure and flood management* (Publication). European Environment Agency, Luxembourg: Publications Office of the European Union.
- EEA. (2017b). *Nationally designated areas (CDDA)*. European Environment Agency, Copenhagen, Denmark.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scr. Geobot.* **18**, 1–248.
- Elton, C.S. (1927). *Animal ecology*. New York: Macmillan Co.
- Enserink, M. & Vogel, G. (2006). The carnivore comeback. *Science* **314**, 746–749.
- EUROSTAT. (2014). *EUROSTAT: Regional Statistics*. Statistical Office of the European Communities, Luxembourg.
- Evans, J.G. (1971). Habitat changes on the calcareous soils of Britain; the impact of Neolithic man. In *Economy and Settlement in Neolithic and Early Bronze Age Britain and Europe: 27–73*. Simpson, D.D.A. (Ed.). Leicester: Leicester University Press.
- FAO. (2015). *FAOSTAT statistics database*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D. & Meyer, C.F.J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *J. Appl. Ecol.* **52**, 1381–1391.
- Feniuk, C. (2015). *Reconciling food production and biodiversity conservation in Europe*. PhD Thesis, University of Cambridge, Cambridge.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O’Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. (2011). Solutions for a cultivated planet. *Nature* **478**, 337–342.
- Fritzemeier, J., Teuffert, J., Greiser-Wilke, I., Staubach, C., Schlüter, H. & Moennig, V. (2000). Epidemiology of classical swine fever in Germany in the 1990s. *Vet. Microbiol.* **77**, 29–41.
- Fruget, J.F. (2006). Ecology of the lower Rhône after 200 years of human influence: A review. *Regul. Rivers Res. Manag.* **7**, 233–246.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J. & Hamilton, R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* **23**, 588–598.
- Fuller, R.J., Williamson, T., Barnes, G. & Dolman, P.M. (2017). Human activities and biodiversity opportunities in pre-industrial cultural landscapes: relevance to conservation. *J. Appl. Ecol.* **54**, 459–469.

- Golfieri, B., Mason, E., Goltara, A. & Silver, E. (2017). *Benefits of European river restoration schemes. An analysis of 13 case studies aiming to integrate improvement of ecological conditions and flood risk mitigation*. European Centre for River Restoration.
- González, E., Sher, A.A., Tabacchi, E., Masip, A. & Poulin, M. (2015). Restoration of riparian vegetation: A global review of implementation and evaluation approaches in the international, peer-reviewed literature. *J. Environ. Manage.* **158**, 85–94.
- Görn, S. & Fischer, K. (2015). Measuring the efficiency of fen restoration on carabid beetles and vascular plants: a case study from north-eastern Germany. *Restor. Ecol.* **23**, 413–420.
- Göthe, E., Timmermann, A., Januschke, K. & Baattrup-Pedersen, A. (2015). Structural and functional responses of floodplain vegetation to stream ecosystem restoration. *Hydrobiologia* **769**, 79–92.
- Goulding, M.J. & Roper, T.J. (2002). Press responses to the presence of free-living Wild Boar (*Sus scrofa*) in southern England. *Mammal Rev.* **32**, 272–282.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005). Farming and the fate of wild nature. *Science* **307**, 550–555.
- Gregory, R. (2006). Birds as biodiversity indicators for Europe. *Significance* **3**, 106–110.
- Gregory, R.D. & Strien, A. van. (2010). Wild bird indicators: Using composite population trends of birds as measures of environmental health. *Ornithol. Sci.* **9**, 3–22.
- Gross, M. (2016). Europe's last wilderness threatened. *Curr. Biol.* **26**, R641–R643.
- Hagy, H.M., Hine, C.S., Horath, M.M., Yetter, A.P., Smith, R.V. & Stafford, J.D. (2017). Waterbird response indicates floodplain wetland restoration. *Hydrobiologia* **804**, 119–137.
- Hanrahan, B.R., Tank, J.L., Dee, M.M., Trentman, M.T., Berg, E.M. & McMillan, S.K. (2018). Restored floodplains enhance denitrification compared to naturalized floodplains in agricultural streams. *Biogeochemistry* 1–19.
- Hatfield, J.H., Orme, C.D.L., Tobias, J.A. & Banks-Leite, C. (2018). Trait-based indicators of bird species sensitivity to habitat loss are effective within but not across data sets. *Ecol. Appl.* **28**, 28–34.
- Hein, T., Schwarz, U., Habersack, H., Nichersu, I., Preiner, S., Willby, N. & Weigelhofer, G. (2016). Current status and restoration options for floodplains along the Danube River. *Sci. Total Environ.* **543**, 778–790.
- Henry, D.A.W. & Cumming, G.S. (2017). Can waterbirds with different movement, dietary and foraging functional traits occupy similar ecological niches? *Landscape Ecol.* **32**, 265–278.
- Herold, B. (2015). *Vergleichende Untersuchungen Der Brutvogelgemeinschaften Wiedervernässter Flusstalmoore Mecklenburg-Vorpommerns*. PhD Thesis, Ernst-Moritz-Arndt-Universität Greifswald.

- Hester, E.T., Guth, C.R., Scott, D.T. & Jones, C.N. (2016). Vertical surface water-groundwater exchange processes within a headwater floodplain induced by experimental floods: Surface Water-groundwater Exchange in Headwater Floodplains. *Hydrol. Process.* **30**, 3770–3787.
- Hobbs, R.J., Valentine, L.E., Standish, R.J. & Jackson, S.T. (2018). Movers and stayers: Novel assemblages in changing environments. *Trends Ecol. Evol.* **33**, 116–128.
- Hodder, K.H., Buckland, P.C., Kirby, K.J. & Bullock, J.M. (2009). Can the pre-Neolithic provide suitable models for re-wilding the landscape in Britain? *Br. Wildl.* **20**, 4–15.
- Hooper, D.U., Chapin Iii, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S. & others. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35.
- Hostert, P., Kuemmerle, T., Prishchepov, A., Sieber, A., Lambin, E.F. & Radeloff, V.C. (2011). Rapid land use change after socio-economic disturbances: the collapse of the Soviet Union versus Chernobyl. *Environ. Res. Lett.* **6**, 045201.
- del Hoyo, J., Collar, N.J., Christie, D.A., Elliott, A., Fishpool, L.D.C., Boseman, P. & Kirwan, G.M. (2016). *HBW and BirdLife International illustrated checklist of the birds of the world*. Barcelona, Spain and Cambridge, UK: Lynx Edicions and BirdLife International.
- del Hoyo, J., Elliott, A., Christie, D.A. & de Juana, E. (Eds.). (2018). *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions.
- Hughes, F.M.R., del Tánago, M.G. & Mountford, J.O. (2012). Restoring floodplain forests in Europe. In *A goal-oriented approach to forest landscape restoration*: 393–422. Stanturf, J., Madsen, P. & Lamb, D. (Eds.). Dordrecht: Springer Netherlands.
- Iacob, O., Rowan, J.S., Brown, I. & Ellis, C. (2014). Evaluating wider benefits of natural flood management strategies: an ecosystem-based adaptation perspective. *Hydrol. Res.* **45**, 774–787.
- Isaac, N.J.B., Cruickshanks, K.L., Weddle, A.M., Marcus Rowcliffe, J., Brereton, T.M., Dennis, R.L.H., Shuker, D.M. & Thomas, C.D. (2011). Distance sampling and the challenge of monitoring butterfly populations. *Methods Ecol. Evol.* **2**, 585–594.
- Januschke, K. & Verdonschot, R.C.M. (2015). Effects of river restoration on riparian ground beetles (Coleoptera: Carabidae) in Europe. *Hydrobiologia* 1–12.
- Jennions, M.D. & Møller, A.P. (2002). Publication bias in ecology and evolution: an empirical assessment using the “trim and fill” method. *Biol. Rev. Camb. Philos. Soc.* **77**, 211–222.
- Jonsson, M., Strasevicius, D. & Malmqvist, B. (2012). Influences of river regulation and environmental variables on upland bird assemblages in northern Sweden. *Ecol. Res.* **27**, 945–954.

- Jørgensen, D. (2015). Rethinking rewilding. *Geoforum* **65**, 482–488.
- Kaplan, J.O., Krumhardt, K.M. & Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. *Quat. Sci. Rev.* **28**, 3016–3034.
- Keenleyside, C. & Tucker, G.M. (2010). *Farmland abandonment in the EU: An assessment of trends and prospects.* , Report prepared for WWF. Institute for European Environmental Policy, London.
- Kent, M. & Ballard, J. (1988). Trends and problems in the application of classification and ordination methods in plant ecology. *Vegetatio* **78**, 109–124.
- Kessell, S.R. & Whittaker, R.H. (1976). Comparisons of three ordination techniques. *Vegetatio* **32**, 21–29.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G. & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends Ecol. Evol.* **26**, 474–481.
- Kleiven, J., Bjerke, T. & Kaltenborn, B.P. (2004). Factors influencing the social acceptability of large carnivore behaviours. *Biodivers. Conserv.* **13**, 1647–1658.
- Knighton, D.A. & Nanson, G.C. (1993). Anastomosis and the continuum of channel pattern. *Earth Surf. Process. Landf.* **18**, 613–625.
- Koch, J.T. (Ed.). (2006). *Celtic culture: a historical encyclopedia.* Santa Barbara, Calif: ABC-CLIO.
- Kovařík, P., Kutal, M. & Machar, I. (2014). Sheep and wolves: Is the occurrence of large predators a limiting factor for sheep grazing in the Czech Carpathians? *J. Nat. Conserv.* **22**, 479–486.
- Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Appl.* **2**, 203–217.
- Krzywicka, A.E., Pociask, G.E., Grimley, D.A. & Matthews, J.W. (2017). Hydrology and soil magnetic susceptibility as predictors of planted tree survival in a restored floodplain forest. *Ecol. Eng.* **103, Part A**, 275–287.
- Kuenzi, C. & McNeely, J. (2008). Nature-based tourism. In *Global Risk Governance*, International Risk Governance Council Bookseries: 155–178. Springer, Dordrecht.
- Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T. & Bebi, P. (2017). A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *For. Ecol. Manag., Ecology of Mountain Forest Ecosystems in Europe* **388**, 120–131.
- Laake, J., Borchers, D., Thomas, L., Miller, D. & Bishop, J. (2015). *mrds: Mark-Recapture Distance Sampling.*

- Lamb, A., Green, R., Bateman, I., Broadmeadow, M., Bruce, T., Burney, J., Carey, P., Chadwick, D., Crane, E., Field, R., Goulding, K., Griffiths, H., Hastings, A., Kasoar, T., Kindred, D., Phalan, B., Pickett, J., Smith, P., Wall, E., zu Ermgassen, E.K.H.J. & Balmford, A. (2016). The potential for land sparing to offset greenhouse gas emissions from agriculture. *Nat. Clim. Change* **6**, 488–492.
- Lamouroux, N., Gore, J.A., Lepori, F. & Stutzner, B. (2015). The ecological restoration of large rivers needs science-based, predictive tools meeting public expectations: an overview of the Rhône project. *Freshw. Biol.* **60**, 1069–1084.
- Lamouroux, N. & Olivier, J.-M. (2015). Testing predictions of changes in fish abundance and community structure after flow restoration in four reaches of a large river (French Rhône). *Freshw. Biol.* **60**, 1118–1130.
- Laundré, J.W., Hernández, L. & Ripple, W.J. (2010). The landscape of fear: Ecological implications of being afraid. *Open Ecol. J.* **3**, 1–7.
- Laurance, W.F. (2000). Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* **15**, 134–135.
- Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P. & Willby, N.J. (2017). Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Sci. Total Environ.* **605**, 1021–1030.
- Law, A., McLean, F. & Willby, N.J. (2016). Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshw. Biol.* **61**, 486–499.
- Lawton, J.H. & May, R.M. (Eds.). (1995). *Extinction rates*. Oxford ; New York: Oxford University Press.
- Legendre, P., Galzin, R. & HarmelinVivien, M.L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology* **78**, 547–562.
- Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., Nilsson, C., Robertson, J.C., Rödel, R., Sindorf, N. & Wisser, D. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Front. Ecol. Environ.* **9**, 494–502.
- Lite, S.J., Bagstad, K.J. & Stromberg, J.C. (2005). Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *J. Arid Environ.* **63**, 785–813.
- Lomba, A., Alves, P., Jongman, R.H.G. & McCracken, D.I. (2015). Reconciling nature conservation and traditional farming practices: a spatially explicit framework to assess the extent of High Nature Value farmlands in the European countryside. *Ecol. Evol.* **5**, 1031–1044.
- Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D.C., Odden, J., Remmen, J. & Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* **123**, 641–651.

- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808.
- Lorimer, J., Sandom, C., Jepson, P., Doughty, C., Barua, M. & Kirby, K.J. (2015). Rewilding: Science, practice, and politics. *Annu. Rev. Environ. Resour.* **40**, 39–62.
- Lovett, R.A. (2014). Dam removals: Rivers on the run. *Nat. News* **511**, 521.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. (2000). Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *J. Environ. Manage.* **59**, 47–69.
- Macdonald, D. w., Tattersall, F. h., Brown, E. d. & Balharry, D. (1995). Reintroducing the European Beaver to Britain: nostalgic meddling or restoring biodiversity? *Mammal Rev.* **25**, 161–200.
- Makaske, B. (2001). Anastomosing rivers: a review of their classification, origin and sedimentary products. *Earth-Sci. Rev.* **53**, 149–196.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C. & Terborgh, J.W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci.* **113**, 838–846.
- Manly, B.F.J. (2007). *Randomization, bootstrap, and Monte Carlo methods in biology.* , Texts in statistical science. 3rd ed. Boca Raton, FL: Chapman & Hall/ CRC.
- May, R.M. (1988). How many species are there on Earth? *Science* **241**, 1441–1449.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185.
- McGranahan, D.A., Hovick, T.J., Elmore, R.D., Engle, D.M. & Fuhlendorf, S.D. (2018). Moderate patchiness optimizes heterogeneity, stability, and beta diversity in mesic grassland. *Ecol. Evol.*
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. (1999). Disturbance response in vegetation – towards a global perspective on functional traits. *J. Veg. Sci.* **10**, 621–630.
- McVittie, A., Cole, L., Wreford, A., Sgobbi, A. & Yordi, B. (2017). Ecosystem-based solutions for disaster risk reduction: Lessons from European applications of ecosystem-based adaptation measures. *Int. J. Disaster Risk Reduct.*
- Melman, T.C.P., Schotman, A.G.M., Hunink, S. & de Snoo, G.R. (2008). Evaluation of meadow bird management, especially black-tailed godwit (*Limosa limosa* L.), in the Netherlands. *J. Nat. Conserv.* **16**, 88–95.

- Menz, M.H.M., Brotons, L. & Arlettaz, R. (2009). Habitat selection by Ortolan Buntings *Emberiza hortulana* in post-fire succession in Catalonia: implications for the conservation of farmland populations. *Ibis* **151**, 752–761.
- Merckx, T. & Pereira, H.M. (2015). Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. *Basic Appl. Ecol.* **16**, 95–103.
- Méridoux, S., Forcellini, M., Dessaix, J., Fruget, J.-F., Lamouroux, N. & Statzner, B. (2015). Testing predictions of changes in benthic invertebrate abundance and community structure after flow restoration in a large river (French Rhône). *Freshw. Biol.* **60**, 1104–1117.
- Meyer, C.F.J., Fründ, J., Lizano, W.P. & Kalko, E.K.V. (2008). Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J. Appl. Ecol.* **45**, 381–391.
- Michelot, J.-L. (1983). Evolution des paysages fluviaux de la vallée du Rhône dans le secteur du Péage-de-Roussillon. *Géocarrefour* **58**, 307–322.
- Mikuś, P., Wyzga, B., Radecki-Pawlik, A., Zawiejska, J., Amirowicz, A. & Oglęcki, P. (2016). Environment-friendly reduction of flood risk and infrastructure damage in a mountain river: Case study of the Czarny Dunajec. *Geomorphology* **272**, 43–54.
- Miller, S.W., Budy, P. & Schmidt, J.C. (2010). Quantifying macroinvertebrate responses to in-stream habitat restoration: Applications of meta-analysis to river restoration. *Restor. Ecol.* **18**, 8–19.
- Milwright, R.D.P. (1998). Breeding biology of the Golden Oriole *Oriolus oriolus* in the fenland basin of eastern Britain. *Bird Study* **45**, 320–330.
- Molloy, D. (2011). *Wildlife at work. The economic impact of white-tailed eagles on the Isle of Mull*. The RSPB, Sandy.
- Morimoto, J., Shibata, M., Shida, Y. & Nakamura, F. (2017). Wetland restoration by natural succession in abandoned pastures with a degraded soil seed bank: Natural wetland restoration. *Restor. Ecol.* **25**, 1005–1014.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177.
- Muhar, S., Januschke, K., Kail, J., Poppe, M., Schmutz, S., Hering, D. & Buijse, A.D. (2016). Evaluating good-practice cases for river restoration across Europe: context, methodological framework, selected results and recommendations. *Hydrobiologia* **769**, 3–19.
- Müller, J., Jarzabek-Müller, A. & Bussler, H. (2013). Some of the rarest European saproxylic beetles are common in the wilderness of Northern Mongolia. *J. Insect Conserv.* **17**, 989–1001.
- Museum im Steintor (Ed.). (2009). *Anklam - Siedlung am Fluss: eine über 1000-jährige Geschichte im Spiegel der Archäologie; [Katalog anlässlich der*

Sonderausstellung "Verschüttet, vergessen, entdeckt" vom 17. Mai 2009 bis 21. September 2009 in Anklam]. Anklam.

- Navarro, L.M. & Pereira, H.M. (2012). Rewilding abandoned landscapes in Europe. *Ecosystems* **15**, 900–912.
- Navarro, L.M., Proença, V., Kaplan, J.O. & Pereira, H.M. (2015). Maintaining disturbance-dependent habitats. In *Rewilding European Landscapes*: 143–167. Pereira, H.M. & Navarro, L.M. (Eds.). Cham; Heidelberg; New York; Dordrecht; London: Springer International Publishing.
- Nichols, S. (1977). On the Interpretation of Principal Components Analysis in Ecological Contexts. *Vegetatio* **34**, 191–197.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science* **308**, 405–408.
- Nilsson, C., Riis, T., Sarneel, J.M. & Svavarsdóttir, K. (2018). Ecological restoration as a means of managing inland flood hazards. *BioScience* **68**, 89–99.
- Nogués-Bravo, D., Simberloff, D., Rahbek, C. & Sanders, N.J. (2016). Rewilding is the new Pandora's box in conservation. *Curr. Biol.* **26**, R87–R91.
- Ockendon, N., Thomas, D.H.L., Cortina, J., Adams, W.M., Aykroyd, T., Barov, B., Boitani, L., Bonn, A., Branquinho, C., Brombacher, M., Burrell, C., Carver, S., Crick, H.Q.P., Duguay, B., Everett, S., Fokkens, B., Fuller, R.J., Gibbons, D.W., Gokhelasvili, R., Griffin, C., Halley, D.J., Hotham, P., Hughes, F.M.R., Karamanlidis, A.A., McOwen, C.J., Miles, L., Mitchell, R., Rands, M.R.W., Roberts, J., Sandom, C.J., Spencer, J.W., ten Broeke, E., Tew, E.R., Thomas, C.D., Timoshyna, A., Unsworth, R.K.F., Warrington, S. & Sutherland, W.J. (2018). One hundred priority questions for landscape restoration in Europe. *Biol. Conserv.* **221**, 198–208.
- OED Online. (2018). *rewild*, v. *OED Online*.
- Olden, J.D., Konrad, C.P., Melis, T.S., Kennard, M.J., Freeman, M.C., Mims, M.C., Bray, E.N., Gido, K.B., Hemphill, N.P., Lytle, D.A., McMullen, L.E., Pyron, M., Robinson, C.T., Schmidt, J.C. & Williams, J.G. (2014). Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Front. Ecol. Environ.* **12**, 176–185.
- Olivier, J.-M., Dole-Olivier, M.-J., Amoros, C., Carrel, G., Malard, F., Lamouroux, N. & Bravard, J.-P. (2009). The Rhône river basin. In *Rivers of Europe*: 247–295. Elsevier.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* **51**, 933–938.

- O'Rourke, E., Charbonneau, M. & Poinot, Y. (2016). High nature value mountain farming systems in Europe: Case studies from the Atlantic Pyrenees, France and the Kerry Uplands, Ireland. *J. Rural Stud.* **46**, 47–59.
- Owen, R. (1848). *On the archetype and homologies of the Vertebrate skeleton*. Paternoster Row: John van Voorst.
- Paillex, A., Castella, E., zu Ermgassen, P.S.E. & Aldridge, D.C. (2015). Testing predictions of changes in alien and native macroinvertebrate communities and their interaction after the restoration of a large river floodplain (French Rhône). *Freshw. Biol.* **60**, 1162–1175.
- Paillex, A., Reichert, P., Lorenz, A.W. & Schuwirth, N. (2017). Mechanistic modelling for predicting the effects of restoration, invasion and pollution on benthic macroinvertebrate communities in rivers. *Freshw. Biol.* **62**, 1083–1093.
- Palmer, M. a., Bernhardt, E. s., Allan, J.D., Lake, P. s., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., Galat, D.L., Loss, S.G., Goodwin, P., Hart, D. d., Hassett, B., Jenkinson, R., Kondolf, G. m., Lave, R., Meyer, J. l., O'donnell, T. k., Pagano, L. & Sudduth, E. (2005). Standards for ecologically successful river restoration. *J. Appl. Ecol.* **42**, 208–217.
- Paracchini, M.L., Petersen, J.-E., Hoogeveen, Y., Bamps, C., Burfield, I. & van Swaay, C. (2008). *High Nature Value Farmland in Europe. An estimate of the distribution patterns on the basis of land cover and biodiversity data*. Institute for Environment and Sustainability, Luxembourg.
- Parajka, J., Kohnova, S., Balint, G., Barbuc, M., Borga, M., Claps, P., Cheval, S., Dumitrescu, A., Gaume, E., Hlavcova, K., Merz, R., Pfaundler, M., Stancalie, G., Szolgay, J. & Blöschl, G. (2010). Seasonal characteristics of flood regimes across the Alpine-Carpathian range. *J. Hydrol.* **394**, 78–89.
- Patthey, P., Signorell, N., Rotelli, L. & Arlettaz, R. (2012). Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. *Eur. J. Wildl. Res.* **58**, 59–70.
- Pearce, F. (2013). A successful push to restore Europe's long-abused rivers. *Yale Environ.* **360**.
- Pedersen, M.L., Andersen, J.M., Nielsen, K. & Linnemann, M. (2007). Restoration of Skjern River and its valley: Project description and general ecological changes in the project area. *Ecol. Eng.*, Wetland restoration at the Society for Ecological Restoration International Conference in Zaragoza, Spain **30**, 131–144.
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Schwartz, A., Sutherland, W.J., Turbé, A., Wulf, F. & Scott, A.V. (2014). EU agricultural reform fails on biodiversity. *Science* **344**, 1090–1092.
- Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A.S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature* **540**, 418–422.

- Pereira, H.M. & Navarro, L.M. (Eds.). (2015). *Rewilding European landscapes*. Cham: Springer International Publishing.
- Pettorelli, N., Barlow, J., Stephens, P.A., Durant, S.M., Connor, B., Schulte to Bühne, H., Sandom, C.J., Wentworth, J. & du Toit, J.T. (2018). Making rewilding fit for policy. *J. Appl. Ecol.* **55**, 1114–1125.
- Pfadenhauer, J. & Klötzli, F. (1996). Restoration experiments in middle European wet terrestrial ecosystems: an overview. *Vegetatio* **126**, 101–115.
- Phalan, B., Green, R.E., Dicks, L.V., Dotta, G., Feniuk, C., Lamb, A., Strassburg, B.B.N., Williams, D.R., Ermgassen, E.K.H.J. zu & Balmford, A. (2016). How can higher-yield farming help to spare nature? *Science* **351**, 450–451.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011). Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. *Science* **333**, 1289–1291.
- Pilkington, M., Mount, D., Walker, J., Allott, T., Ashton-Waird, R., Evans, M., Hammond, G., Huggett, D., Nisbet, T. & Rose, S. (2015). *Appraisal of the three UK multi-demonstration projects*. Moors for the Future Partnership, Edale, Derbyshire, UK.
- Poff, N.L. & Hart, D.D. (2002). How dams vary and why it matters for the emerging science of dam removal. *BioScience* **52**, 659–668.
- Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biol. Conserv.* **12**, 115–134.
- Pons, P., Lambert, B., Rigolot, E. & Prodon, R. (2003). The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. *Biodivers. Conserv.* **12**, 1843–1860.
- POST. (2011). *Natural flood management* (POSTnote No. 396). The Parliamentary Office of Science and Technology, London.
- Potter, K., Ludwig, C. & Beattie, C. (2016). Responding to a ‘flood of criticism’: analysing the ebbs and flows of planning and floodplain development in England (1926–2015). *Town Plan. Rev.* **87**, 125–138.
- Powell, S.J., Jakeman, A. & Croke, B. (2014). Can NDVI response indicate the effective flood extent in macrophyte dominated floodplain wetlands? *Ecol. Indic.* **45**, 486–493.
- Price, T.D. (Ed.). (2000). *Europe’s first farmers*. New York: Cambridge University press.
- Princé, K. & Jiguet, F. (2013). Ecological effectiveness of French grassland agri-environment schemes for farmland bird communities. *J. Environ. Manage.* **121**, 110–116.
- Princé, K., Moussus, J.-P. & Jiguet, F. (2012). Mixed effectiveness of French agri-environment schemes for nationwide farmland bird conservation. *Agric. Ecosyst. Environ.* **149**, 74–79.

- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rackham, O. (2000). *The history of the countryside: the classic history of Britain's landscape, flora and fauna*. London: Phoenix Press.
- Raith, S. (1999). The Rhine Action Program: Restoring value to the Rhine river. *Restor. Reclam. Rev.* **4**, 1–9.
- Ratajczak, Z., Nippert, J.B., Briggs, J.M. & Blair, J.M. (2014). Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *J. Ecol.* **102**, 1374–1385.
- Raven, P. (1986). Changes in the breeding bird population of a small clay river following flood alleviation works. *Bird Study* **33**, 24–35.
- REFORM Policy brief*. (2015). . REFORM.
- Regos, A., Domínguez, J., Gil-Tena, A., Brotons, L., Ninyerola, M. & Pons, X. (2016). Rural abandoned landscapes and bird assemblages: winners and losers in the rewilding of a marginal mountain area (NW Spain). *Reg. Environ. Change* **16**, 199–211.
- RESTORE. (2017). RiverWiki [WWW Document]. URL https://restorerivers.eu/wiki/index.php?title=Main_Page
- Ribeiro, P.F., Santos, J.L., Bugalho, M.N., Santana, J., Reino, L., Beja, P. & Moreira, F. (2014). Modelling farming system dynamics in High Nature Value Farmland under policy change. *Agric. Ecosyst. Environ.* **183**, 138–144.
- Richards, K., Brasington, J. & Hughes, F. (2002). Geomorphic dynamics of floodplains: ecological implications and a potential modelling strategy. *Freshw. Biol.* **47**, 559–579.
- Richards, K., Girel, J., Moss, T., Muller, E., Nilsson, C. & Rood, S. (2003). *The Flooded Forest: Guidance for policy makers and river managers in Europe on the restoration of floodplain forests*. FLOBAR2 Project, Department of Geography, University of Cambridge, Cambridge, UK.
- Richter, B.D., Baumgartner, J.V., Braun, D.P. & Powell, J. (1998). A spatial assessment of hydrologic alteration within a river network. *Regul. Rivers Res. Manag.* **14**, 329–340.
- Ridout, M., Hinde, J. & DeméAtrio, C.G.B. (2001). A score test for testing a zero-inflated Poisson regression model against zero-inflated negative binomial alternatives. *Biometrics* **57**, 219–223.
- Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.* **35**, 491–522.

- Riquier, J., Piégay, H. & Šulc Michalková, M. (2015). Hydromorphological conditions in eighteen restored floodplain channels of a large river: linking patterns to processes. *Freshw. Biol.* **60**, 1085–1103.
- Roni, P., Hanson, K. & Beechie, T. (2008). Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North Am. J. Fish. Manag.* **28**, 856–890.
- Room for the River (English) [WWW Document]. (2014). *Ruimte Voor Rivier*. URL <https://www.ruimtevoorderivier.nl/english/>
- Rost, J., Clavero, M., Brotons, L. & Pons, P. (2012). The effect of postfire salvage logging on bird communities in Mediterranean pine forests: the benefits for declining species. *J. Appl. Ecol.* **49**, 644–651.
- Rottier, T. (2013). Le Rhône : un enjeu lyonnais, un enjeu européen [WWW Document]. *Solidar. Prog. Lyon*. URL <http://lyon.solidariteetprogres.org/le-rhone-un-enjeu-lyonnais-un-enjeu-europeen/>
- Rubenstein, D.R. & Rubenstein, D.I. (2016). From Pleistocene to trophic rewilding: A wolf in sheep's clothing. *Proc. Natl. Acad. Sci.* **113**, E1–E1.
- Rundlöf, M., Bengtsson, J. & Smith, H.G. (2008). Local and landscape effects of organic farming on butterfly species richness and abundance. *J. Appl. Ecol.* **45**, 813–820.
- Sandel, B., Corbin, J.D. & Krupa, M. (2011). Using plant functional traits to guide restoration: A case study in California coastal grassland. *Ecosphere* **2**, 1–16.
- Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. (2014a). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. Lond. B Biol. Sci.* **281**, 20133254.
- Sandom, C.J., Clouttick, D., Manwill, M. & Bull, J.W. (2016). *Rewilding knowledge hub: Bibliography*. Wild Business Ltd, London.
- Sandom, C.J., Ejrnæs, R., Hansen, M.D.D. & Svenning, J.-C. (2014b). High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proc. Natl. Acad. Sci.* **111**, 4162–4167.
- Sandom, C.J., Hughes, J. & Macdonald, D.W. (2013). Rooting for rewilding: Quantifying wild boar's *Sus scrofa* rooting rate in the Scottish Highlands. *Restor. Ecol.* **21**, 329–335.
- Sandom, C.J. & MacDonald, D.W. (2015). What next? Rewilding as a radical future for the British countryside. In *Wildlife Conservation on Farmland*: 291. MacDonald, D.W. & Feber, R.E. (Eds.). Oxford: Oxford University Press.
- Schepers, F. & Bosman, I. (2015). *Rewilding Europe Annual Review 2014*. Rewilding Europe, Nijmegen.
- Schindler, S., O'Neill, F.H., Biró, M., Damm, C., Gasso, V., Kanka, R., van der Sluis, T., Krug, A., Lauwaars, S.G., Sebesvari, Z., Pusch, M., Baranovsky, B., Ehlert, T., Neukirchen, B., Martin, J.R., Euler, K., Mauerhofer, V. & Wrška, T. (2016).

Multifunctional floodplain management and biodiversity effects: a knowledge synthesis for six European countries. *Biodivers. Conserv.* **25**, 1349–1382.

Schindler, U., Behrendt, A. & Müller, L. (2003). Change of soil hydrological properties of fens as a result of soil development. *J. Plant Nutr. Soil Sci.* **166**, 357–363.

Schneider, E. (2014). Aspects of wetland habitat restoration and monitoring in the Danube Delta: Water macrophytes as quality indicators in evaluation processes. *Acta Zool. Bulg.* **7**, 97–102.

Schrautzer, J., Breuer, V., Holsten, B., Jensen, K. & Rasran, L. (2016). Long-term effects of large-scale grazing on the vegetation of a rewetted river valley. *Agric. Ecosyst. Environ.* **216**, 207–215.

Seidl, R., Schelhaas, M. & Lexer, M.J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Change Biol.* **17**, 2842–2852.

Sellheim, K.L., Vaghti, M. & Merz, J.E. (2016). Vegetation recruitment in an enhanced floodplain: ancillary benefits of salmonid habitat enhancement. *Limnol. - Ecol. Manag. Inland Waters* **58**, 94–102.

Shafroth, P.B., Stromberg, J.C. & Patten, D.T. (2002). Riparian vegetation response to altered disturbance and stress regimes. *Ecol. Appl.* **12**, 107–123.

Sills, N. & Hirons, G. (2011). From carrots to cranes: the creation of RSPB Lakenheath Fen, Suffolk. *Br. Wildl.* **22**, 381–390.

Sirami, C., Brotons, L. & Martin, J. (2011). Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment. *Bird Study* **58**, 99–106.

Skublics, D., Blöschl, G. & Rutschmann, P. (2016). Effect of river training on flood retention of the Bavarian Danube. *J. Hydrol. Hydromech.* **64**, 349–356.

Šmilauer, P. & Lepš, J. (2014). *Multivariate analysis of ecological data using Canoco 5*. Second edition. Cambridge, United Kingdom ; New York: Cambridge University Press.

Smith, P.L. (2018). Copying ancient woodlands: a positive perspective. *Biodivers. Conserv.* **27**, 1041–1053.

Snow, D., Perrins, C.M. & Gillmor, R. (1998). *The birds of the Western Palearctic*. Concise ed. Oxford ; New York: Oxford University Press.

Society for Ecological Restoration International Science & Policy Working Group. (2004). *The SER International primer on ecological restoration*. Society for Ecological Restoration International, Tuscon, Arizona.

Sourial, N., Wolfson, C., Zhu, B., Quail, J., Fletcher, J., Karunanathan, S., Bandeen-Roche, K., Béland, F. & Bergman, H. (2010). Correspondence analysis is a useful tool to uncover the relationships among categorical variables. *J. Clin. Epidemiol.* **63**, 638–646.

- Stammel, B., Fischer, P., Gelhaus, M. & Cyffka, B. (2016). Restoration of ecosystem functions and efficiency control: case study of the Danube floodplain between Neuburg and Ingolstadt (Bavaria/Germany). *Environ. Earth Sci.* **75**, 1174.
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R. de & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* **63**, 337–365.
- Streitberger, M. & Fartmann, T. (2016). Vegetation heterogeneity caused by an ecosystem engineer drives oviposition-site selection of a threatened grassland insect. *Arthropod-Plant Interact.* **10**, 545–555.
- Strohbach, M.W., Kohler, M.L., Dauber, J. & Klimek, S. (2015). High Nature Value farming: From indication to conservation. *Ecol. Indic.* **57**, 557–563.
- Sutfin, N.A., Wohl, E.E. & Dwire, K.A. (2015). Banking carbon: a review of organic carbon storage and physical factors influencing retention in floodplains and riparian ecosystems. *Earth Surf. Process. Landf.* **41**, 38–60.
- Sutherland, W.J. (Ed.). (1996). *Ecological census techniques: a handbook*. Cambridge ; New York: Cambridge University Press.
- Svenning, J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biol. Conserv.* **104**, 133–148.
- Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.M., Sandel, B., Sandom, C.J., Terborgh, J.W. & Vera, F.W.M. (2015). Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci.* 201502556.
- Svensson, L., Grant, P.J., Mullarney, K., Zetterström, D. & Christie, D.S. (2009). *Collins bird guide: the most complete field guide to the birds of Britain and Europe*. 2nd Edition. London: HarperCollins.
- van Swaay, C., Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašić, M., Settele, J., Verovnik, R., Verstrael, T., Warren, M., Wiemers, M. & Wynhof, I. (2010). *European Red List of Butterflies*. Publications Office of the European Union, Luxembourg.
- van Swaay, C., Warren, M. & Lois, G. (2006). Biotope use and trends of European butterflies. *J. Insect Conserv.* **10**, 189–209.
- van Swaay, C.A.M., Brereton, T., Kirkland, P. & Warren, M.S. (2012). *Manual for butterfly monitoring* (No. VS2012.010). De Vlinderstichting/Dutch Butterfly Conservation, Butterfly Conservation UK & Butterfly Conservation Europe, Wageningen.
- Tansley, A.G. (1939). *The British Islands and their vegetation*. Cambridge University Press.
- Terrier, C. & Bouffard, W. (2003). *Assessment of developments and water management along the Rhone river - France, for the past 60 years*. Zhengzhou: Yellow River Conservancy Press.

- Thomas, C.D. (2009). A speculative history of open-country species in Britain and northern Europe. *Br. Wildl.* **20**, 21.
- Thomas, C.D. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends Ecol. Evol.* **26**, 216–221.
- Thomas, J.A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos. Trans. R. Soc. B Biol. Sci.* **360**, 339–357.
- Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**, 1879–1881.
- Ticehurst, C., Guerschman, J.P. & Chen, Y. (2014). The strengths and limitations in using the daily MODIS open water likelihood algorithm for identifying flood events. *Remote Sens.* **6**, 11791–11809.
- Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *Am. Nat.* **125**, 827–852.
- Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011). Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad. Sci.* **108**, 20260–20264.
- Timmermann, T., Margóczy, K., Takács, G. & Vegelin, K. (2006). Restoration of peat-forming vegetation by rewetting species-poor fen grasslands. *Appl. Veg. Sci.* **9**, 241–250.
- Tockner, K. & Stanford, J.A. (2002). Riverine flood plains: present state and future trends. *Environ. Conserv.* **29**, 308–330.
- Tolman, T. & Lewington, R. (2009). *Collins butterfly guide: the most complete guide to the butterflies of Britain and Europe*. London: Collins.
- Toth, L.A. (2017). Variant restoration trajectories for wetland plant communities on a channelized floodplain: River floodplain restoration. *Restor. Ecol.* **25**, 342–353.
- van Turnhout, C. a. M., Leuven, R.S.E.W., Hendriks, A.J., Kurstjens, G., van Strien, A., Foppen, R.P.B. & Siepel, H. (2012). Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds. *River Res. Appl.* **28**, 269–282.
- UNEP-WCMC & IUCN. (2018). Protected planet: The world database on protected areas (WDPA) [WWW Document]. URL <https://www.protectedplanet.net/555540855>
- USDA. (2018). National nutrient database for standard reference [WWW Document]. URL <https://ndb.nal.usda.gov/ndb/search/list?home=true>
- USGS. (2017). *Landsat collection 1 level 1 product definition* (No. LSDS-1656). Department of the Interior, U.S. Geological Survey, Sioux Falls, South Dakota.

- USGS. (2018). SLC-off products: Background [WWW Document]. URL <https://landsat.usgs.gov/slc-products-background>
- Van Dijk, A., Mueller, N., Lymburner, L., Byrne, G., Warren, G. & Guerschman, J. (2011). *MODIS-based standing water detection for flood and large reservoir mapping: Algorithm development and applications for the Australian continent* (National Flagship Report). , Water for a Healthy Country Flagship Report. CSIRO, Canberra.
- Vaughan, I.P. & Ormerod, S.J. (2005). Increasing the value of principal components analysis for simplifying ecological data: a case study with rivers and river birds. *J. Appl. Ecol.* **42**, 487–497.
- Veblen, T. (1992). Revegetation dynamics. In *Plant succession. An analysis of the development of vegetation*, Population and Community Biology. Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (Eds.). London: Chapman and Hall.
- Vera, F.W.M. (2000). *Grazing ecology and forest history*. Wallingford, Oxon; New York, NY: CABI Pub.
- WallisDeVries, M.F. (2014). Linking species assemblages to environmental change: Moving beyond the specialist-generalist dichotomy. *Basic Appl. Ecol.* **15**, 279–287.
- Ward, J.V. & Stanford, J.A. (2006). Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regul. Rivers Res. Manag.* **11**, 105–119.
- Ward, J.W. & Stanford, J.A. (1983). Intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. *Dyn. Lotic Syst. Ann Arbor Sci. Ann Arbor MI 1983 347-356 P 2 Fig 35 Ref.*
- Waterstraat, A. & Krappe, M. (1998). Distribution and abundance of *Lampetra planan* populations in the Peene drainage (NE Germany) in relation to isolation and habitat conditions. *Ital. J. Zool.* **65**, 137–143.
- Watt, A.S. (1947). Pattern and process in the plant community. *J. Ecol.* **35**, 1–22.
- Waylen, K.A., Holstead, K.L., Colley, K. & Hopkins, J. (2018). Challenges to enabling and implementing Natural Flood Management in Scotland: Challenges to enabling and implementing NFM. *J. Flood Risk Manag.* **11**, S1078–S1089.
- Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Wigier, M. (2014). The competitiveness of Polish agriculture after accession to the EU. *Econ. Agric.* **61**.
- Wilkinson, D.M. (1999). The disturbing history of intermediate disturbance. *Oikos* **84**, 145–147.
- Williams, D.R., Alvarado, F., Green, R.E., Manica, A., Phalan, B. & Balmford, A. (2017). Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico. *Glob. Change Biol.* **23**, 5260–5272.

- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.*, Conserving complexity: Global change and community-scale interactions **143**, 2280–2291.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027.
- Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. (1997). Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *J. Appl. Ecol.* **34**, 1462–1478.
- Wohl, E. (2015). Legacy effects on sediments in river corridors. *Earth-Sci. Rev.* **147**, 30–53.
- Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture—a key element for conservation in the developing world. *Conserv. Lett.* **5**, 11–19.
- xeno-canto.org [WWW Document]. (2018). *Xeno-Canto Shar. Bird Sounds World*. URL <https://www.xeno-canto.org/>
- Xu, H. (2006). Modification of normalised difference water index (NDWI) to enhance open water features in remotely sensed imagery. *Int. J. Remote Sens.* **27**, 3025–3033.
- Zak, D. & Gelbrecht, J. (2007). The mobilisation of phosphorus, organic carbon and ammonium in the initial stage of fen rewetting (a case study from NE Germany). *Biogeochemistry* **85**, 141–151.
- Zerbe, S., Steffenhagen, P., Parakenings, K., Timmermann, T., Frick, A., Gelbrecht, J. & Zak, D. (2013). Ecosystem service restoration after 10 years of rewetting peatlands in NE Germany. *Environ. Manage.* **51**, 1194–1209.
- Zhang, F., Zhu, X. & Liu, D. (2014). Blending MODIS and Landsat images for urban flood mapping. *Int. J. Remote Sens.* **35**, 3237–3253.
- Zimov, S.A. (2005). Pleistocene Park: Return of the mammoth's ecosystem. *Science* **308**, 796–798.
- Zingraff-Hamed, A., Greulich, S., Pauleit, S. & Wantzen, K.M. (2017). Urban and rural river restoration in France: a typology. *Restor. Ecol.*
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). Zero-truncated and zero-inflated models for count data. In *Mixed effects models and extensions in ecology with R*, Statistics for Biology and Health: 261–293. Springer, New York, NY.
- Zweckverband Peenetal-Landschaft [WWW Document]. (2018). *Zweckverb. Peen.-Landsch.* URL <http://peenetal-landschaft.de/>

APPENDICES

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APPENDIX 1. LIST OF TYPES OF DISTURBANCE RECORDED

Type of Disturbance	Category	Score	Description
Animal Prints	Other Animal Signs	1 for each animal's prints	Footprints from an animal (species not identified)
Animal Trail	Other Animal Signs	1 for each trail (for example a trail with a fork would be scored 2)	A trail of disturbed vegetation or bare ground made by animals (species not identified) walking the same route repeatedly.
Ants' Nest	Other Animal Signs	1 for each patch (NB – nests may have multiple entrances/exits, each of which has a patch)	Patch of bare ground or mound of soil around an ants' nest
Badger Hole	Other Animal Signs	1 for each hole (a sett may have multiple holes)	Entrance/exit to a badger sett
Beaver Canal	Beaver	1 for each canal	Deep, flooded trail made by beavers.
Beaver Dam	Beaver	1 for each dam	Dam of wood/mud made by beavers.
Beaver Gnawed Stump	Beaver	1 for each stump (multiple gnawed stems of the same plant score multiply)	Stump of a tree having being felled by beavers.
Beaver Hole	Beaver	1 for each hole	Entrance to a beaver lodge.
Beaver Lodge	Beaver	1 for each lodge	Large structure of wood and mud made by beavers as a residence.
Beaver Trail	Beaver	1 for each trail	As animal trail, but evidently made by beavers (based on for example size, circumstance)

Type of Disturbance	Category	Score	Description
Boar	Boar	1 for each animal	Boar seen during transect
Boar “nest”	Boar	1 for each nest	Area of flattened vegetation where a boar has overnighted
Boar Poo	Boar	1 for each defecation event (regardless of size)	Droppings from a wild boar
Boar Scrape	Boar	Area in m ²	Area of disturbed ground where boars have been foraging
Canal	Human	1 for each canal	Artificial waterway created by humans for transport or drainage
Cow Pat	Human	1 for each pat	A cow pat
Cow Prints	Human	1 for each animal’s prints	Footprints from a cow
Deer “nest”	Deer	1 for each nest	Area of flattened vegetation where a deer has overnighted
Deer Poo	Deer	1 for each defecation event (regardless of number of pellets)	Droppings from a deer (species not identified)
Deer Prints	Deer	1 for each animal’s prints	Footprints from a deer (species not identified)
Deer Scrape	Deer	Area in m ²	Area of bare ground created by deer foraging
Deer Trail	Deer	1 for each trail	As animal trail, but evidently made by deer (based on for example size, circumstance)
Deer/boar “nest”	Other animal signs	1 for each nest	Area of flattened vegetation where a deer/boar (species not identified) has overnighted

Type of Disturbance	Category	Score	Description
Elk Poo	Elk	1 for each defecation event (regardless of number of pellets)	Droppings from an elk
Elk Prints	Elk	1 for each animal's prints	Footprints from an elk
Elk Trail	Elk	1 for each trail	As animal trail, but evidently made by elk (based on for example size, circumstance)
Excavation	Human	Area in m ²	Area where peat has been removed by humans (for burning etc.)
Fire	Fire	Area in m ²	Area showing evidence of recent fire (for example burnt vegetation)
Fire break	Human	1 for each break	Large trench dug in ground to reduce chances of fire spreading
Furrows	Human	Area in m ²	Trenches dug for agricultural purposes
Grazing	Human	Area in m ²	Area with evidence of grazing by livestock
Horse	Human	1 for each horse	Horses present
Horse Poo	Human	1 for each defecation event	Droppings from a horse
Logging	Human	Area in m ²	Area of logged forest
Mole Hill	Other Animal Signs	1 for each mound	Mound of soil created by moles
Mowing	Human	Area in m ²	Area of mown vegetation

Type of Disturbance	Category	Score	Description
Poo	Other Animal Signs	1 for each defecation event	Droppings (species not identified)
Rodent Burrow	Other Animal Signs	1 for each burrow	Burrow of a rodent (species not identified)
Roe Deer	Deer	1 for each animal	Roe deer seen during transect
Scrape	Other Animal Signs	Area in m ²	Area of disturbed vegetation and soil (species not identified)
Track (Human)	Human	1 for each track	Artificially surfaced path (not suitable for vehicles)
Track (Vehicle)	Human	1 for each track	Artificially surfaced path (suitable for vehicles)
Trail	Human	1 for each trail	A trail of disturbed vegetation or bare ground made by people walking the same route repeatedly.

APPENDIX 2. LIST OF HNV SPECIES

Lists of species associated with HNV farming systems. From (Paracchini *et al.*, 2008)

HNV Birds

Black-crowned night-heron <i>Nycticorax nycticorax</i>	Booted eagle <i>Hieraaetus pennatus</i>
White stork <i>Ciconia ciconia</i>	Bonelli's eagle <i>Hieraaetus fasciatus</i>
Mute swan <i>Cygnus olor</i>	Lesser kestrel <i>Falco naumanni</i>
Tundra swan <i>Cygnus columbianus</i>	Kestrel <i>Falco tinnunculus</i>
Whooper swan <i>Cygnus cygnus</i>	Red-footed falcon <i>Falco vespertinus</i>
Bean goose <i>Anser fabalis</i>	Lanner falcon <i>Falco biarmicus</i>
Pink-footed goose <i>Anser brachyrhynchus</i>	Saker falcon <i>Falco cherrug</i>
Greater white-fronted goose <i>Anser albifrons</i>	Black grouse <i>Tetrao tetrix</i>
Lesser white-fronted goose <i>Anser erythropus</i>	Chukar <i>Alectoris chukar</i>
Greylag goose <i>Anser anser</i>	Red-legged partridge <i>Alectoris rufa</i>
Barnacle goose <i>Branta leucopsis</i>	Black francolin <i>Francolinus francolinus</i>
Brent goose <i>Branta bernicla</i>	Grey partridge <i>Perdix perdix</i>
Red-breasted goose <i>Branta ruficollis</i>	Common quail <i>Coturnix coturnix</i>
Garganey <i>Anas querquedula</i>	Spotted crake <i>Porzana porzana</i>
Black-winged kite <i>Elanus caeruleus</i>	Corncrake <i>Crex crex</i>
Black kite <i>Milvus migrans</i>	Crane <i>Grus grus</i>
Red kite <i>Milvus milvus</i>	Little bustard <i>Tetrax tetrax</i>
Egyptian vulture <i>Neophron percnopterus</i>	Houbara bustard <i>Chlamydotis undulata</i>
Griffon vulture <i>Gyps fulvus</i>	Great bustard <i>Otis tarda</i>
Cinereous vulture <i>Aegypius monachus</i>	Oystercatcher <i>Haematopus ostralegus</i>
Short-toed snake-eagle <i>Circaetus gallicus</i>	Stone curlew <i>Burhinus oediconemus</i>
Hen harrier <i>Circus cyaneus</i>	Cream-coloured courser <i>Cursorius cursor</i>
Montagu's harrier <i>Circus pygargus</i>	Collared pratincole <i>Glareola pratincola</i>
Levant sparrowhawk <i>Accipiter brevipes</i>	Golden plover <i>Pluvialis apricaria</i>
Long-legged buzzard <i>Buteo rufinus</i>	Lapwing <i>Vanellus vanellus</i>
Lesser spotted eagle <i>Aquila pomarina</i>	Ruff <i>Philomachus pugnax</i>
Greater spotted eagle <i>Aquila clanga</i>	Snipe <i>Gallinago gallinago</i>
Eastern imperial eagle <i>Aquila heliaca</i>	Great snipe <i>Gallinago media</i>
Spanish imperial eagle <i>Aquila adalberti</i>	Black-tailed godwit <i>Limosa limosa</i>
	Curlew <i>Numenius arquata</i>
	Redshank <i>Tringa totanus</i>
	Black-bellied sandgrouse <i>Pterocles orientalis</i>

Pin-tailed sandgrouse <i>Pterocles alchata</i>	Fieldfare <i>Turdus pilaris</i>
Stock dove <i>Columba oenas</i>	Redwing <i>Turdus iliacus</i>
Turtle dove <i>Streptopelia turtur</i>	Grasshopper warbler <i>Locustella naevia</i>
Barn owl <i>Tyto alba</i>	River warbler <i>Locustella fluviatilis</i>
Scops owl <i>Otus scops</i>	Aquatic warbler <i>Acrocephalus paludicola</i>
Little owl <i>Athene noctua</i>	Olivaceous warbler <i>Hippolais pallida</i>
Short-eared owl <i>Asio flammeus</i>	Olive-tree warbler <i>Hippolais olivetorum</i>
Bee-eater <i>Merops apiaster</i>	Orphean Warbler <i>Sylvia hortensis</i>
Roller <i>Coracias garrulus</i>	Barred Warbler <i>Sylvia nisoria</i>
Hoopoe <i>Upupa epops</i>	Whitethroat <i>Sylvia communis</i>
Wryneck <i>Jynx torquilla</i>	Red-backed shrike <i>Lanius collurio</i>
Green woodpecker <i>Picus viridis</i>	Lesser grey shrike <i>Lanius minor</i>
Syrian woodpecker <i>Dendrocopos syriacus</i>	Great grey shrike <i>Lanius excubitor</i>
Dupont's lark <i>Chersophilus duponti</i>	Woodchat shrike <i>Lanius senator</i>
Calandra lark <i>Melanocorypha calandra</i>	Masked shrike <i>Lanius nubicus</i>
Greater short-toed lark <i>Calandrella brachydactyla</i>	Red-billed chough <i>Pyrrhocorax pyrrhocorax</i>
Lesser short-toed lark <i>Calandrella rufescens</i>	Jackdaw <i>Corvus monedula</i>
Crested lark <i>Galerida cristata</i>	Rook <i>Corvus frugilegus</i>
Thekla lark <i>Galerida theklae</i>	Tree sparrow <i>Passer montanus</i>
Wood lark <i>Lullula arborea</i>	Canary <i>Serinus canaria</i>
Skylark <i>Alauda arvensis</i>	Eurasian linnet <i>Carduelis cannabina</i>
Swallow <i>Hirundo rustica</i>	Twite <i>Carduelis flavirostris</i>
Tawny pipit <i>Anthus campestris</i>	Trumpeter Finch <i>Bucanetes githagineus</i>
Yellow wagtail <i>Motacilla flava</i>	Yellowhammer <i>Emberiza citrinella</i>
Rufous-tailed scrub-robin <i>Erythropygia galactotes</i>	Cirl bunting <i>Emberiza cirlus</i>
Whinchat <i>Saxicola rubetra</i>	Ortolan bunting <i>Emberiza hortulana</i>
Stonechat <i>Saxicola torquatus</i>	Reed bunting <i>Emberiza schoeniclus</i>
Wheatear <i>Oenanthe oenanthe</i>	Black-headed bunting <i>Emberiza melanocephala</i>
Black-eared wheatear <i>Oenanthe hispanica</i>	Corn bunting <i>Miliaria calandra</i>

HNV Butterflies

Lorkovic's brassy ringlet <i>Erebia calcaria</i>	Corsican swallowtail <i>Papilio hospiton</i>
Rätzer's ringlet <i>Erebia Christi</i>	Spanish zephyr blue <i>Plebeius hespericus</i>
Sudeten ringlet <i>Erebia sudetica</i>	Alpine zephyr blue <i>Plebeius trappi</i>
Apollo <i>Parnassius apollo</i>	Mesopotamian blue <i>Polyommatus dama</i>
Sierra Nevada blue <i>Polyommatus golgus</i>	Gallo's anomalous blue <i>Polyommatus galloi</i>
Corsican fritillary <i>Argynnis elisa</i>	Piedmont anomalous blue <i>Polyommatus humedasaë</i>
Spring ringlet <i>Erebia epistygne</i>	<i>Pseudochazara euxina</i>
Azores grayling <i>Hipparchia azorina/H. occidentalis</i>	Cinquefoil skipper <i>Pyrgus cirsii</i>
Le Cerf's grayling <i>Hipparchia miguelensis</i>	Scarce heath <i>Coenonympha hero</i>
Grecian copper <i>Lycaena ottomanus</i>	False ringlet <i>Coenonympha oedippus</i>
Large blue <i>Maculinea arion</i>	Marsh fritillary <i>Euphydryas aurinia</i>
Mountain Alcon blue <i>Maculinea rebeli</i>	Dusky large blue <i>Maculinea nausithous</i>
Italian marbled white <i>Melanargia arge</i>	Scarce large blue <i>Maculinea teleius</i>

APPENDIX 3. SENSITIVITY ANALYSES OF COMPARISONS BETWEEN BIRD SPECIES' POPULATION DENSITIES IN POLAND AND UKRAINE

These plots compare population densities in Poland and Ukraine, in farmland and in natural habitats and are thus similar to Figure 3.20 and Figure 3.21; please refer to Chapter 3 for full details. Two variations on the analysis are presented here. In the first analysis, the density in Polish farmland in these plots is the maximum estimated density at any yield. In the second analysis, the density in Polish sites is the estimated density in sites on wetland soils only (including both natural baseline sites and farmland on wetland soils; see Feniuk, 2015, for full details).

Maximum farmland density: HNV species

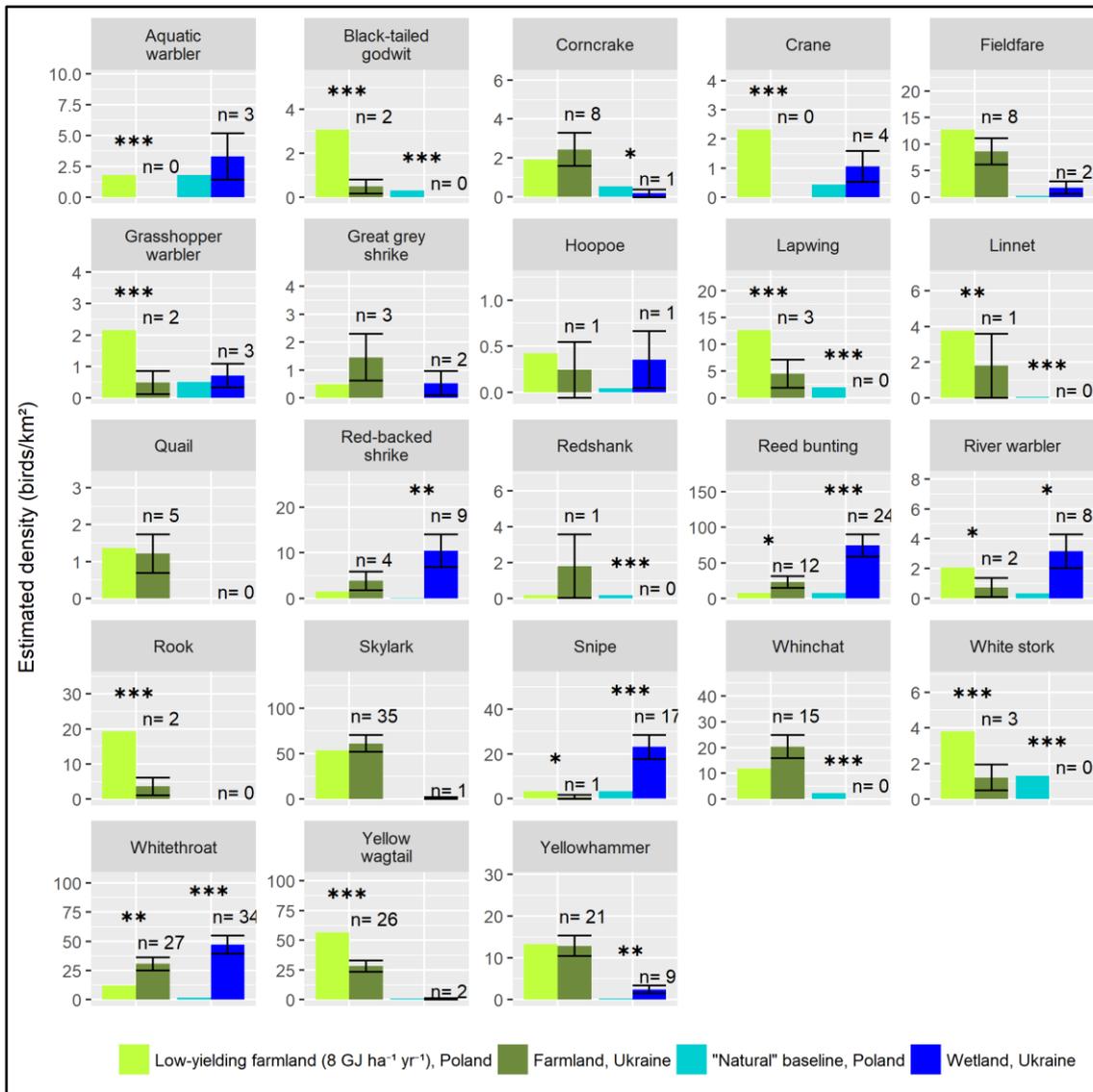


Figure A2.0.1 – Estimated population density of HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from Feniuk (2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and choosing the maximum density at any yield for farmland. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine. There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

Maximum farmland density: Non-HNV species

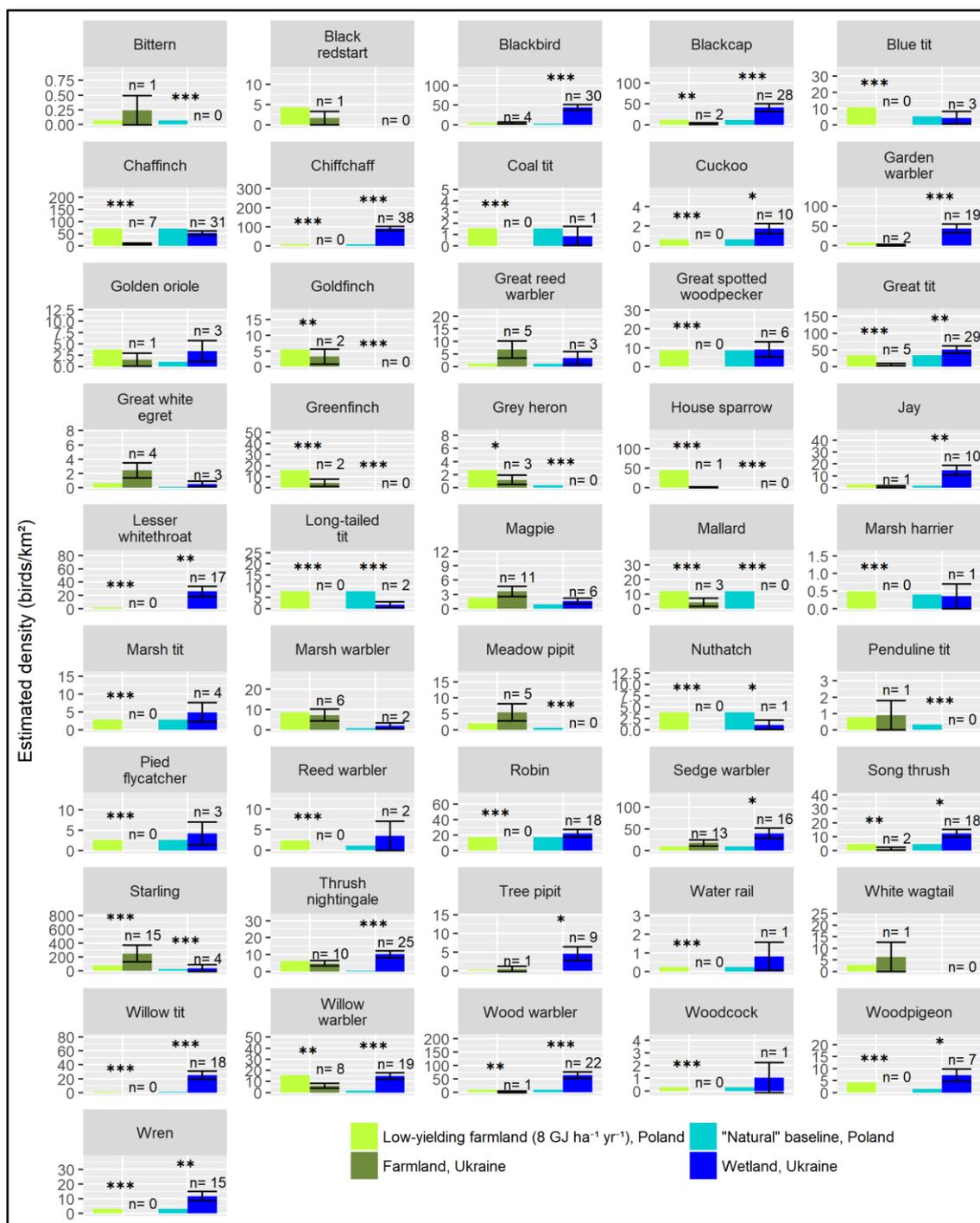


Figure A2.0.2 – Estimated population density of non-HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from (Feniuk, 2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and choosing the maximum density at any yield for farmland. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine. There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

Wetland soils only: HNV species

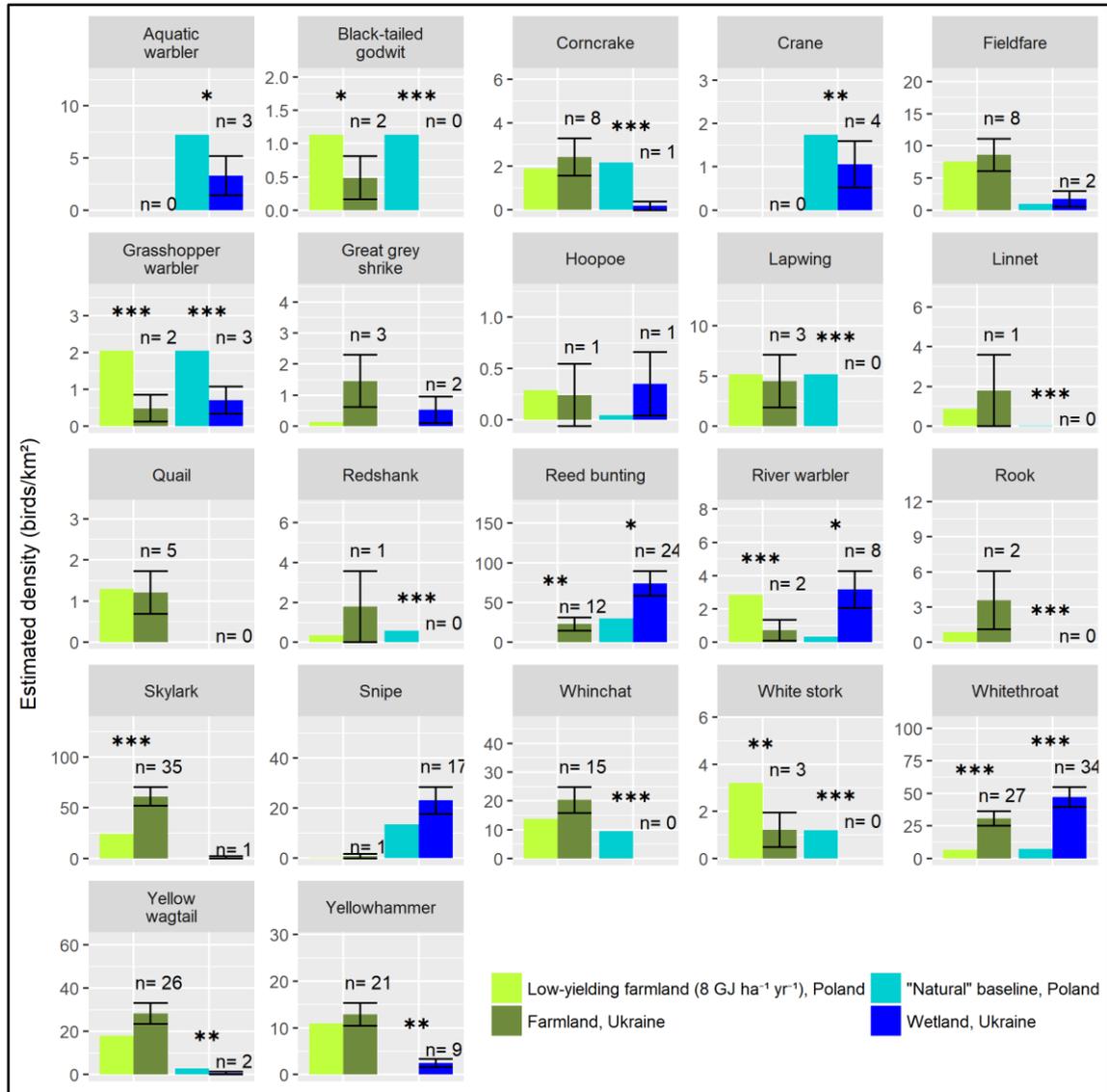


Figure A2.0.3 – Estimated population density of HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from Feniuk (2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland, both on wetland soils only. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine). There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

Wetland soils only: Non-HNV species

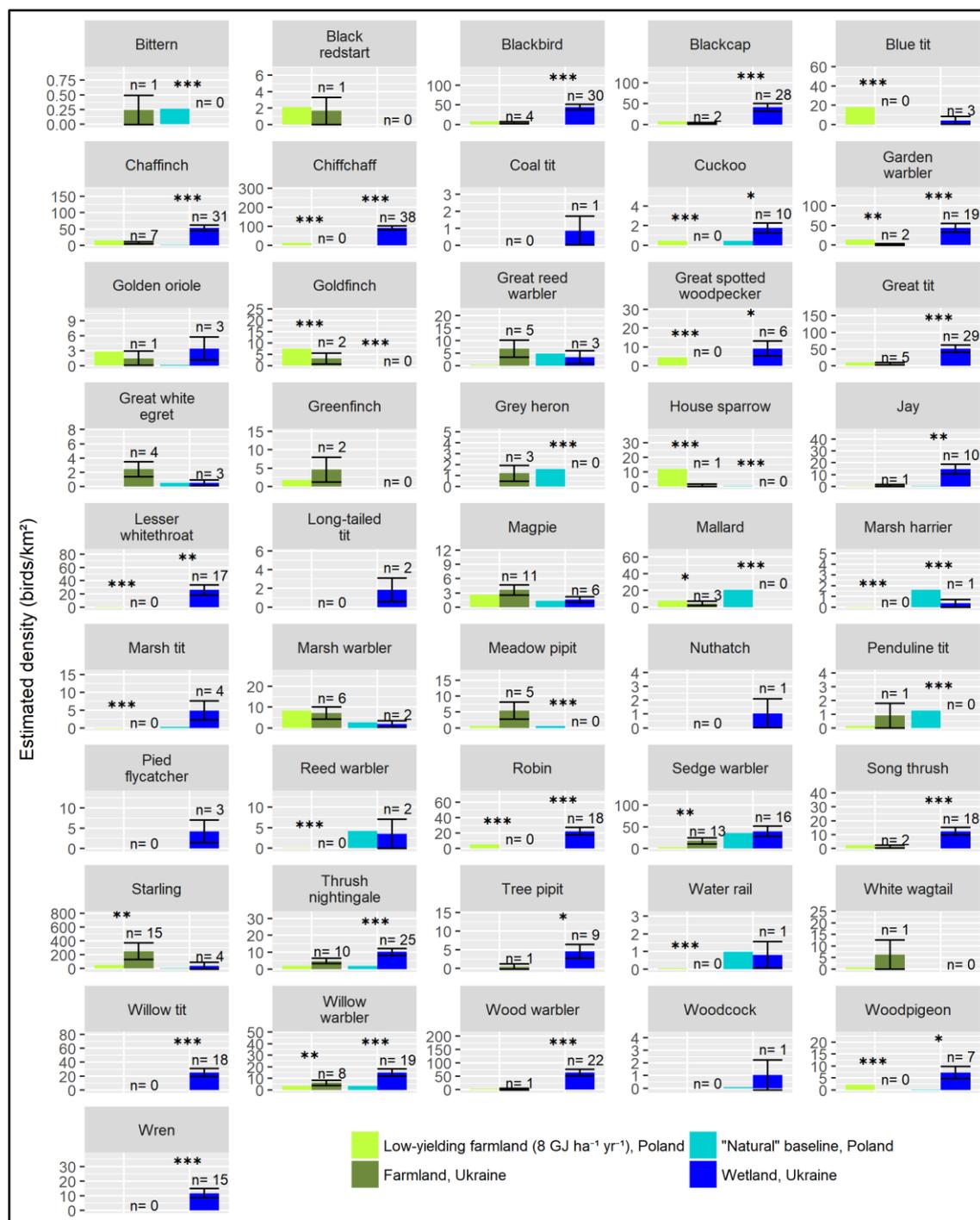
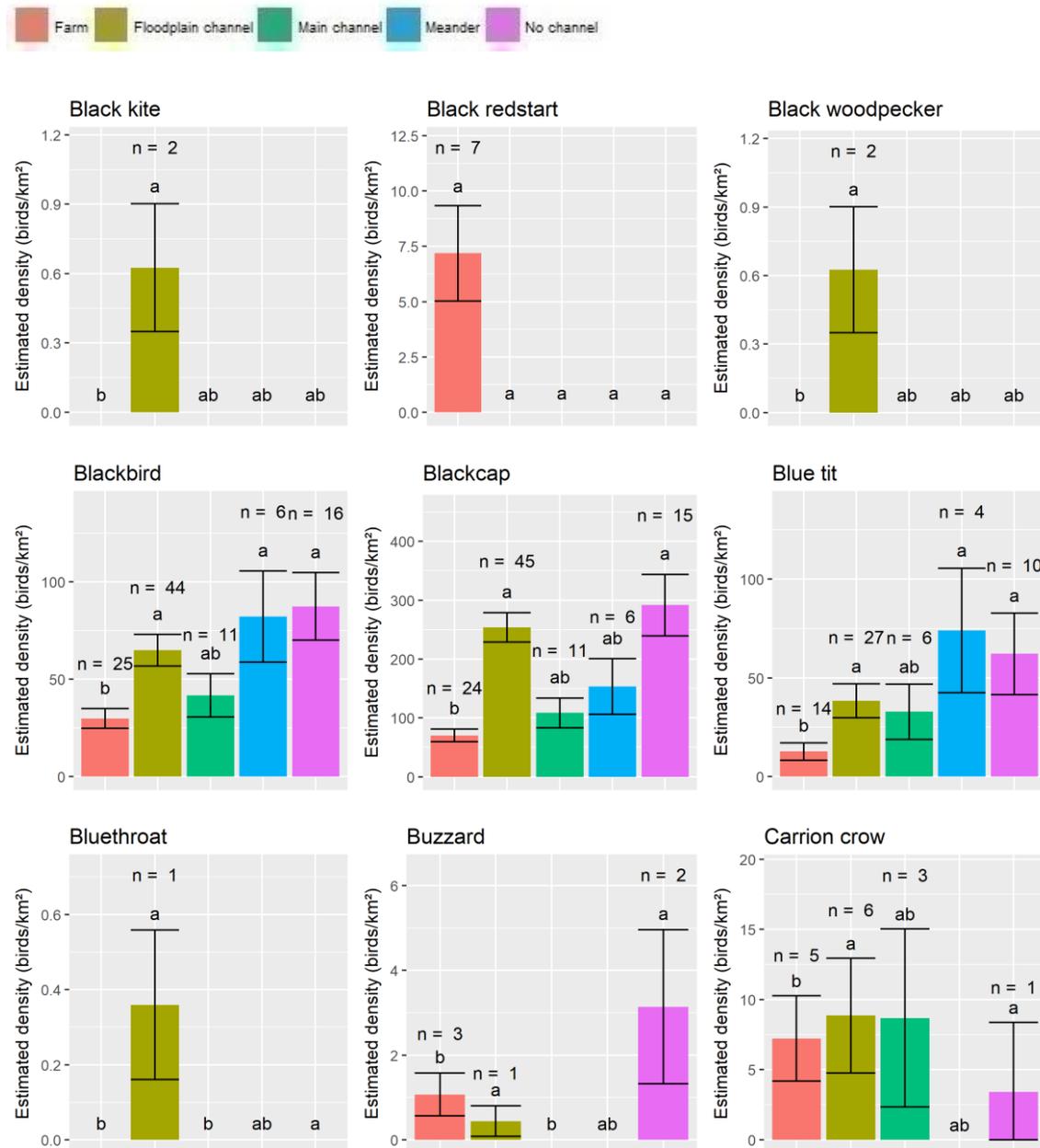


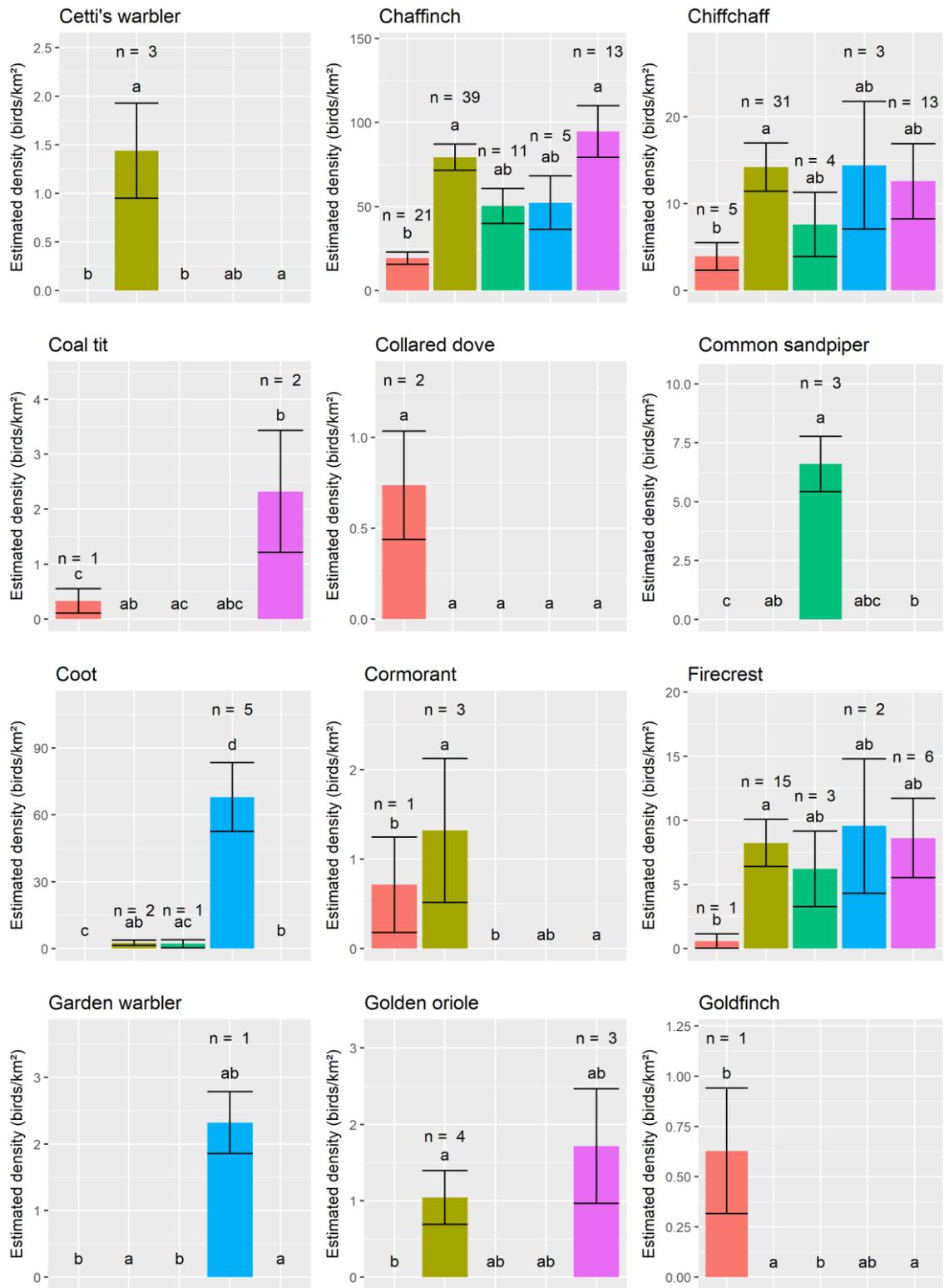
Figure A2.0.4 – Estimated population density of non-HNV bird species in farmland (green) and wetland (blue), in Poland (left) and in Ukraine (right). Population densities in Poland were estimated using density-yield functions from Feniuk (2015), at 0 GJ ha⁻¹ yr⁻¹ for natural baseline and at 8 GJ ha⁻¹ yr⁻¹ for low-yielding farmland, both on wetland soils only. Population densities in Ukraine were estimated using quasi-Poisson models. Black lines on Ukrainian bars indicate ± one Standard Error in the modelled estimates. Stars indicate the statistical significance of one-sample t-tests, comparing densities in natural habitats in Poland versus Ukraine, and comparing densities in farmland in Poland versus Ukraine. There were 44 Agricultural sites and 48 Wetland sites in Ukraine; n values in the figure refer to the number of Agricultural or Wetland sites in Ukraine with at least one observation of that species.

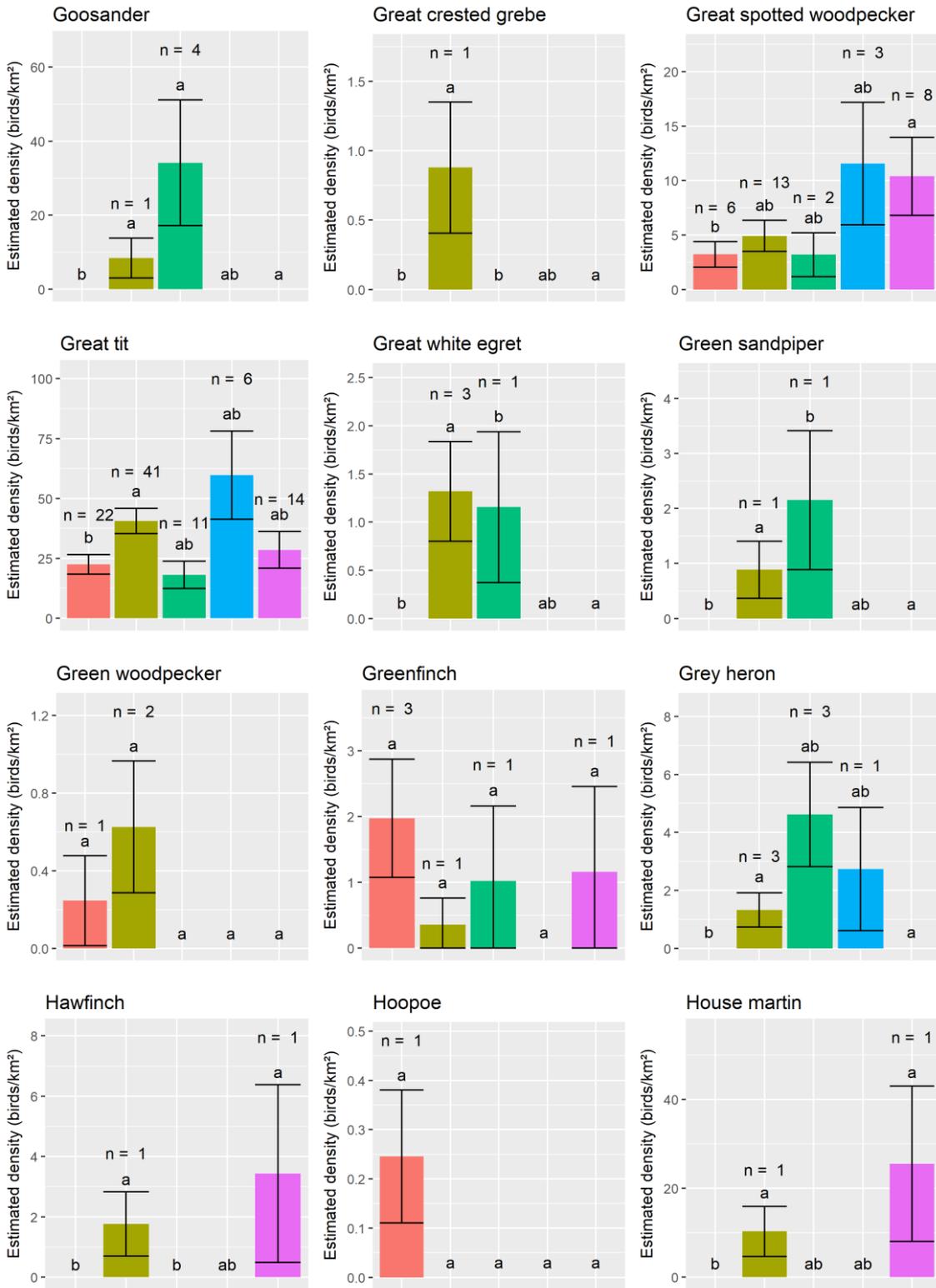
APPENDIX 4. SPECIES' POPULATION DENSITIES COMPARED IN DIFFERENT STUDY SITE CATEGORIES IN FRANCE

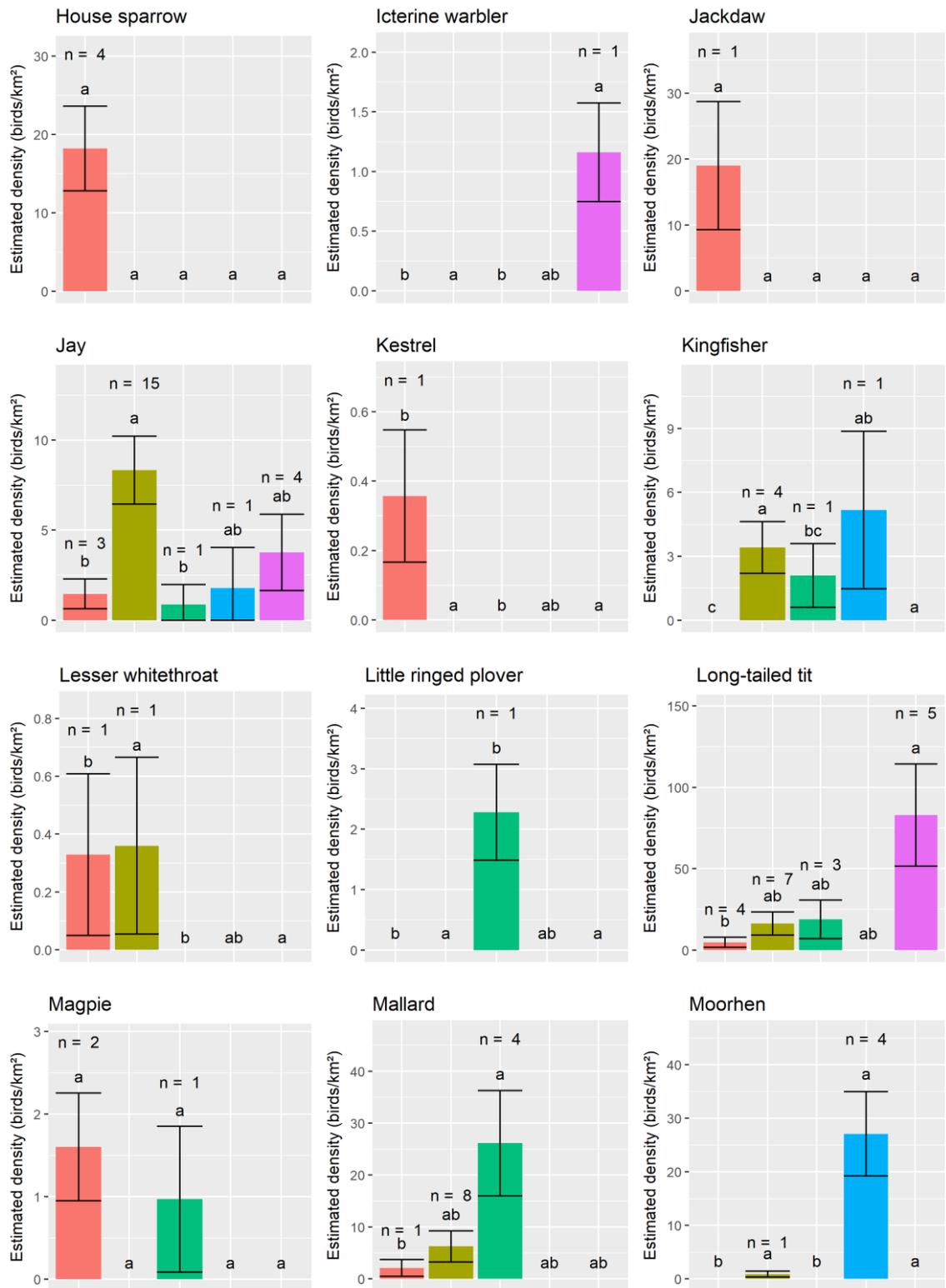
This appendix shows the same results as from Figure 4.14 and Figure 4.15, but enlarged to display more detail. Please refer to Chapter 4 for full details. Categories marked with the same letter do not differ significantly from each other, based on Tukey Honest Significant Differences test, with a significance level of 0.05 throughout. N values indicate the number of sites in each category in which the species was observed at least once.

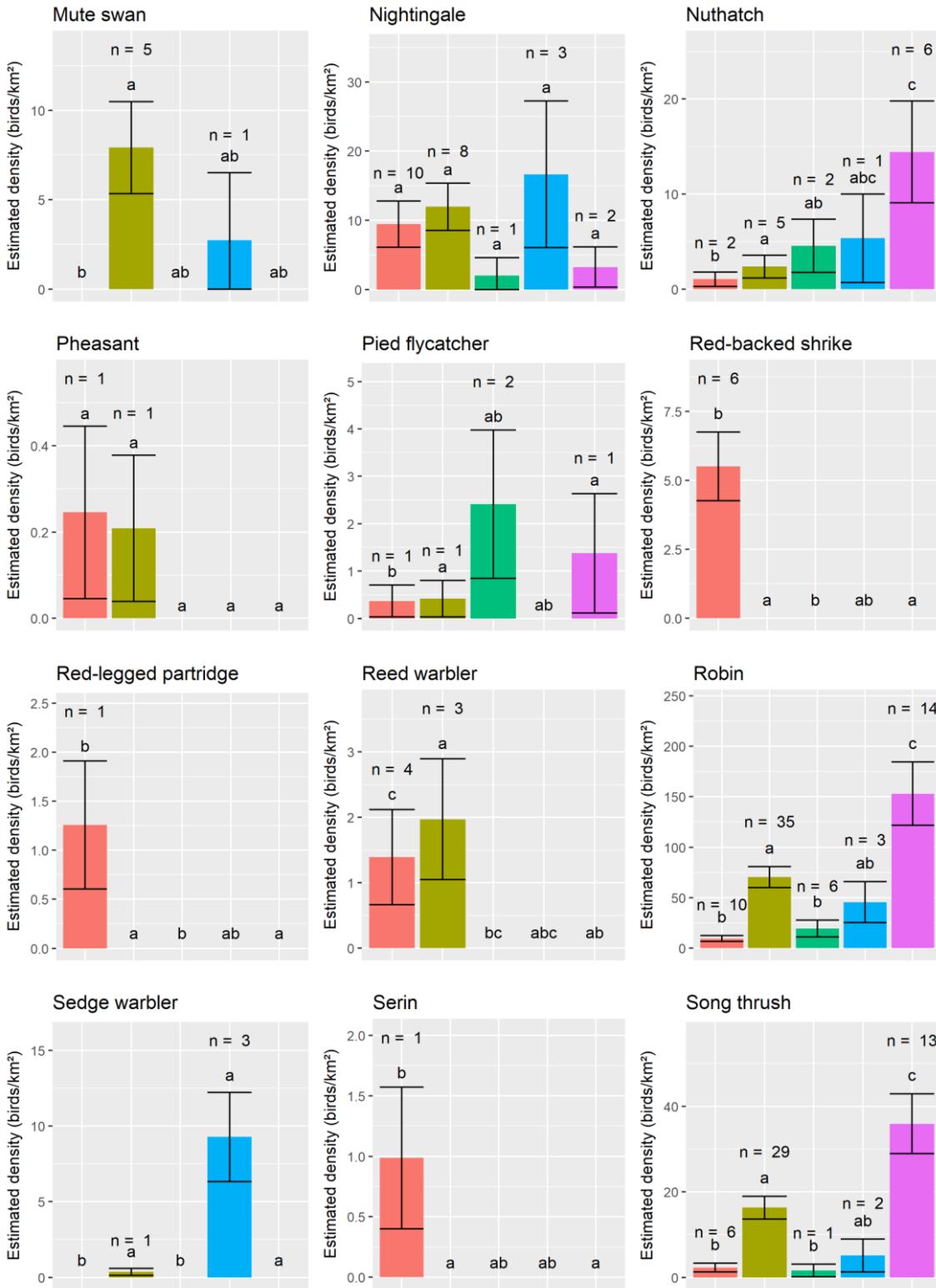
Birds

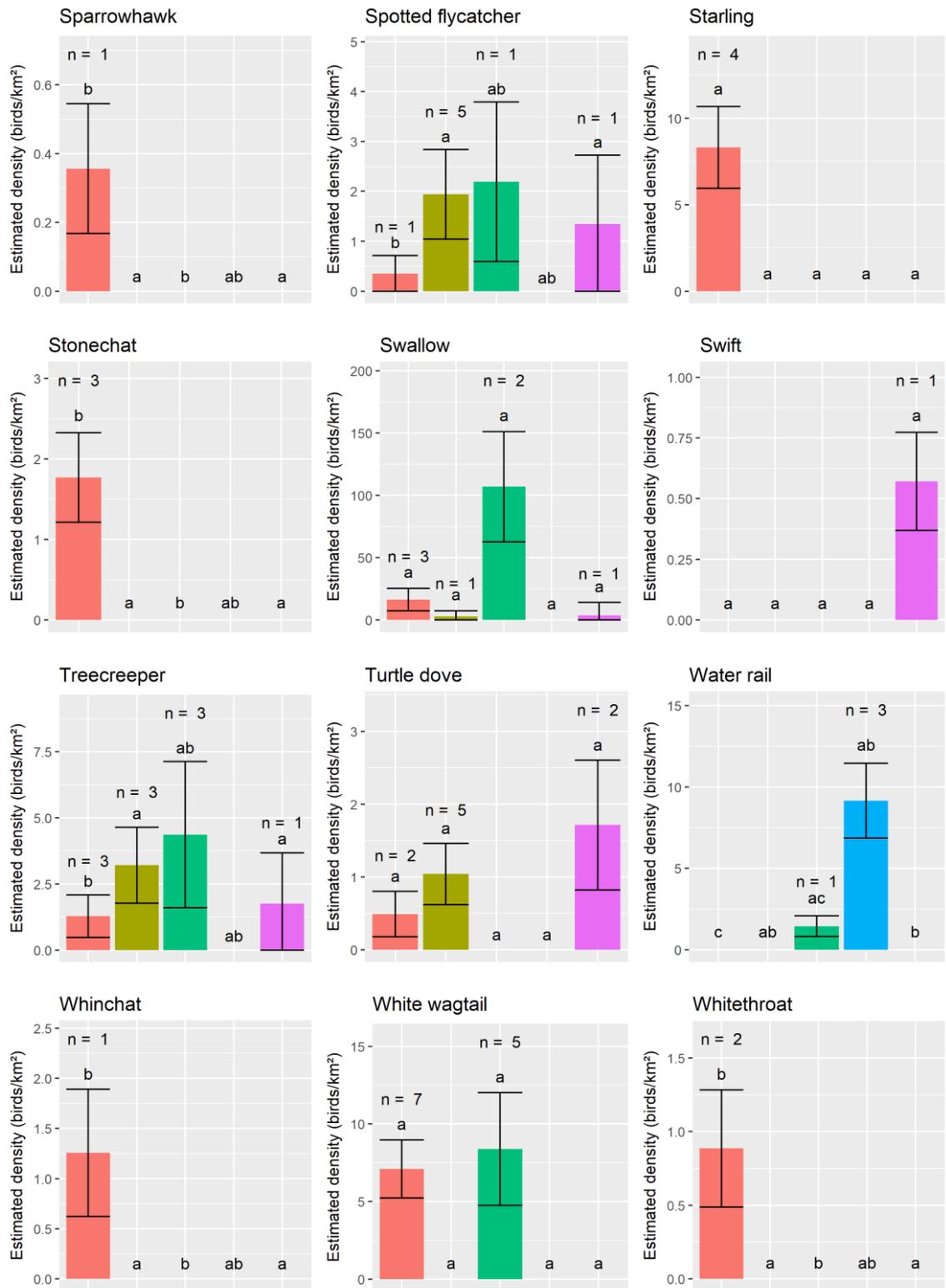




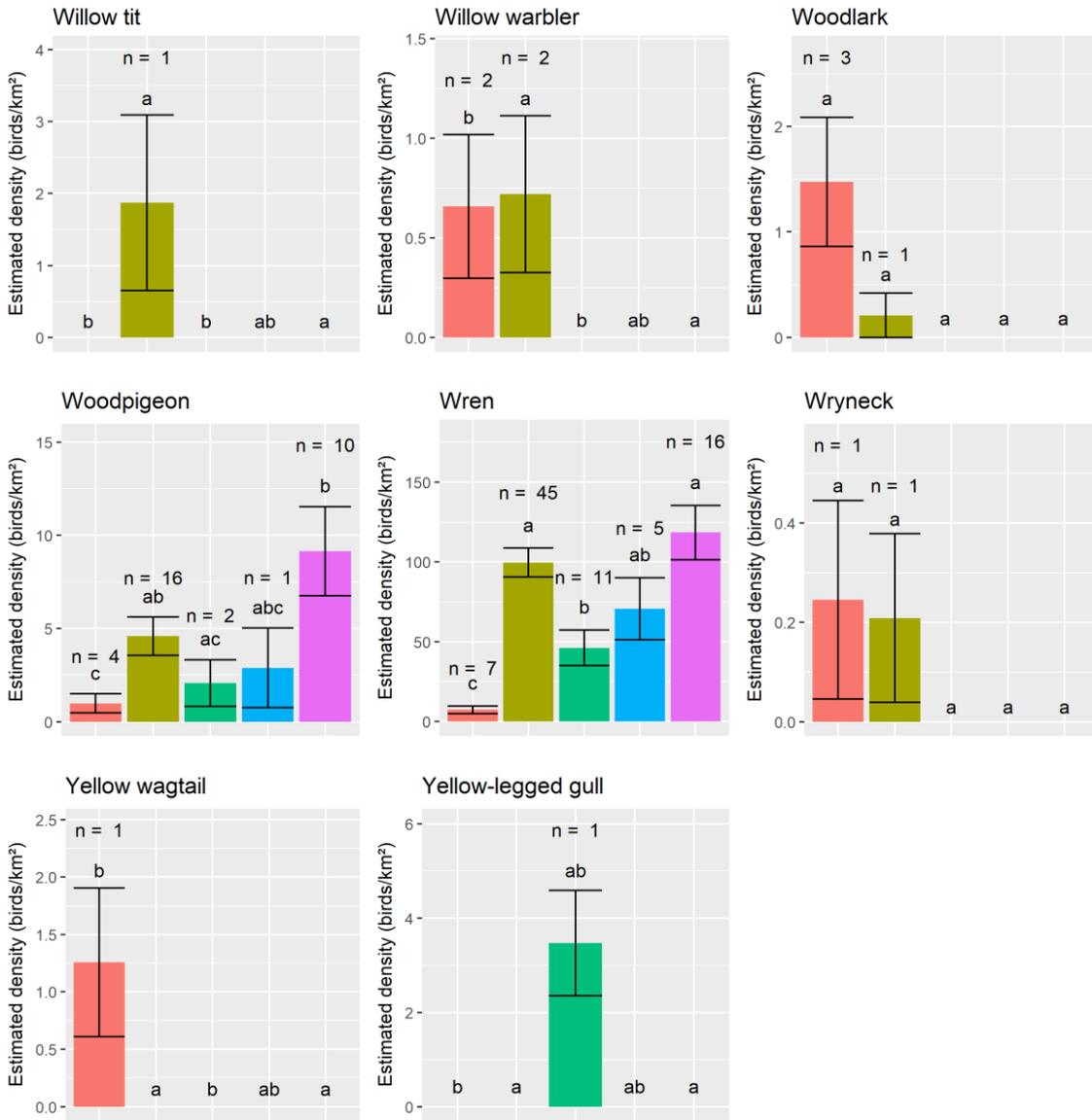




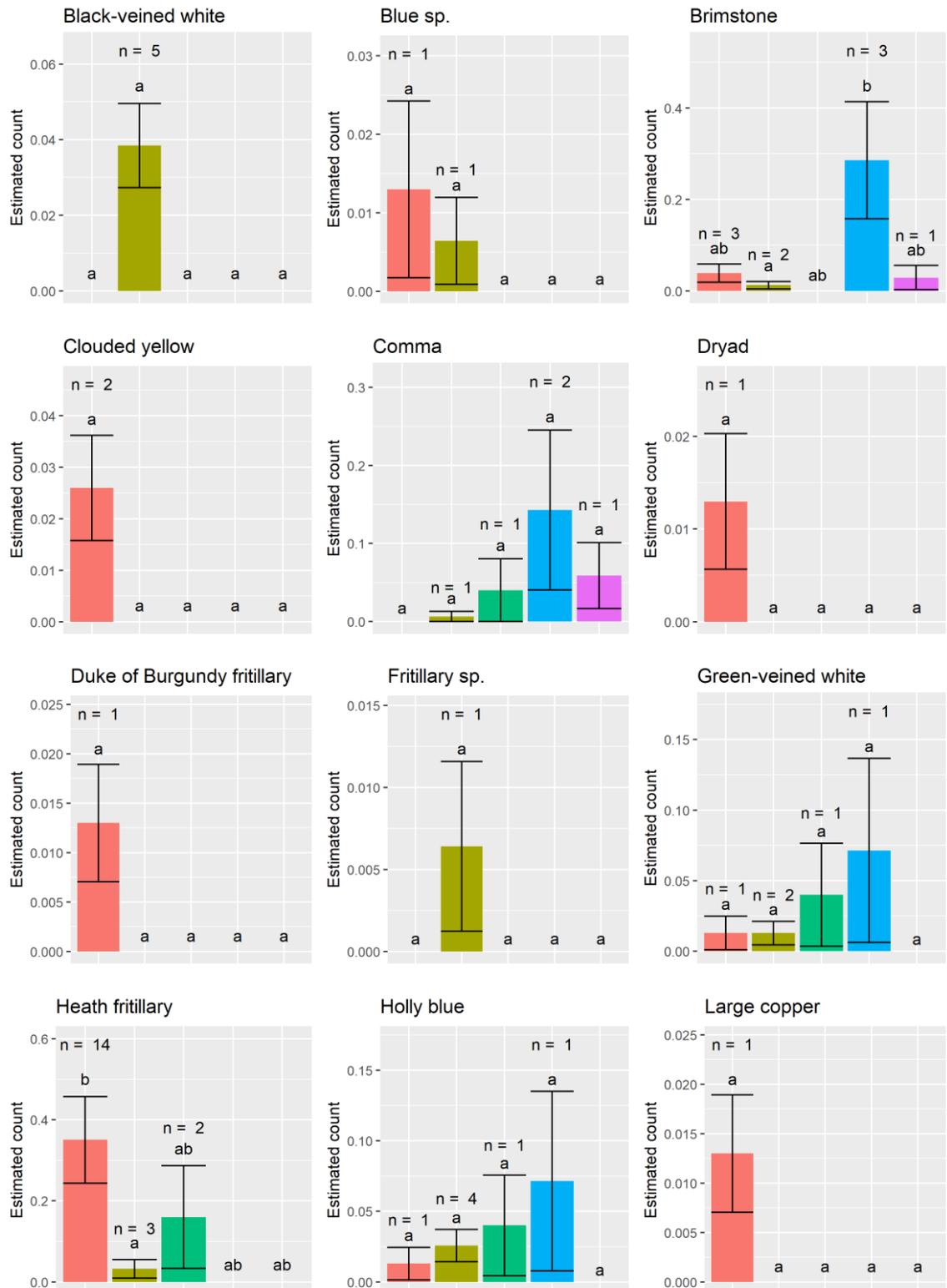




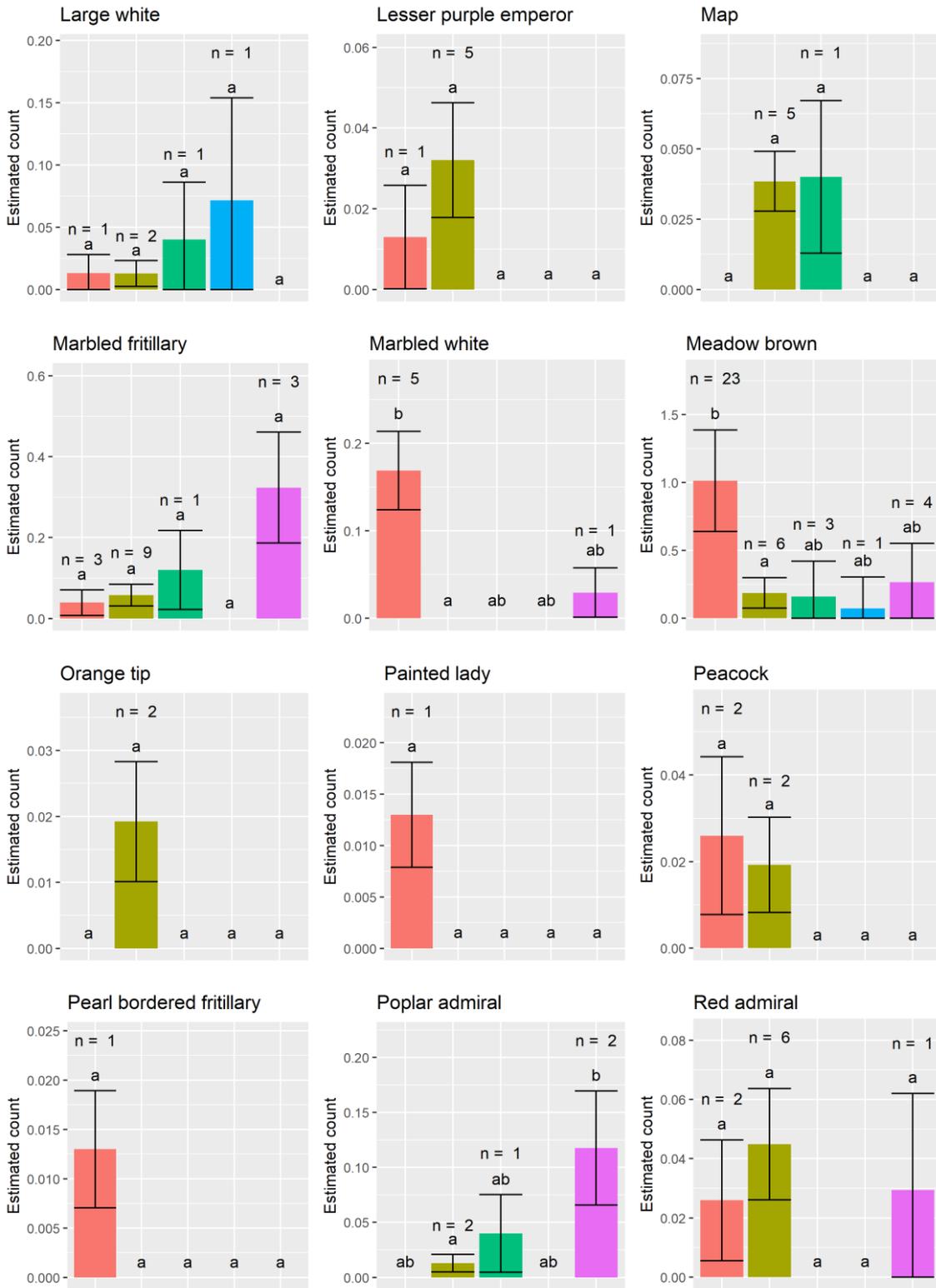
Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

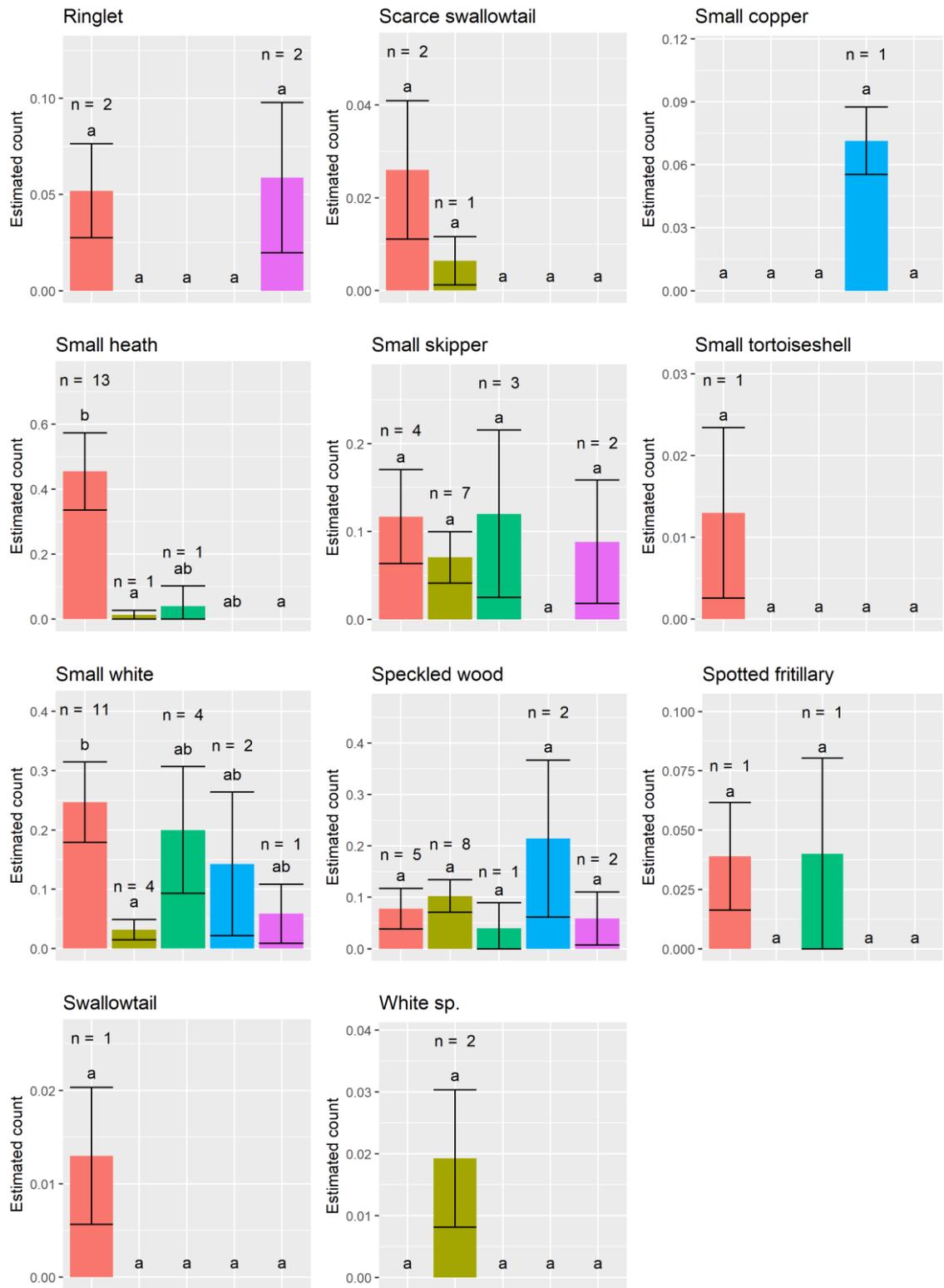


Butterflies



Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

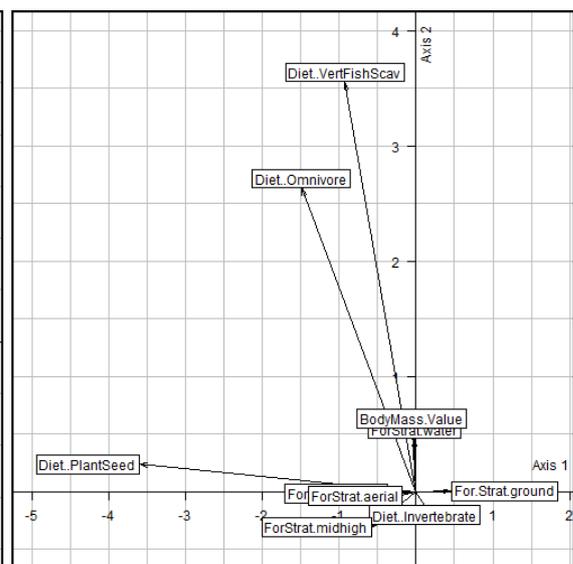
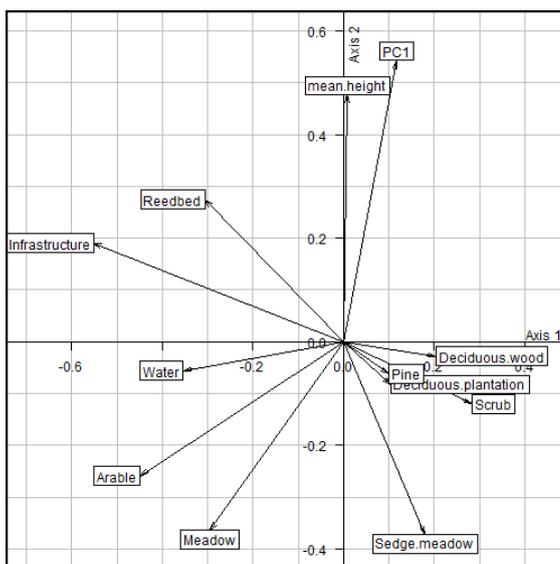
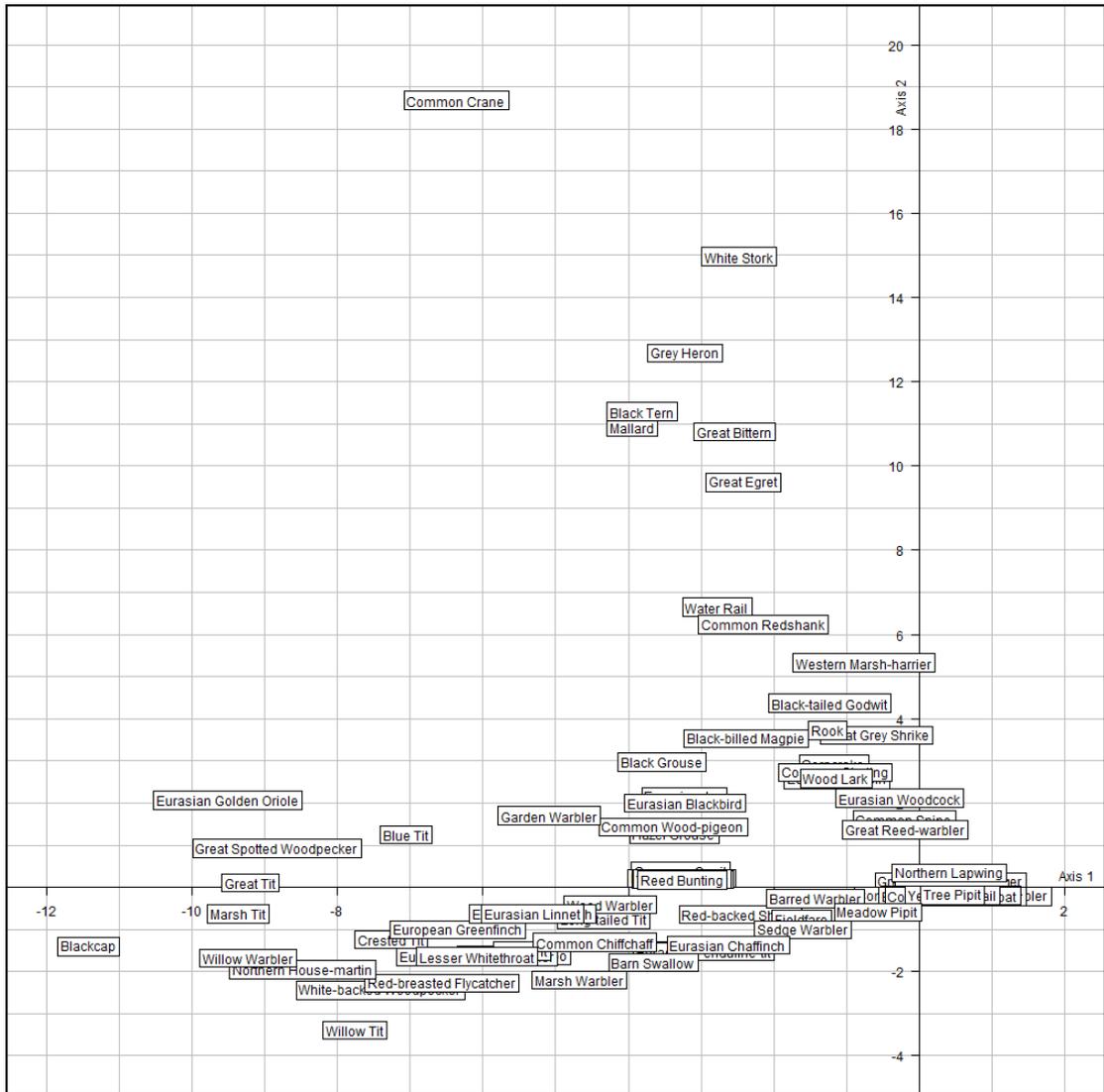




APPENDIX 5. TRAIT-BASED ANALYSIS BY REGION AND USING ONLY SPECIES COMMON TO ALL THREE REGIONS

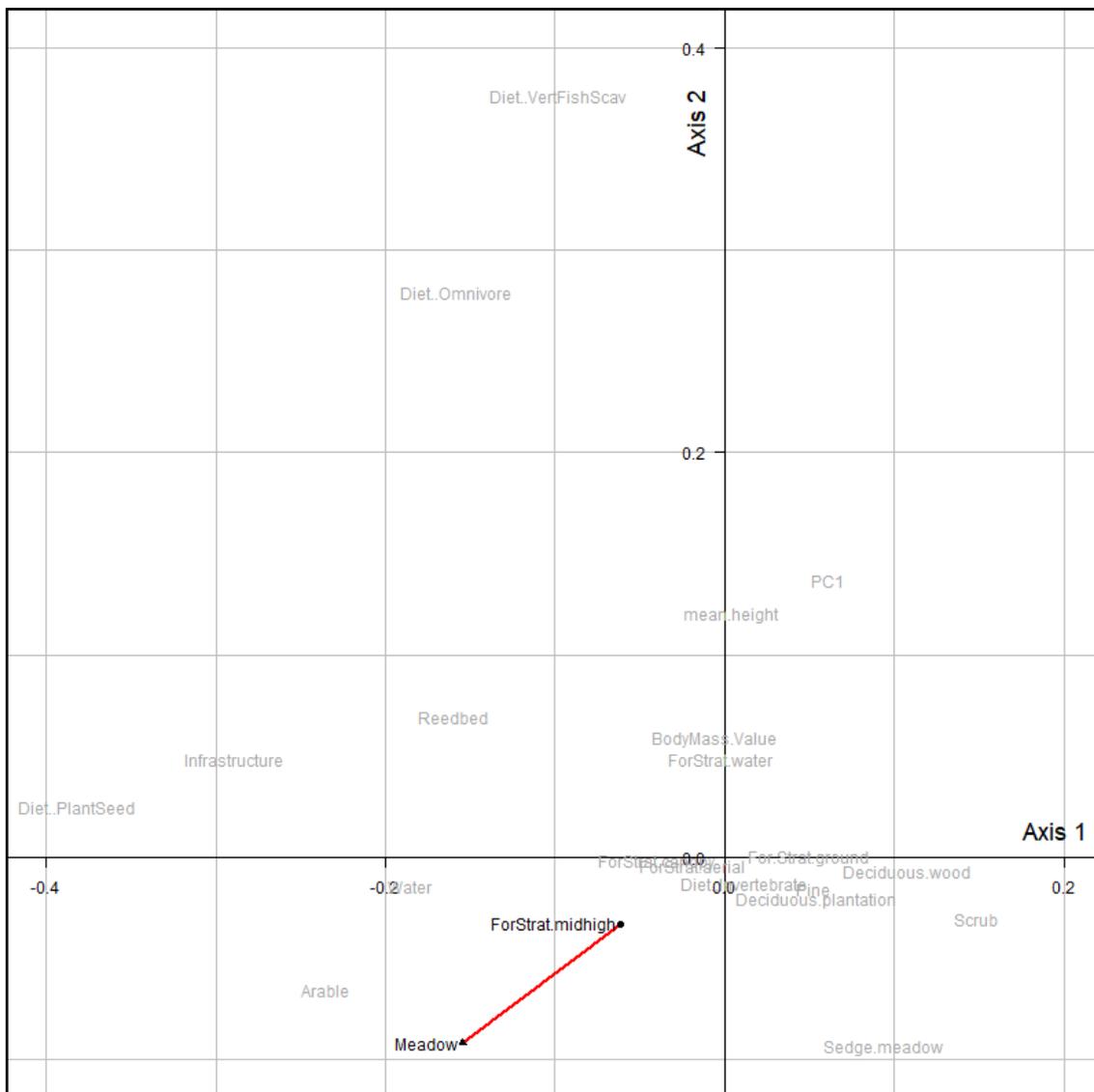
These plots show the same analyses carried out in Chapter 6, but firstly carried out separately for each study region, and secondly carried out only considering the subset of species which I observed in all three study regions. Please refer back to Chapter 6 for details and methodology. In each case, I present the results of RLQ analyses, showing species, environmental variables and species' traits in the same ordination space; the table of association strengths, with significant associations highlighted in **bold** and coloured blue for negative associations and red for positive associations; and the combined results, plotting species' traits and habitat variables in the same ordination space and highlighting significant associations. To minimize repetition, figures are not individually captioned other than to identify them.

Birds, Ukraine

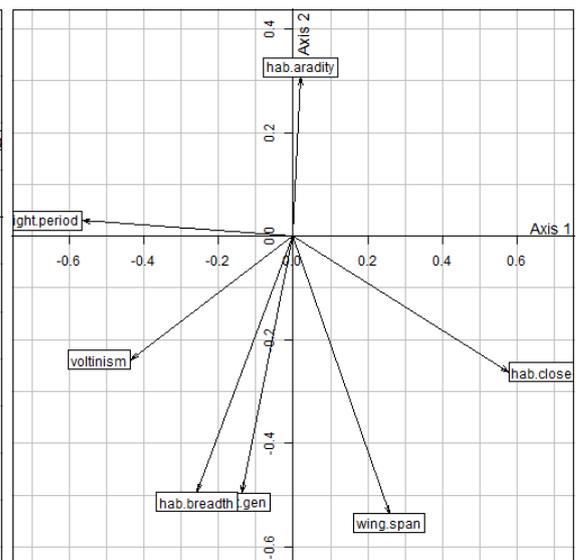
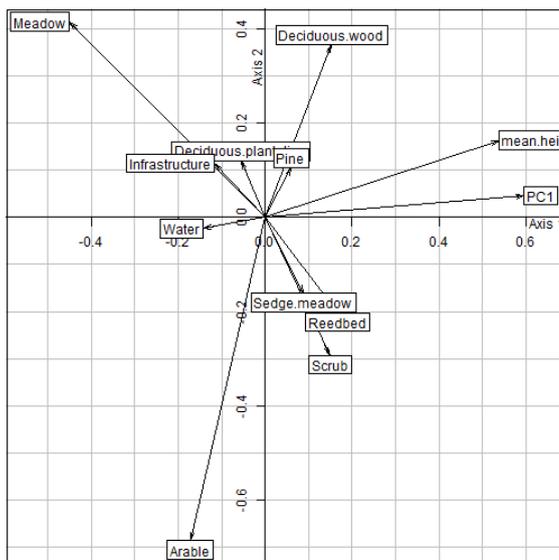
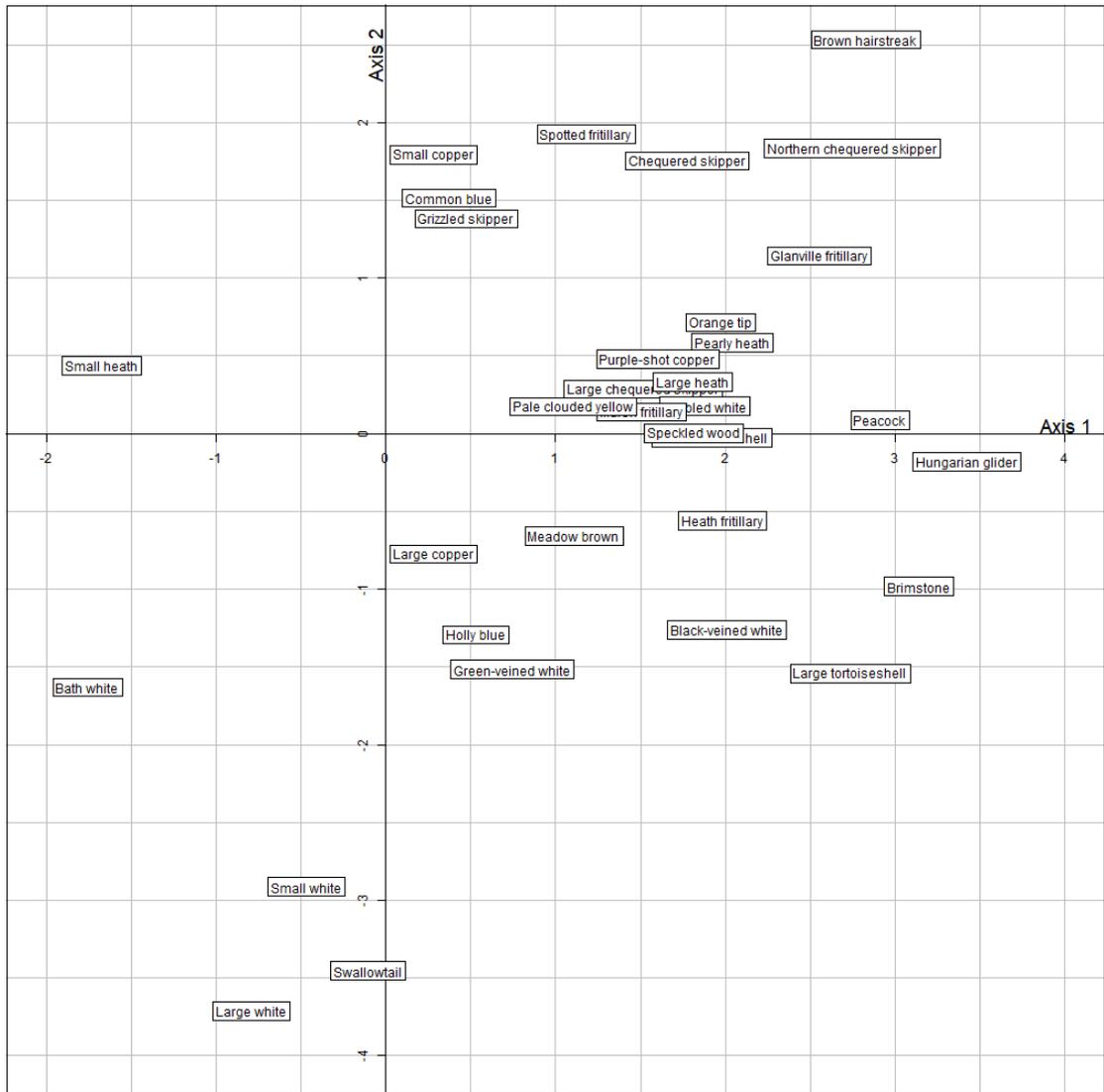


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

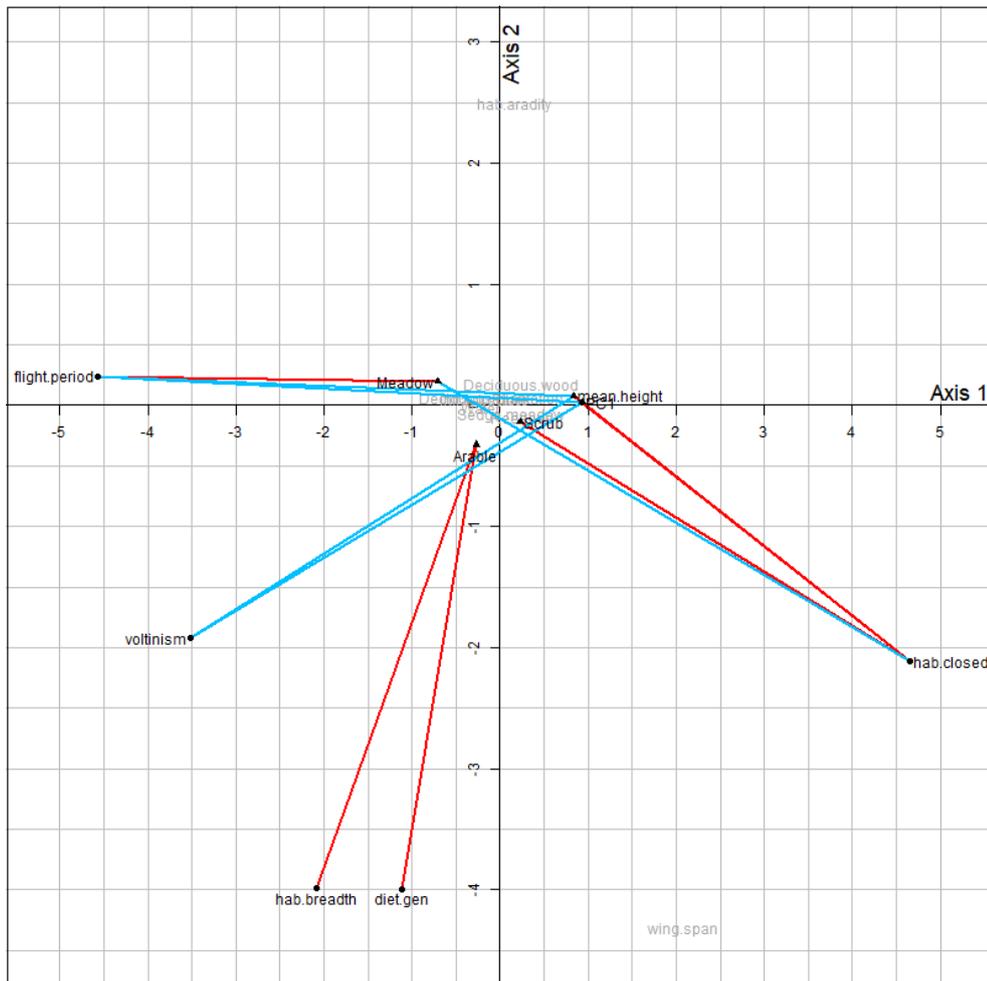
		Species' Traits									
		Diet Category				Foraging: water	Foraging: ground	Foraging: mid-height	Foraging: canopy	Foraging: aerial	Body mass
		Invertebrate	Omnivore	Plant/ seed	Vertebrate/ Fish/ Scavenger						
Environmental Variables	Mean height	0.909	0.031	0.024	0.026	0.035	0.023	-0.017	-0.032	-0.062	0.058
	Arable	0.720	0.047	0.191	0.021	-0.028	-0.092	0.181	0.047	-0.008	-0.020
	Deciduous plantation	0.973	0.005	0.010	0.011	-0.023	0.036	-0.028	-0.024	-0.019	-0.018
	Infrastructure	0.474	0.198	0.260	0.036	0.025	-0.134	0.110	0.155	0.065	0.025
	Water	0.736	0.050	0.129	0.069	-0.014	-0.070	0.123	0.045	-0.003	-0.002
	Deciduous wood	0.959	0.013	0.010	0.018	-0.021	0.066	-0.055	-0.048	-0.057	-0.015
	Meadow	0.887	0.031	0.046	0.031	-0.054	-0.062	0.145	0.039	-0.010	-0.042
	Reedbed	0.929	0.009	0.016	0.043	0.064	-0.119	0.049	0.093	0.150	0.069
	Scrub	0.938	0.015	0.014	0.024	-0.001	0.061	-0.097	-0.037	-0.002	-0.025
	Sedge meadow	0.964	0.010	0.007	0.007	-0.040	0.032	-0.054	0.000	0.033	-0.060
	Pine	0.930	0.035	0.016	0.019	-0.033	0.040	-0.018	-0.034	-0.029	-0.024
	PC1	0.936	0.019	0.023	0.016	0.055	0.043	-0.064	-0.048	-0.059	0.071



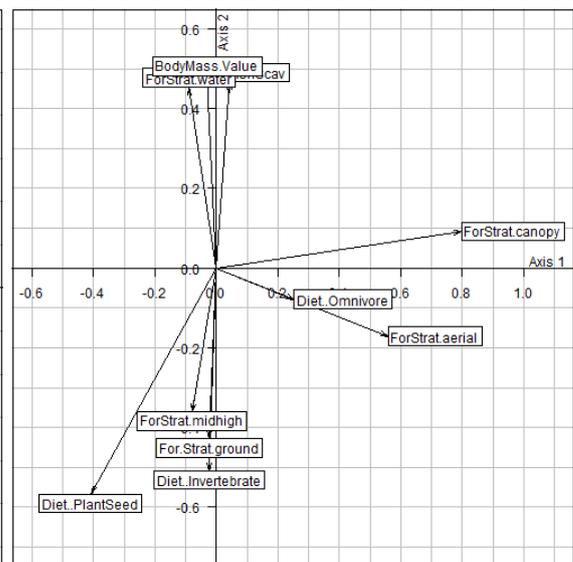
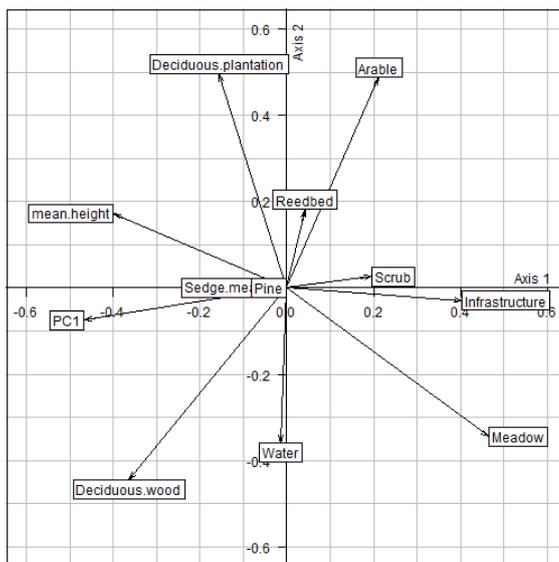
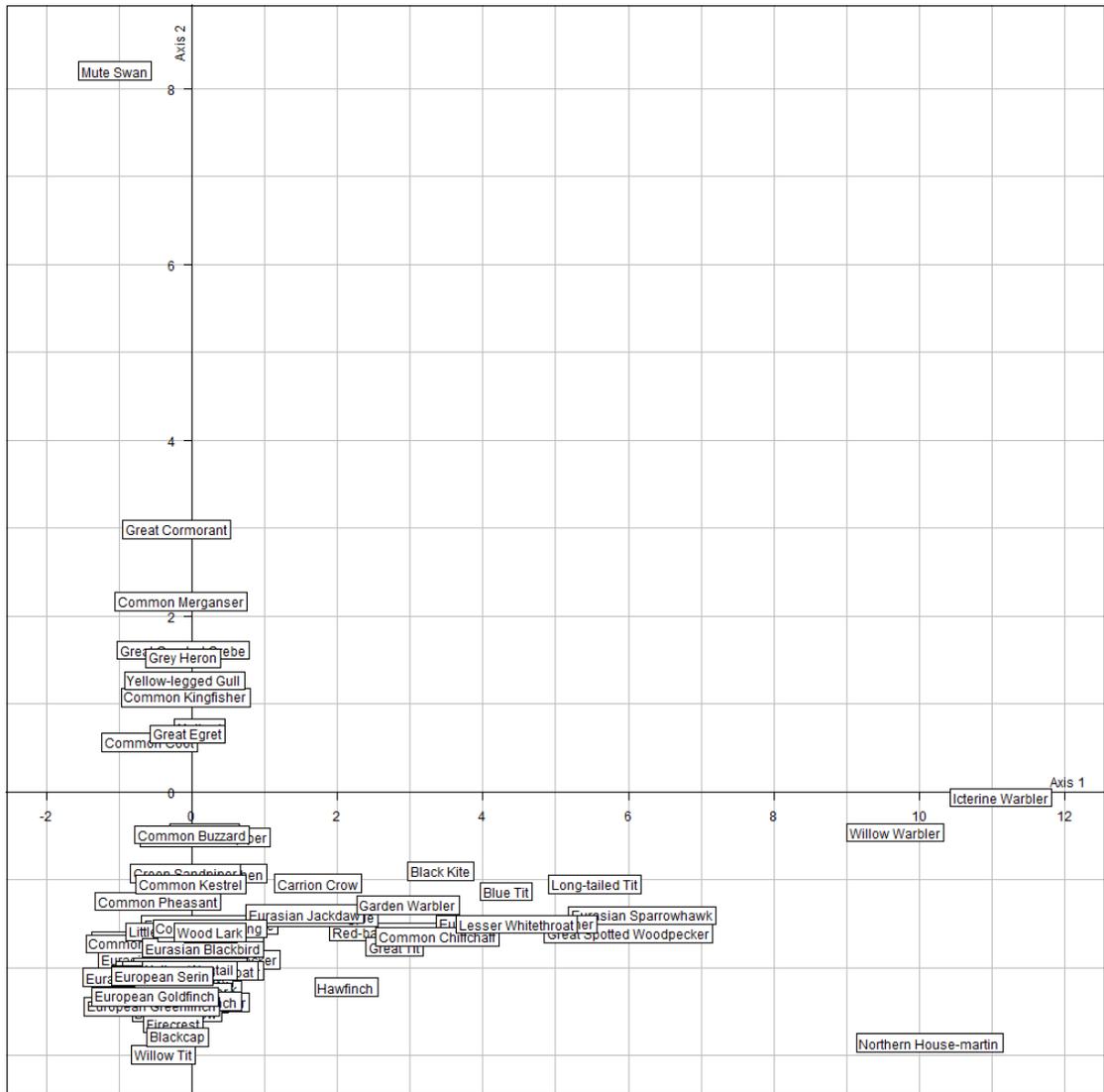
Butterflies, Ukraine



		Species' Traits						
		Wing span	Flight period	Voltinism	Diet generality	Habitat breadth	Habitat aridity	Habitat closedness
Environmental Variables	Mean height	0.161	-0.487	-0.423	-0.121	-0.245	0.042	0.448
	Arable	0.132	0.151	0.144	0.274	0.225	-0.008	-0.100
	Deciduous plantation	-0.058	0.034	-0.009	-0.046	0.047	0.001	-0.087
	Infrastructure	-0.086	0.098	0.047	0.001	0.043	0.015	-0.126
	Water	-0.039	0.112	0.044	0.034	0.099	-0.014	-0.172
	Deciduous wood	0.020	-0.100	-0.138	-0.059	-0.191	0.181	0.097
	Meadow	-0.286	0.409	0.271	0.008	0.082	0.069	-0.450
	Reedbed	0.112	-0.168	-0.079	-0.081	0.043	-0.067	0.181
	Scrub	0.156	-0.108	-0.005	0.030	-0.042	-0.010	0.211
	Sedge meadow	0.031	-0.116	-0.024	-0.014	0.016	-0.112	0.099
	Pine	0.013	-0.090	-0.110	-0.051	-0.012	-0.018	-0.031
	PC1	0.241	-0.522	-0.425	-0.129	-0.247	0.059	0.531

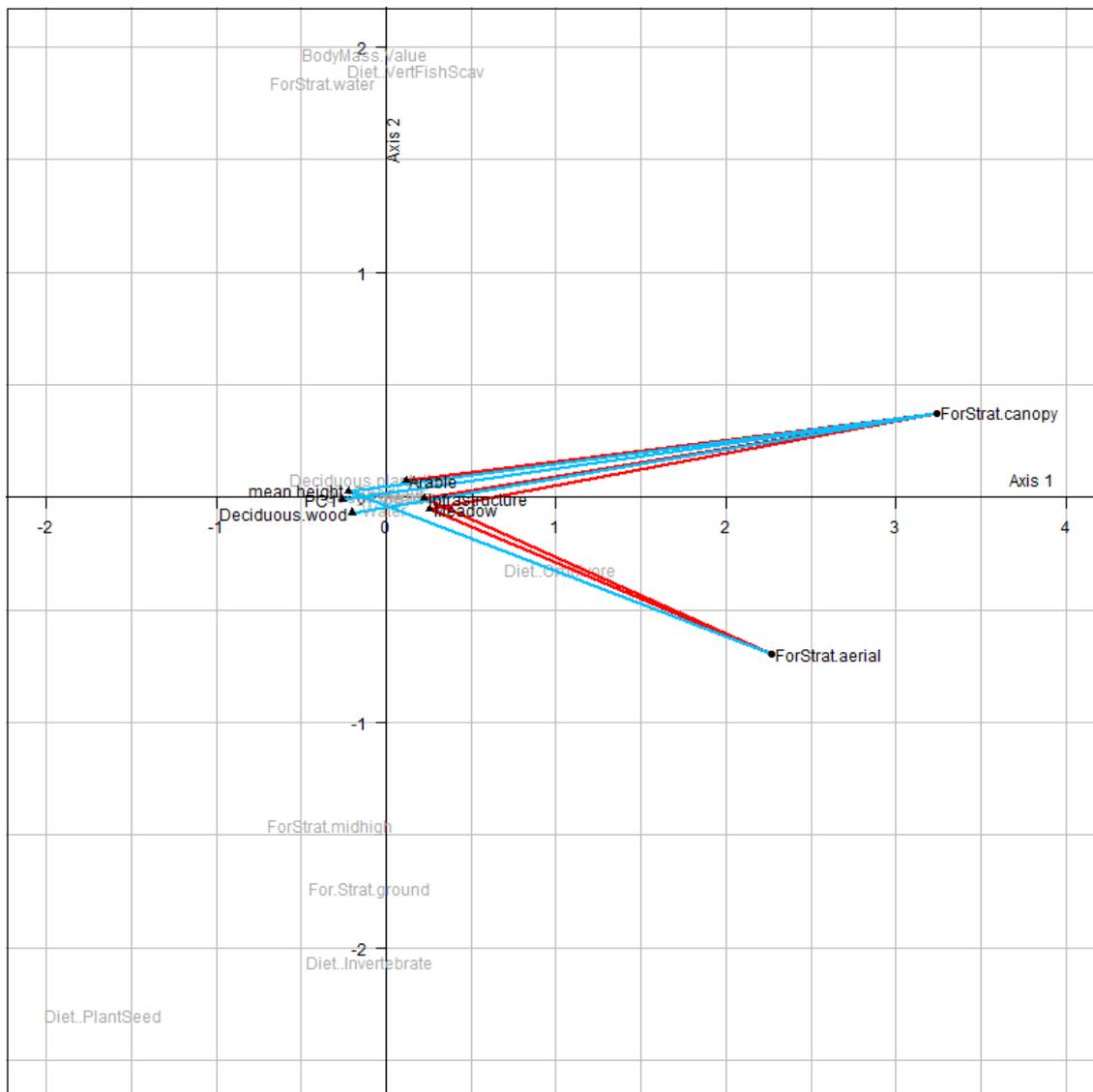


Birds, France

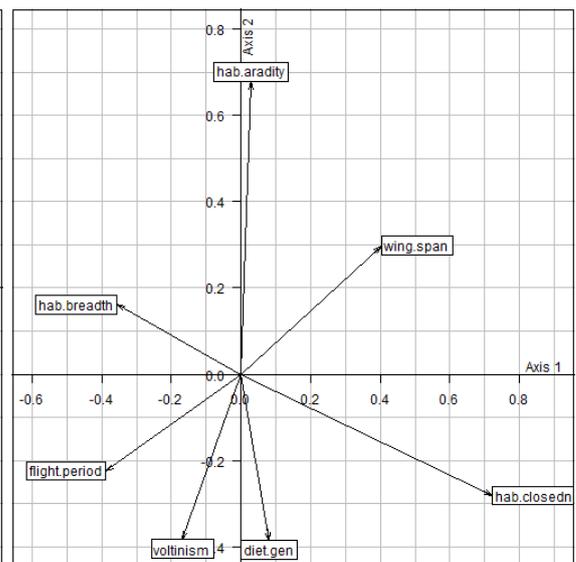
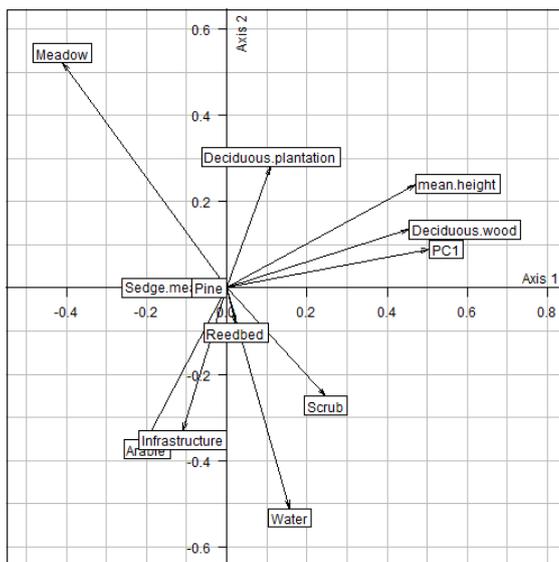
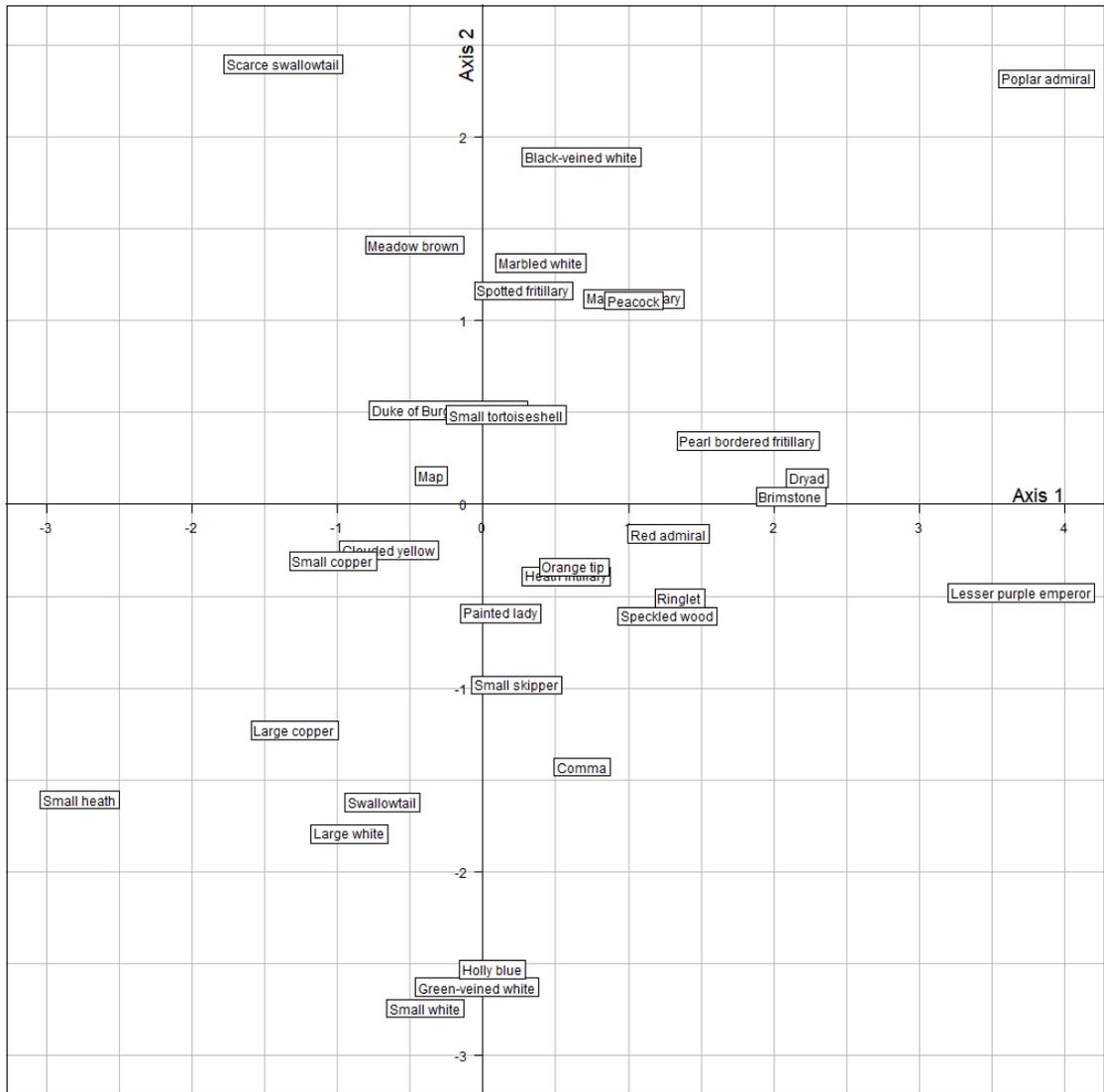


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

		Species' Traits									
		Diet Category				Foraging: water	Foraging: ground	Foraging: mid-height	Foraging: canopy	Foraging: aerial	Body mass
		Invertebrate	Omnivore	Plant/ seed	Vertebrate/ Fish/ Scavenger						
Environmental Variables	Mean height	0.241	0.162	0.129	0.464	0.039	-0.018	0.015	-0.174	-0.120	0.013
	Arable	0.264	0.156	0.082	0.494	0.025	-0.034	-0.043	0.105	0.039	0.021
	Deciduous plantation	0.231	0.103	0.167	0.495	0.039	-0.033	-0.008	-0.061	-0.049	0.052
	Infrastructure	0.238	0.191	0.122	0.447	-0.014	-0.018	-0.006	0.166	0.147	-0.011
	Water	0.256	0.155	0.143	0.445	-0.030	0.032	0.019	-0.006	0.001	-0.036
	Deciduous wood	0.258	0.178	0.119	0.441	-0.010	0.033	0.037	-0.168	-0.106	-0.028
	Meadow	0.260	0.191	0.130	0.418	-0.047	0.011	0.008	0.208	0.155	-0.025
	Reedbed	0.188	0.292	0.090	0.428	0.008	-0.001	-0.029	0.026	-0.007	0.016
	Scrub	0.233	0.212	0.128	0.423	-0.009	0.004	-0.023	0.072	0.067	0.005
	Sedge meadow	NA	NA	NA	NA	0.000	0.000	0.000	0.000	0.000	0.000
	Pine	NA	NA	NA	NA	0.000	0.000	0.000	0.000	0.000	0.000
PC1	0.278	0.186	0.102	0.431	0.020	0.009	0.026	-0.214	-0.134	0.011	

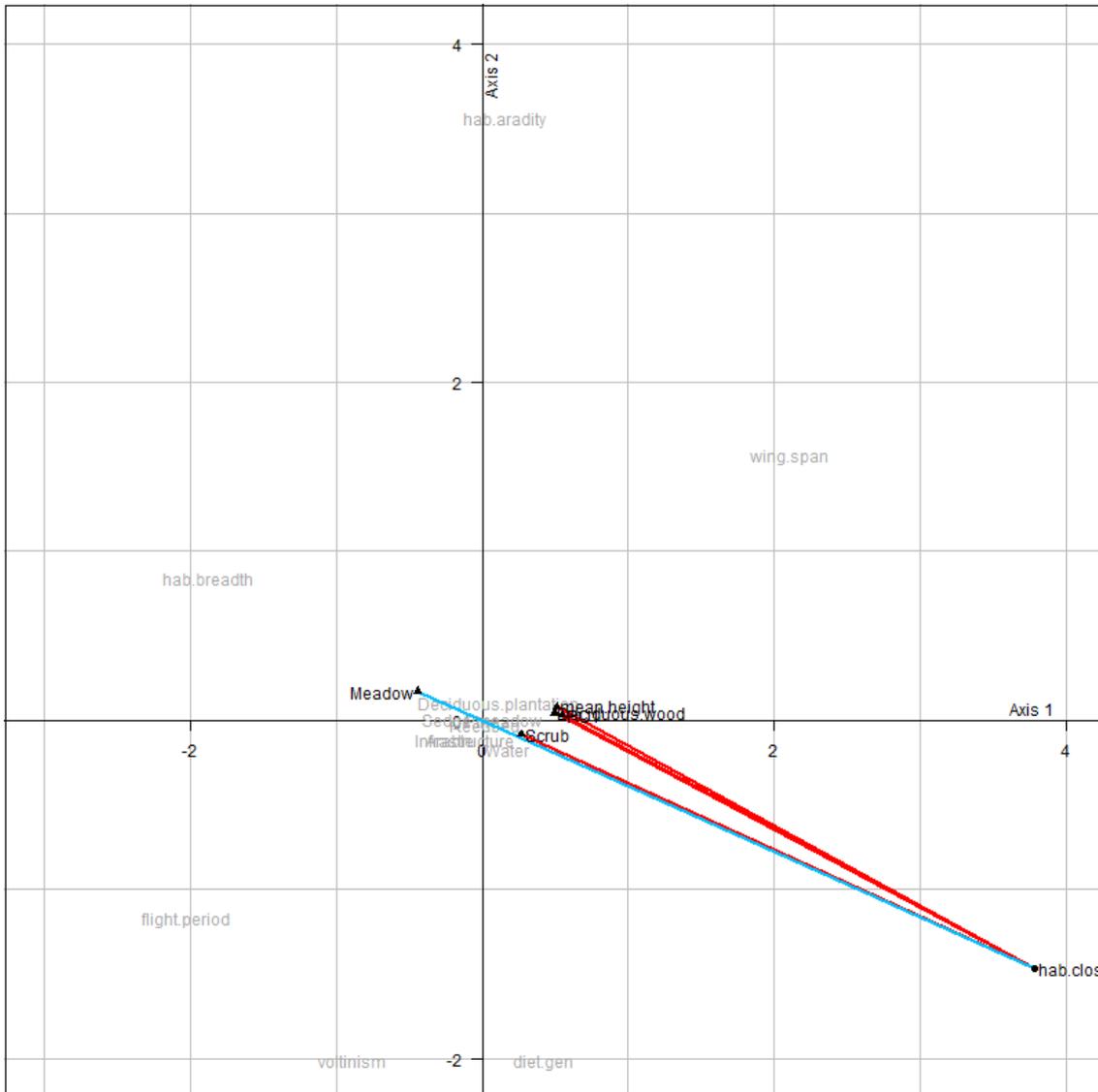


Butterflies, France

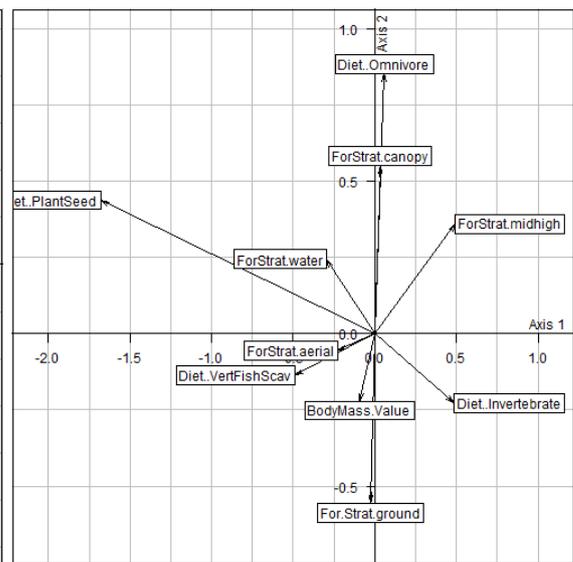
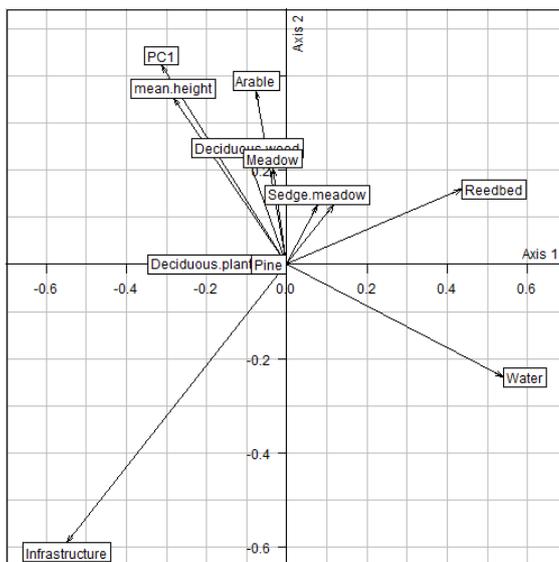
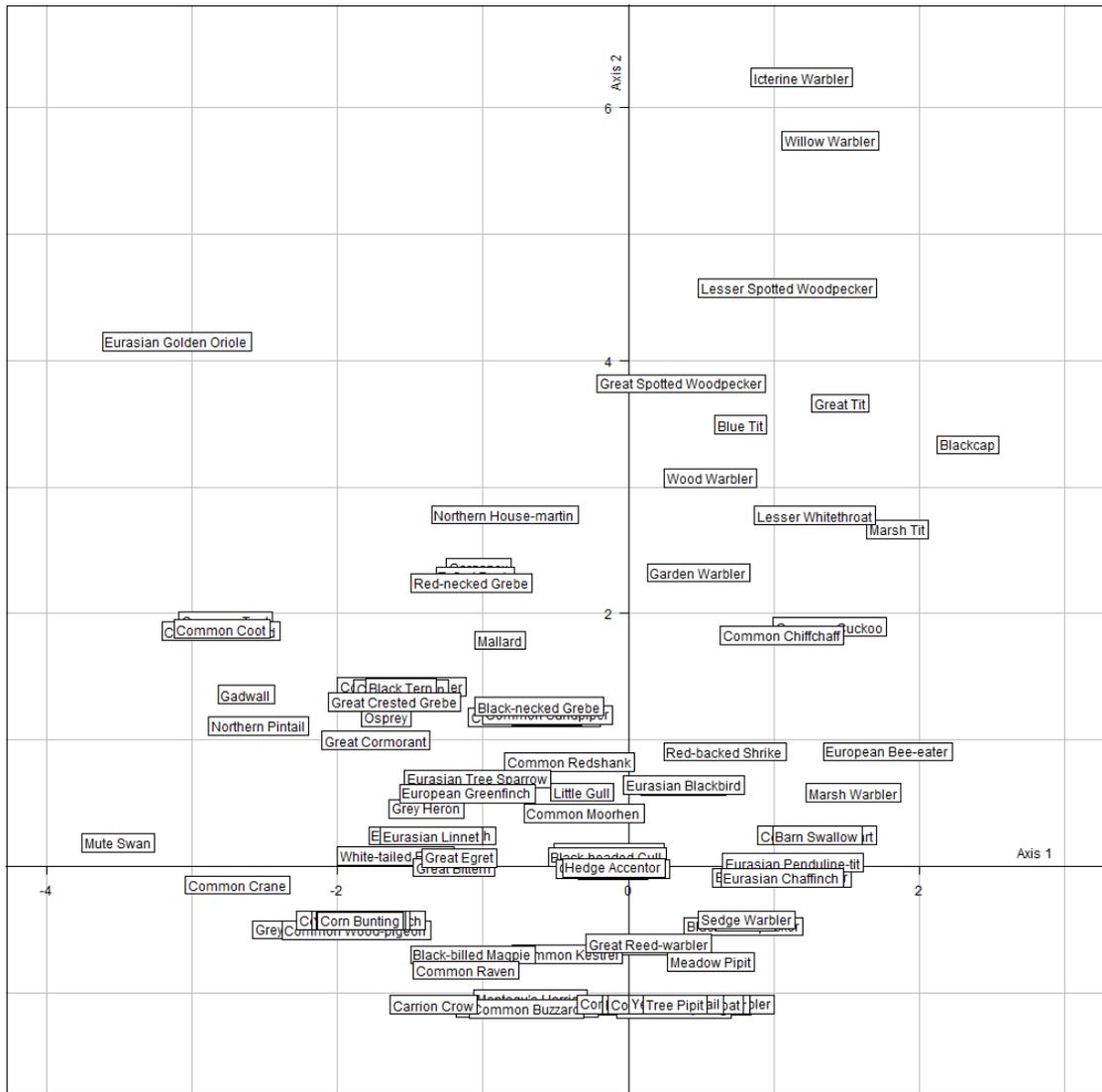


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

		Species' Traits						
		Wing span	Flight period	Voltinism	Diet generality	Habitat breadth	Habitat aridity	Habitat closedness
Environmental Variables	Mean height	0.243	-0.202	-0.115	0.023	-0.174	0.077	0.346
	Arable	-0.122	0.130	0.108	0.010	0.032	-0.067	-0.119
	Deciduous plantation	0.035	-0.061	-0.049	-0.122	0.022	0.051	0.124
	Infrastructure	-0.065	0.075	0.041	0.032	0.055	-0.101	-0.051
	Water	0.008	-0.028	0.025	0.101	-0.088	-0.100	0.170
	Deciduous wood	0.225	-0.212	-0.104	0.042	-0.189	0.040	0.320
	Meadow	-0.127	0.120	-0.012	-0.082	0.196	0.094	-0.380
	Reedbed	-0.023	-0.048	0.023	-0.025	0.025	-0.036	0.043
	Scrub	0.064	-0.114	-0.039	0.011	-0.068	-0.092	0.234
	Sedge meadow	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Pine	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	PC1	0.234	-0.212	-0.100	0.050	-0.200	0.049	0.384

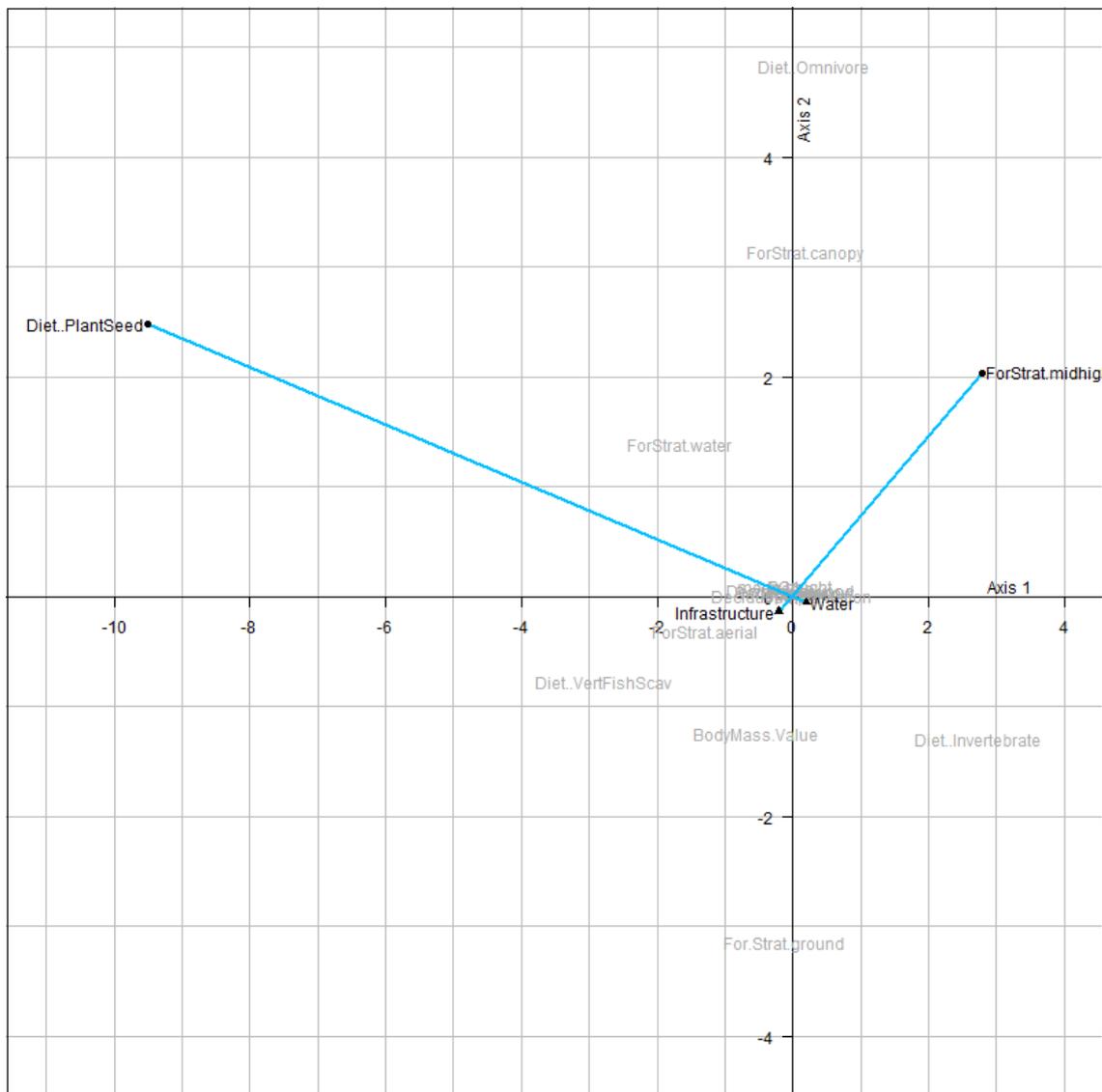


Birds, Germany

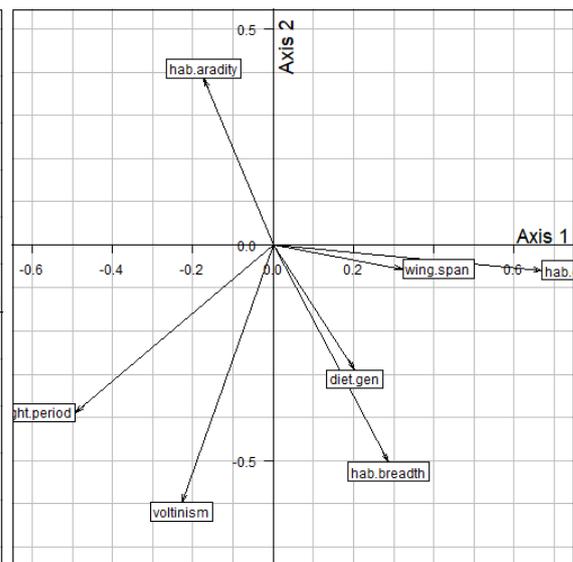
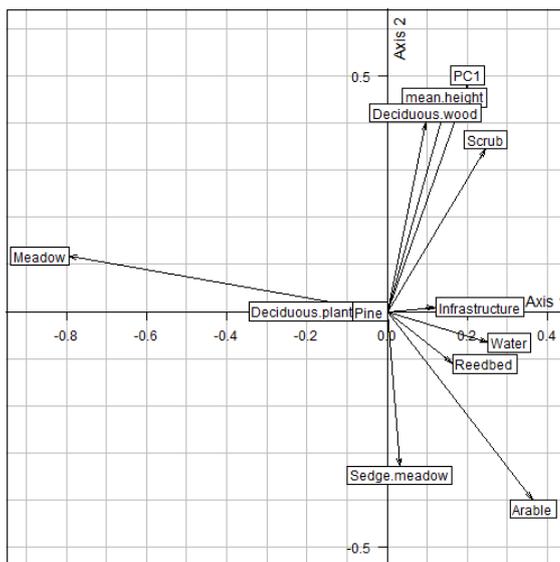
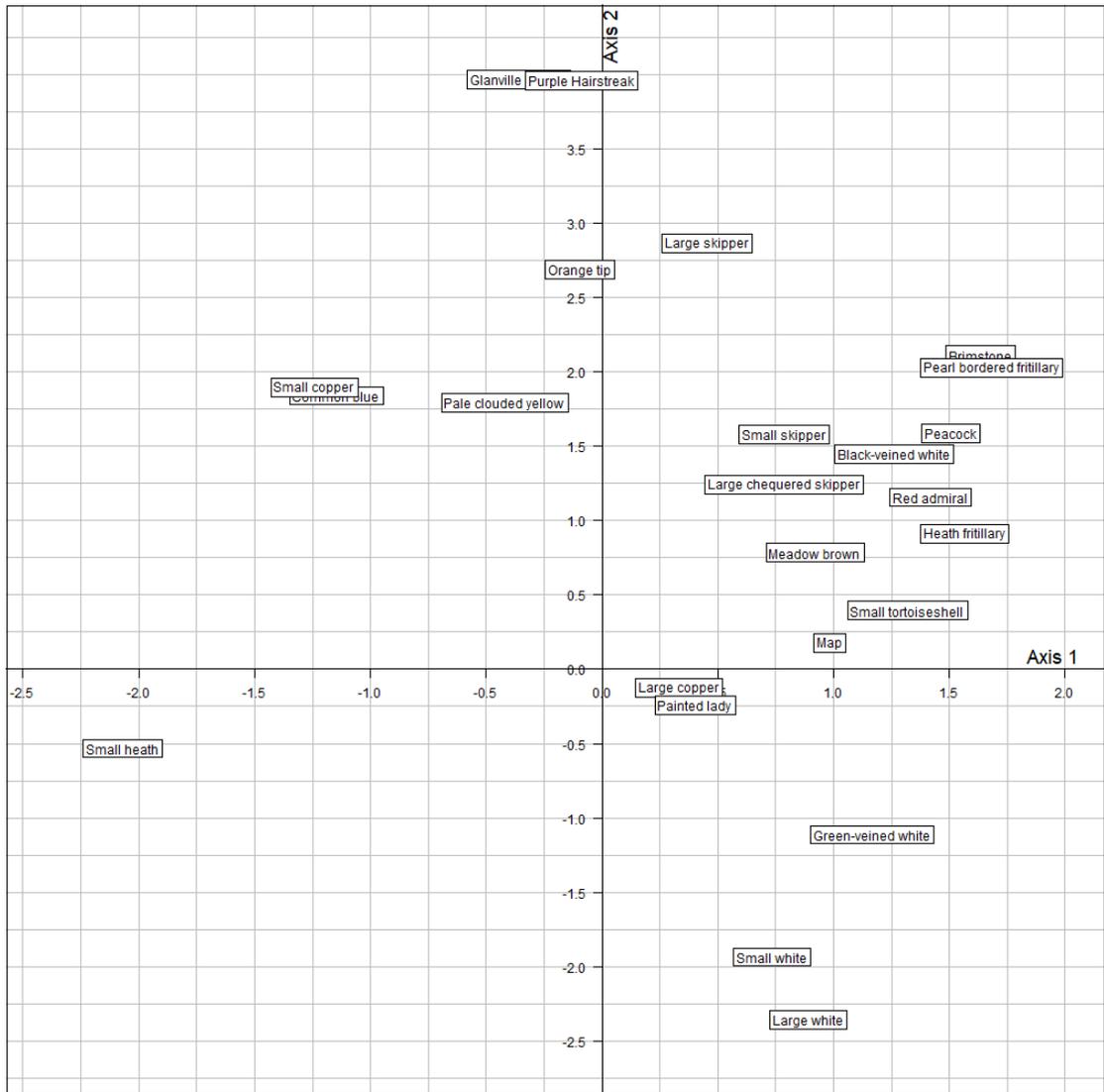


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

		Species' Traits									
		Diet Category				Foraging: water	Foraging: ground	Foraging: mid-height	Foraging: canopy	Foraging: aerial	Body mass
		Invertebrate	Omnivore	Plant/ seed	Vertebrate/ Fish/ Scavenger						
Environmental Variables	Mean height	0.358	0.179	0.358	0.093	0.051	-0.042	-0.024	0.038	0.018	-0.013
	Arable	0.399	0.195	0.283	0.122	0.025	-0.037	-0.013	0.092	0.004	-0.011
	Deciduous plantation	NA	NA	NA	NA	0.000	0.000	0.000	0.000	0.000	0.000
	Infrastructure	0.607	0.096	0.167	0.112	0.022	0.089	-0.165	-0.062	0.053	0.042
	Water	0.617	0.111	0.135	0.104	-0.071	0.026	0.072	-0.013	-0.040	-0.004
	Deciduous wood	0.296	0.179	0.447	0.077	0.023	-0.026	-0.006	0.036	0.005	-0.011
	Meadow	0.533	0.186	0.202	0.078	0.014	-0.020	-0.007	0.047	0.001	-0.013
	Reedbed	0.639	0.124	0.141	0.080	-0.049	-0.013	0.088	0.032	-0.046	-0.040
	Scrub	0.839	0.036	0.061	0.063	-0.006	-0.023	0.045	0.011	-0.011	-0.013
	Sedge meadow	0.893	0.015	0.068	0.024	-0.007	-0.017	0.028	0.027	-0.007	-0.009
	Pine	NA	NA	NA	NA	0.000	0.000	0.000	0.000	0.000	0.000
PC1	0.498	0.145	0.238	0.103	0.062	-0.057	-0.011	0.028	0.023	-0.010	

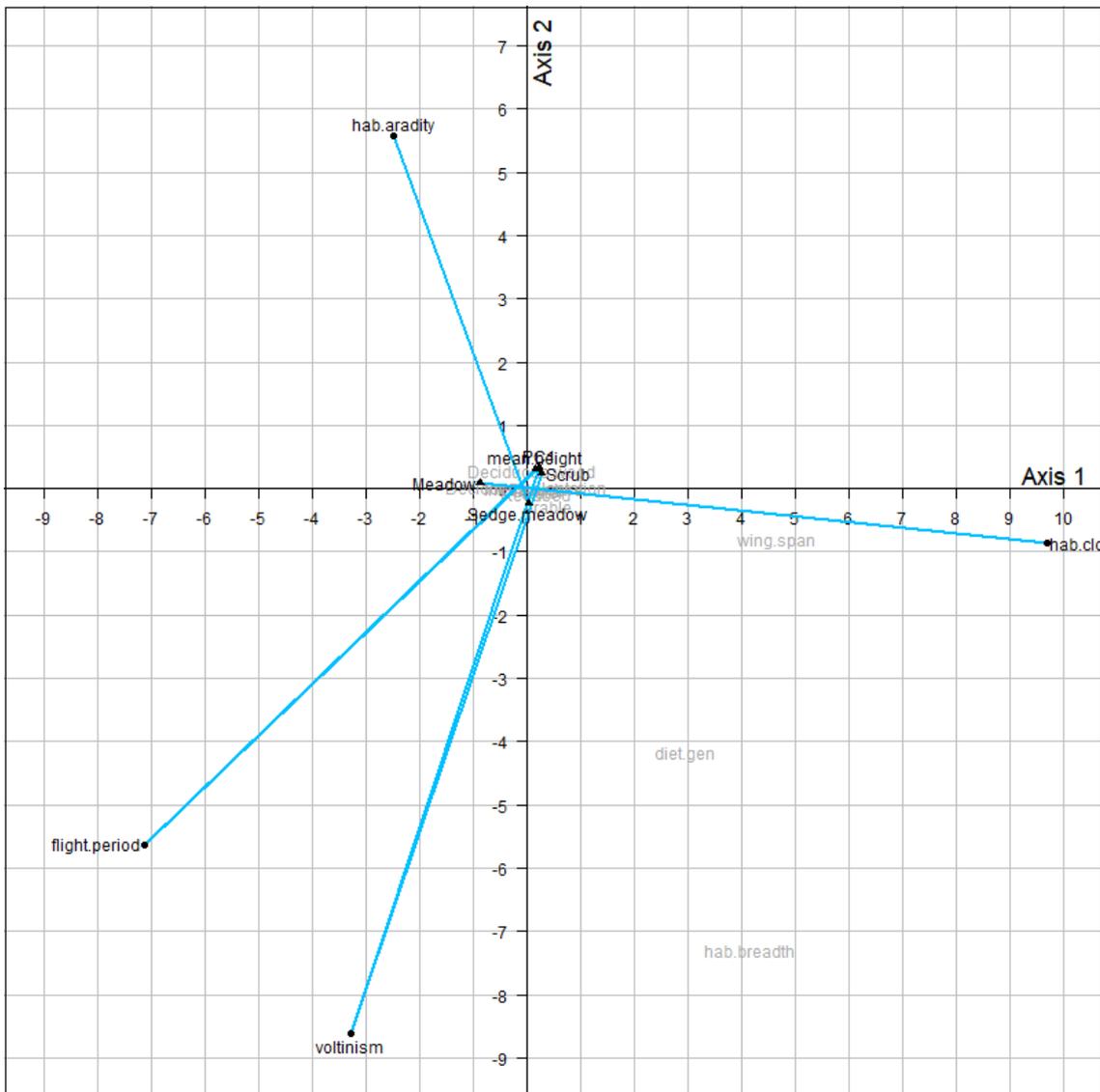


Butterflies, Germany

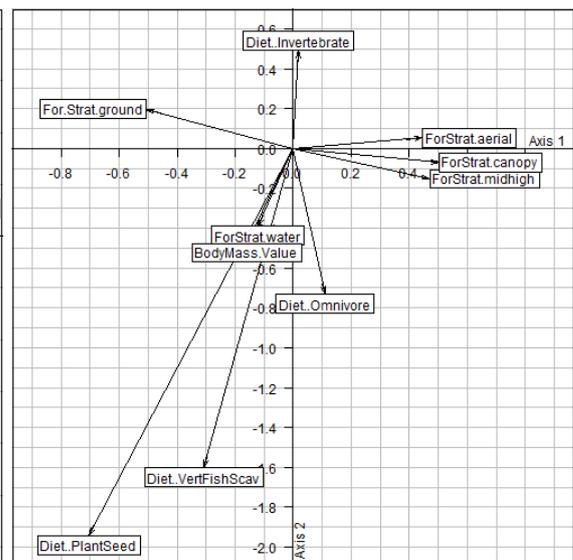
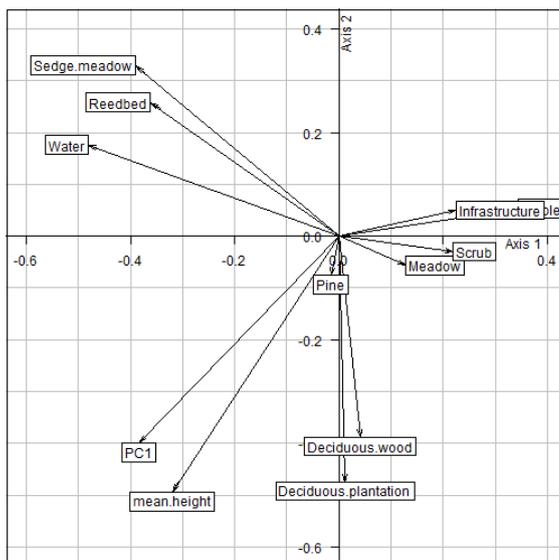
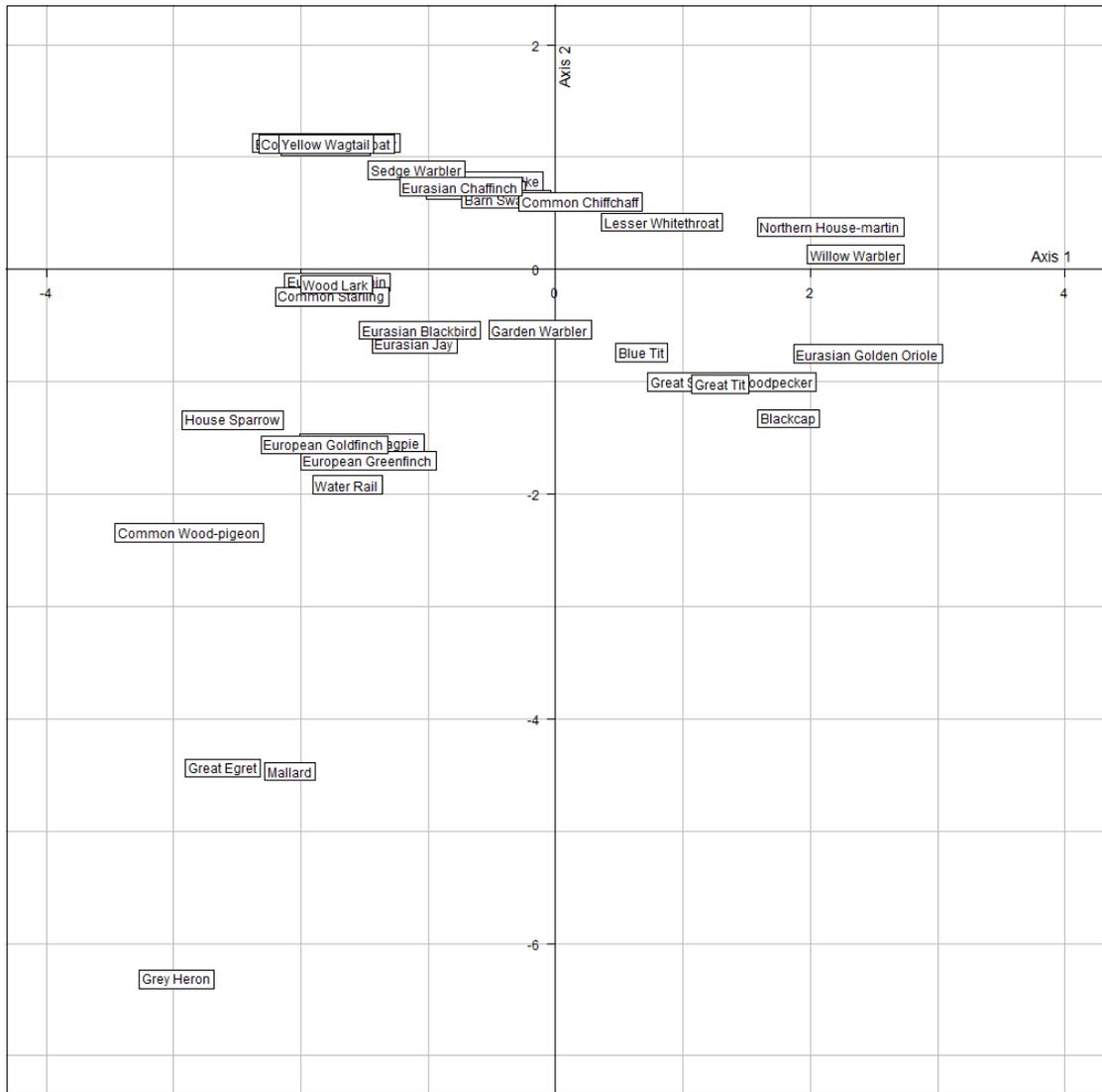


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

		Species' Traits						
		Wing span	Flight period	Voltinism	Diet generality	Habitat breadth	Habitat aridity	Habitat closedness
Environmental Variables	Mean height	0.033	-0.232	-0.196	-0.025	-0.108	0.113	0.067
	Arable	0.189	-0.066	0.092	0.308	0.234	-0.049	0.283
	Deciduous plantation	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Infrastructure	0.138	0.018	-0.050	0.139	0.038	0.149	0.108
	Water	0.112	-0.128	-0.025	-0.039	0.108	-0.132	0.190
	Deciduous wood	0.036	-0.193	-0.147	-0.029	-0.158	0.098	0.051
	Meadow	-0.246	0.421	0.151	-0.168	-0.298	0.233	-0.589
	Reedbed	0.155	-0.023	-0.031	0.074	0.121	-0.025	0.086
	Scrub	0.026	-0.176	-0.247	-0.078	-0.052	-0.018	0.219
	Sedge meadow	-0.087	-0.019	0.183	-0.072	0.110	-0.253	0.051
	Pine	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	PC1	0.046	-0.267	-0.242	-0.064	-0.088	0.098	0.111

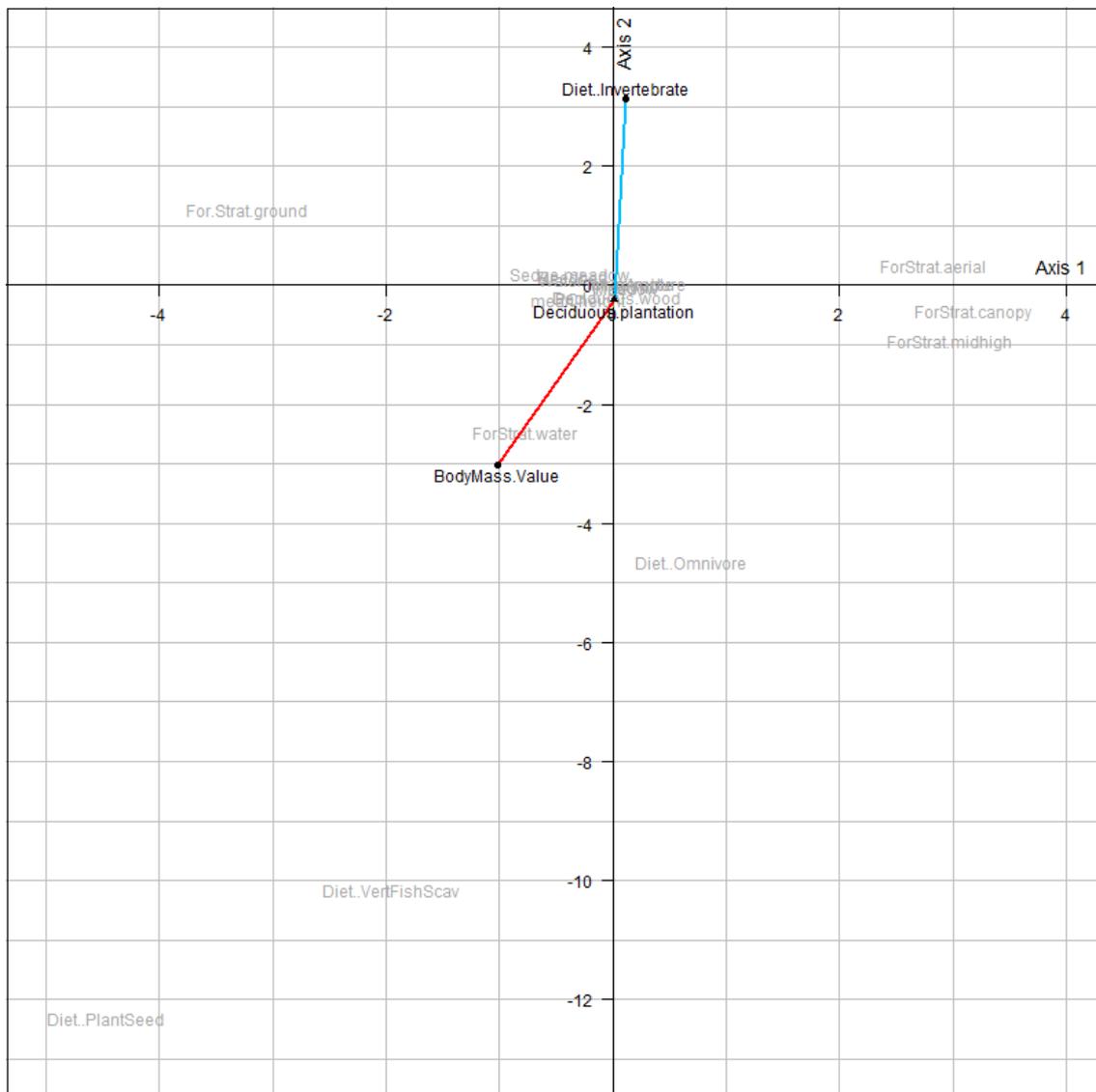


Birds, subset of species recorded in all three study regions

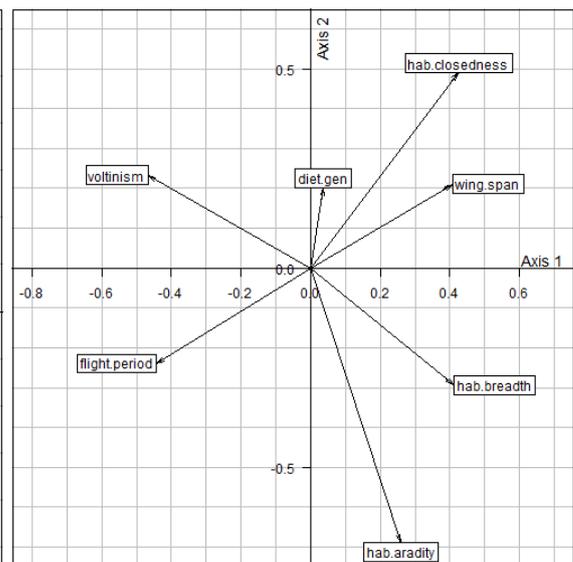
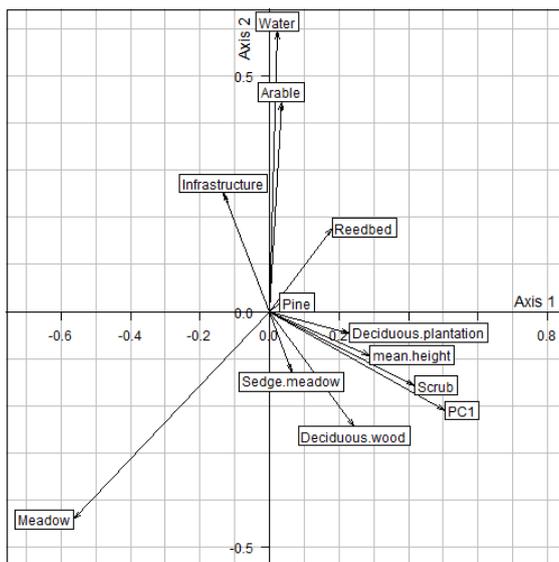
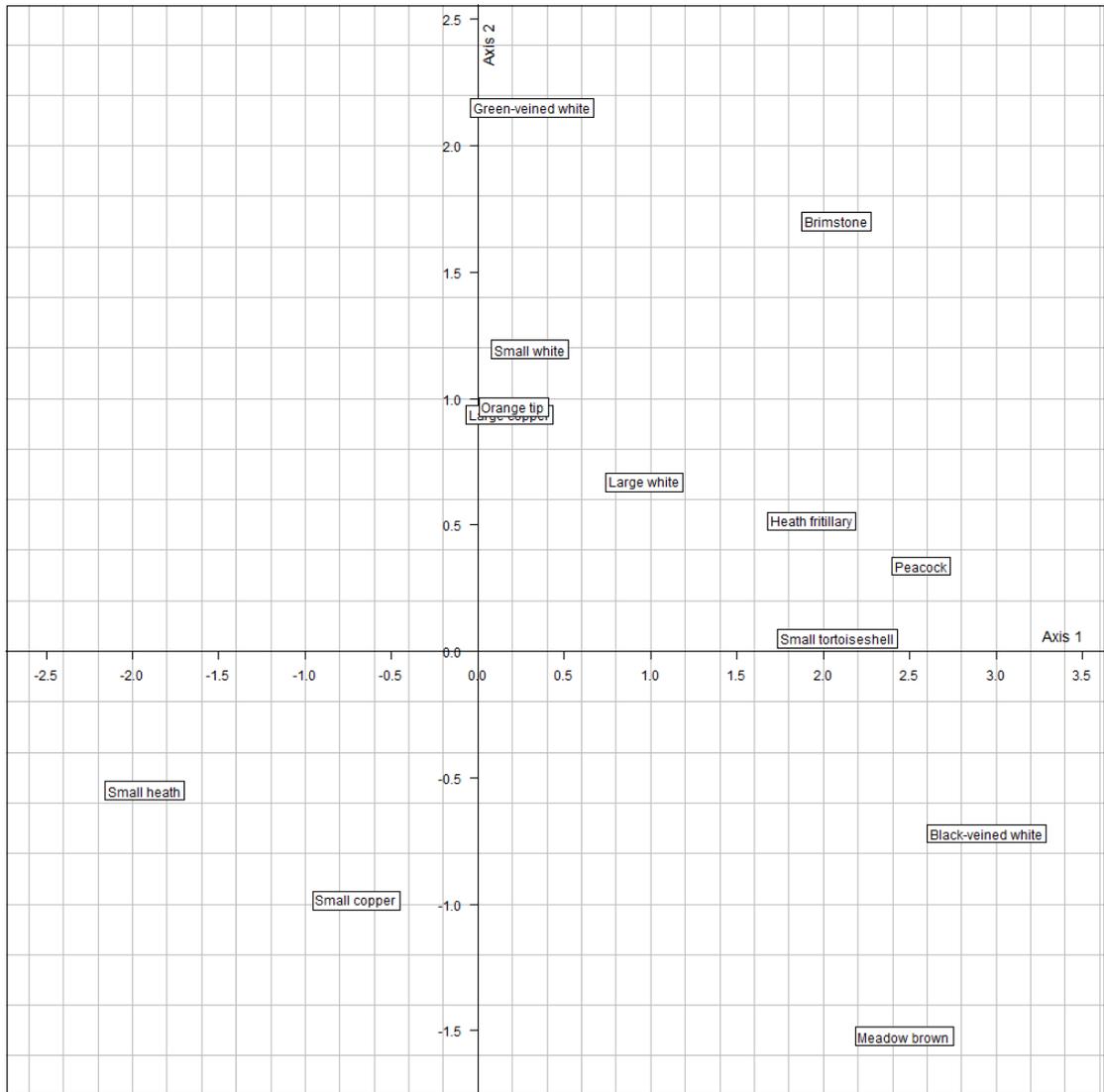


Impacts of Flood-Mediated Disturbance on Species of High Nature Value Farmland

		Species' Traits									
		Diet Category				Foraging: water	Foraging: ground	Foraging: mid-height	Foraging: canopy	Foraging: aerial	Body mass
		Invertebrate	Omnivore	Plant/ seed	Vertebrate/ Fish/ Scavenger						
Environmental Variables	Mean height	0.430	0.376	0.082	0.047	0.117	0.111	-0.089	-0.144	-0.160	0.139
	Arable	0.709	0.214	0.026	0.038	-0.030	-0.175	0.094	0.178	0.222	-0.059
	Deciduous plantation	0.362	0.414	0.102	0.095	0.126	-0.063	0.046	0.028	-0.020	0.167
	Infrastructure	0.643	0.290	0.020	0.029	-0.064	-0.088	0.146	0.084	0.038	-0.082
	Water	0.808	0.108	0.062	0.017	0.010	0.253	-0.222	-0.236	-0.207	0.027
	Deciduous wood	0.572	0.325	0.039	0.033	0.067	-0.061	0.032	0.042	0.030	0.082
	Meadow	0.692	0.225	0.019	0.053	0.034	-0.078	0.040	0.074	0.065	0.038
	Reedbed	0.880	0.068	0.017	0.027	-0.004	0.199	-0.183	-0.182	-0.146	-0.002
	Scrub	0.568	0.373	0.005	0.025	-0.070	-0.085	0.173	0.078	0.008	-0.075
	Sedge meadow	0.923	0.036	0.013	0.014	-0.019	0.221	-0.203	-0.197	-0.154	-0.019
	Pine	0.035	0.737	0.061	0.167	0.017	0.000	0.001	-0.005	-0.011	0.027
PC1	0.480	0.377	0.058	0.043	0.130	0.141	-0.145	-0.167	-0.165	0.152	



Butterflies, subset of species recorded in all three study regions



		Species' Traits						
		Wing span	Flight period	Voltinism	Diet generality	Habitat breadth	Habitat aridity	Habitat closedness
Environmental Variables	Mean height	0.109	-0.131	-0.156	0.010	0.145	0.112	0.138
	Arable	0.059	-0.048	0.009	0.066	-0.042	-0.091	0.084
	Deciduous plantation	0.109	-0.111	-0.135	0.035	0.081	0.095	0.099
	Infrastructure	-0.057	0.033	0.095	-0.013	-0.090	-0.096	-0.008
	Water	0.037	-0.067	0.033	0.029	-0.053	-0.136	0.124
	Deciduous wood	0.085	-0.123	-0.173	-0.052	0.101	0.127	0.072
	Meadow	-0.290	0.308	0.255	-0.068	-0.226	-0.054	-0.344
	Reedbed	0.121	-0.122	-0.080	-0.040	0.057	-0.005	0.096
	Scrub	0.189	-0.194	-0.216	0.020	0.237	0.151	0.160
	Sedge meadow	0.009	0.007	-0.027	0.060	0.083	0.053	0.020
	Pine	0.016	0.035	0.010	0.111	0.040	0.032	0.043
	PC1	0.206	-0.238	-0.286	-0.015	0.241	0.200	0.213

