Overview

The theory of island biogeography (IBT) states that island size, isolation and distance from the mainland influence the immigration and extinction of species on the island. The interplay of these factors is expected to reach an equilibrium of species richness. The original IBT focused on oceanic islands, but this framework can also be applied to other island-like systems. I investigated the applicability of the IBT on the waterbird species richness on lakes during the winter migration period. Moreover, I looked at the influence of habitat diversity on lake selection and if certain ecological characteristics such as migration status, size and feeding clade (terrestrial herbivore, aquatic herbivore, aquatic predator and omnivore) influence the applicability of the IBT. I did this by identifying and counting waterbird species on 14 lakes around the Dutch cities of Ede and Wageningen. Lake size and distance from the river had a significant impact on species richness, with larger lakes containing more species and lakes further from the river having fewer species. Habitat diversity was not representative for a larger species richness but lakes with larger coastal reed coverage did have more waterbird species. All feeding clades followed the expected patterns of the IBT except for terrestrial herbivores species which were not correlated with both lake size and river proximity. The species distribution of resident waterbirds and species with both resident and wintering populations followed the IBT species distribution. Waterbird species with only wintering population positively correlated with lake size but not with distance from the river, which suggest they stay close to the river during migration. This study could be replicated during the spring migration to further analyse the migration routes and lake preferences of migratory waterbirds. Additionally, the effects of climate change could be taken into account, waterbird species richness patterns might change through delayed migration and habitat destruction by the more frequent droughts in certain lakes.

The island biogeography theory and its applicability on the waterbird species richness of lakes during the winter migration period

By: Menno van der Waal

Supervisor: Jente Ottenburghs

Date: 20-12-2022

Introduction

The Island Biogeography Theory (IBT) was developed to explore patterns in the number of species on oceanic islands (MacArthur & Wilson 1967). The theory states that each island has an equilibrium in the number of species that is defined by the immigration of new species and the local extinction of resident species (figure 1). The immigrating species originate from the mainland or other islands within the archipelago while the extinction represents the disappearance of the species from the island. Both the immigration and extinction rates are influenced by geographic features of the islands and the archipelago. Larger islands generally support a larger habitat diversity, as described by the habitat diversity hypothesis (Williams, 1964), and a larger area can support more individuals of a species which creates more stable populations. Thus, the extinction rates are expected to decrease with increasing island size (figure 2A). In addition, islands that are closer to each other and to the mainland experience a higher immigration rate (figure 2B).

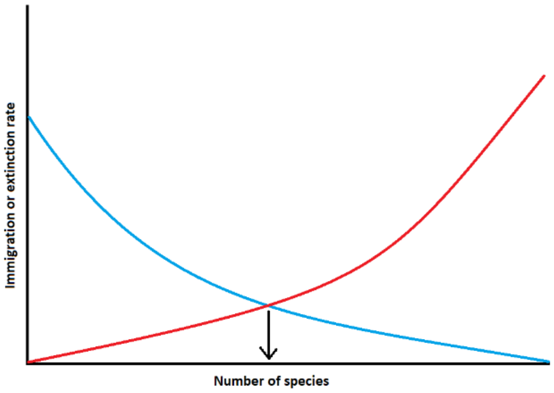

Figure 1. The number of species found on an island is the equilibrium of the intersection of the species immigration rate (blue) and extinction rate (red)

The IBT has often been applied to oceanic island communities and archipelagos (Simberloff, 1974). However, it can also be applied to other isolated habitats with island-like characteristics, such as fragmented forest habitats, tidepools and lakes (MacArthur & Wilson, 1967). Isolated freshwater bodies, such as lakes, fens and ponds, could been seen as an archipelago where aquatic species are isolated from traveling to other water bodies by land (Elmberg et al., 1994). Large freshwater bodies, such as rivers and large lakes, could serve as the source or “mainland” for these lakes.

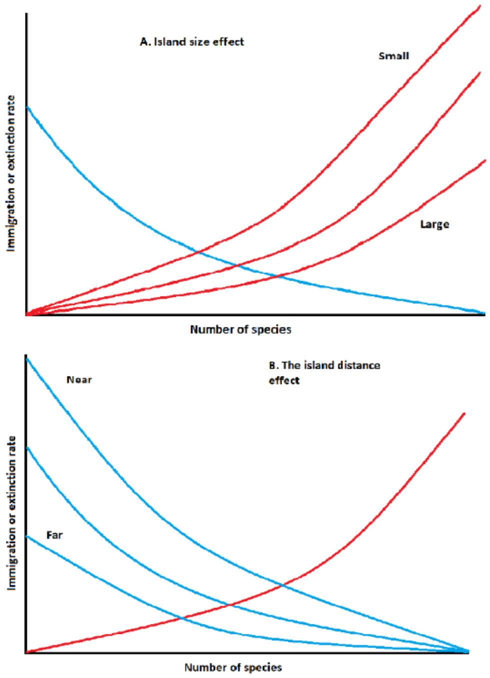

Figure 2. A. Larger islands experience a lower extinction rate (red). B. Closer interconnected islands experience a larger immigration rate (blue)

Island size and interconnectivity are not the only important environmental factors that determine the establishment and persistence of a species. Habitat diversity is an important characteristic for lakes and influences the species richness through habitat selection by different species. Firstly, food availability is one of the most important factors, especially during periods of scarcity such as winter. For example, barnacle geese (*Branta leucopsis)* and greater white fronted geese (*Anser albifrons)* move southward to ensure the availability of food. The migration path moves southward from their Russian and Scandinavian breeding grounds following the west European Atlantic coast. These species stop in the Netherlands due to the large grassy plains and pastures and large availability of fresh water. During the spring migration they follow the “green wave” of budding grass back home for the breeding season (Graaf et al., 2006). Secondly, other habitats and features besides foraging grounds, such as roosting spots and hiding spots in case of lakes, may influence habitat selection. However, the habitat features could be influenced by island size as larger islands could generally support a larger habitat diversity (i.e. habitat diversity theory, Williams, 1964), which in turn support more individuals of a species and keep a species form local extinction (Paracuellos & Tellería, 2004). The effect of habitat diversity is implicit in the IBT, where island size is assumed to correlate with the habitat diversity (MacArthur and Wilson, 1967).

Winter migration

The waterbird species composition constantly changes during the migratory period. Especially The Netherlands, which is home to a large population of year-round resident waterbird populations which are supplemented by breeding birds during the spring migration and by wintering and stopover populations during the winter migration (Sluis et al., 2004, Peterson et al., 1993). During the colder period of the year, waterbirds are dependent on the presence of fresh water and local food resources, which creates waterbird congregations on the fresh water bodies. This results in an assemblage of different waterbird species with different migration strategies. Therefore, lakes and other fresh water bodies become hotspots for waterbird species diversity during the winter migration period (Rajpar et al., 2010).

Most of the waterbirds which use the Netherlands as their wintering grounds or stopover site originate from Scandinavia and the northern Russian coast. They follow landmarks such as coasts and rivers during their travel southward (Aurbach et al., 2020). Hence, these species move south and westward over the Netherlands. However, some wintering guests and resident waterbirds generally stay at one location, but may move to other lakes if the food availability is reduced. The resident waterbirds congregate during the colder parts of winter to share the load of keeping a waterhole open when it freezes (Severcan & Yamaç ,2011). These movements could create a larger abundance and diversity of resident waterbirds. However, a mild winter could lessen the need to congregate and create more separate smaller groups due to a larger food availability (Paracuellos & Tellería, 2004). Both the movement of migratory guests and the congregation behaviour could influence the waterbird species richness distribution patterns as set up by the IBT.

Feeding clade

Feeding clade is also an important factor for habitat selection in waterbirds, especially in periods of scarcity such as the winter months. If a lake is rich with a certain food source favourable for a clade, it could cause a concentration of different species from the same feeding clade (Jeong et al., 2004, Kersten et al., 1991). Most of the winter guests are large herbivores, such as Greylag geese (*Anser anser*) and Greater white-fronted geese (*Anser albifrons*). These populations mainly focus on large pastures near water and floodplains where grass serves as the main food source (Graaf et al., 2006). This creates an assemblage of grass feeding herbivorous waterbirds. Piscivores generally select larger bodies of water, such as rivers, because these larger waterbodies generally support healthier fish populations (Moyle, 1949). Altogether, the food availability could thus influence the species richness distribution and cause it to deviate from the IBT distribution.

All the local and migratory movements of waterbird species during the winter turn the lakes into a dynamic system. These dynamics might influence species richness on the lakes, leading to deviations in the expected patterns of the island biogeographic theory. That is why I looked at the waterbird species compositions of lakes and floodplains around Wageningen and Ede. I explored whether this “archipelago” of lakes follows the predictions of the island biogeography theory during the winter migration period. Therefore, I tested the tree main IBT characteristics: lake size, lake isolation and distance from mainland. I hypothesized that species richness will be influenced by the lake characteristics according to the IBT. In addition, I measured habitat diversity around each lake to explore how it relates to lake size and how it influences the species richness of the lakes. Lastly, I investigated if the ecological characteristics of the waterbird species, such as migration status, size, wingspan and feeding clade, will impact the general predictions of the IBT.

Research questions:

- Does the waterbird species richness distribution follow the predictions of the island biogeography theory in terms of lake size, distance from river and lake isolation?
- How do different bird species traits, feeding clade and migration status, influence the applicability of the island biogeography theory to freshwater bodies?

Hypotheses

H1: My first hypothesis is that the species richness of lakes around Wageningen and Ede during the winter migration period will follow the predictions of the island biogeography theory. This means that the species richness increases with lake size and proximity to the mainland (represented by the river Rhine) and decreases with the degree of isolation of the lake (MacArthur & Wilson, 1967). Lakes are often used as islands, as animals in the water can't leave the confines of the coasts (Elmberg et al., 1994). Just like island birds are dependent on the resources of the islands mainland, waterbirds are dependent on the lakes for resources. Which creates a reverse archipelago of lakes with similar parameters (Browne, 1981).

H2: My second hypothesis is that coastal habitat diversity has a larger positive effect on waterbird species richness compared to lake size. MacArthur & Wilson implied that larger islands have a larger habitat diversity and can thus support a larger species richness. Although lake size tends to be positively correlated with habitat diversity (Ricklefs and Lovette, 1999), it doesn't automatically mean that lake size is representative for the level of habitat diversity. Larger lakes do generally support more individuals of a species through a larger availability of resources (Pöysä et al., 2019) and more niche diversity (MacDonald et al., 2018). However, most of the water vegetation might be gone during the fall and winter period and the available habitats will be located on the coasts of the lake. Taken together, I expect that coastal habitat diversity will be more important than other lake characteristics during the winter migration period.

H3: My last two hypotheses will focus on the impact of ecological characteristics of the bird species on the species richness of the lakes and IBT applicability. With regard to feeding clade, I expect that aquatic predators and terrestrial herbivores are found closer to the river and their species richness will not correlate with river distance, whereas omnivores and aquatic herbivores species are more widespread and will follow the IBT species distribution. Floodplains near the river generally contain a larger abundance of fish and have larger number of grassy plains compared to more inland lakes. Hence, aquatic predators and terrestrial herbivores will concentrate near the river. On the contrary, omnivores do not dependent on a particular niche and rely on the directly available resources. Larger lakes have more resources and more interconnected lakes allow for easy relocation if there is too much competition or when the resources are depleted (Paracuellos & Tellería, 2004). Therefore, these species will likely follow the IBT in terms of river distance, lake size and lake isolation.

H4: Lastly, I expect that the species richness patterns of waterbirds with migratory populations do not follow the IBT distribution whereas resident species richness will be correlated with the IBT parameters. During the winter migration, many migratory birds use landmarks like coasts and rivers to navigate southward (Aurbach et al., 2020). Waterbirds also use the river estuaries as stopover sites or wintering locations. This means that migratory birds do not tend to move land inwards and the species richness increases around the river lakes, resulting in the species richness distribution which is not correlated with the distance from the river. For resident waterbirds the individuals only migrate short distances to congregate and spend most of their time near the same lakes (Severcan & Yamaç ,2011).These movement patterns could result in a species richness distribution according to the IBT parameters.

Methods

Waterbird species selection

I examined the waterbird species present in lakes, fens and river floodplains around Wageningen and Ede. I went to each lake six times over a period of two months to count individuals of Anatidae (ducks, geese and swans), Rallidae (rails), Gaviidae (divers), Podicipedidae (grebes), Ciconiidae (stocks), Phalacrocoracidae (cormorants), Ardeidae (herons) and Laridea (gulls). I chose these families because these birds are dependent on the availability of fresh water as part of their habitat and are mostly found in and around lakes and floodplains and the surrounding vegetation (Green and Elmberg, 2014).

Measuring lake environmental factors

To determine the environmental factors, I measured each lakes surface area, coastal length, distance to the closest neighbouring lake, nearest distance to the river, which was the Nederrijn in all cases, and the habitat diversity score. The first three factors are related to the IBT with the river functioning as a possible "mainland", as the Nederrijn is the northmost river of the Rijn-Waal delta. The habitat diversity was calculated with the Simpsons diversity score, taking into account the coastal vegetation length and the following habitat types; woody vegetation, reeds, grassy coast and sandy coasts and sandbanks. I measured the area, distances and coastal circumference using Google Earth of which the pictures are taken around May 2021.

Taking measurements and locations

Over a period of 2 months from the 17th of October 2022 till the 16th of December 2022, each workday (i.e. Monday to Friday) I visited two lakes to take a measurement, with one visit in the morning and one in the afternoon. During the measuring period I visited each lake 6 times, 3 times in the morning and 3 times during the afternoon. During a visit in this period, I tried to identify and count all waterbirds present in the water and around the lake. I tried to find lookout spots with as much vision over the whole lake. This meant that smaller lakes have 1 or 2 lookout spots and larger lakes have up to 5 lookout spots. For each spot I took 15 minutes to document all species present with added time when I had difficulty identifying the species, and larger lakes with less lookout spots have more time. During the examination I looked at all birds present in the water, within a 5m radius on the coast and included all new arrivals. To aid me in spotting I used binoculars, the Vogelgids app

Figure 3. The locations of the 14 lakes selected for this research. The red markers represent the cities and the locations of the lakes are represented by the blue markers.

of the “Vogelbescherming Nederland” and a Rebo mini guide to birdwatching (2021). I tried to select as many lakes as possible with a close proximity to Wageningen and Ede with a variety of distances from the Nederrijn river. I selected the 14 lakes (figure 3.) because of their relative reachability and the possible overview of the largest part of the lake to make measurements possible. Additionally, I selected lakes which are not directly connected to any other bodies of water and are not in close proximity to urban areas, as some species are more tolerant to human presence compared to other species and reduce the possible effect it could have on the species richness of a lake.

Data analysis

I compiled all the data in an excel sheet where I also classified the birds according to their life history traits; feeding clade, migration status in the Netherlands, mass, wing length, tail length and hand-wing index, provided by the AVONET database (Tobias et al., 2022) and the official website of the Dutch “Vogelbescherming” (Vogelgids Nederland, 2022). I used R studio V 4.2.2 to look at the influence of these life history traits such as migration status, feeding clades and physical characteristics on the lake selection.

First, I created a Species Effort Curves to determine if I captured the maximum species diversity on each lake. The maximum number of species of six visits was used as a direct measure of species richness of each lake. For the first hypothesis I analysed the effect of different IBT parameters on the species richness distribution. I used a generalized linear model with a Poisson distribution with all lake variables and backward selection and a Principal Component Analysis (PCA) to visualize the results. For the second hypothesis I first correlated habitat diversity and lake size. Next, I used a generalized linear model to analyse the influence of the different habitat types (trees, reeds, sand/mud and grass) on the species richness. For the feeding clade and migration status, I created subsets of species and tested each IBT parameter for each feeding clade and migration status group separately with a generalized linear model with a backward selection. Finally I created separate triplots, for feeding clade and migration status, with a Redundancy Analysis (RDA) to visualize the effect of the waterbird life history traits with the species and the lakes.

Results

A total of 29 waterbird species were spotted over the course of the observational period at 14 different lakes (appendix 1), with the Wageningse nevengeul containing the largest species richness with 21 species, and the Heidebloemplas containing none. The species richness of the lakes was measured over 6 visits per lake (figure 4). Species effort curves show that Wageningse Geul, Palmerswaard and the Surfvijver have the potential for a larger species richness than observed. The other lakes show a flattening species effort curve, suggesting that I have captured their maximum species diversity within 6 visits. Finally, I excluded the domestic duck (Anas platyrhynchos domesticus) from all analysis due to it being a blanket subspecies for all domestic and hybrid duck and the resulting variance in its life history traits.

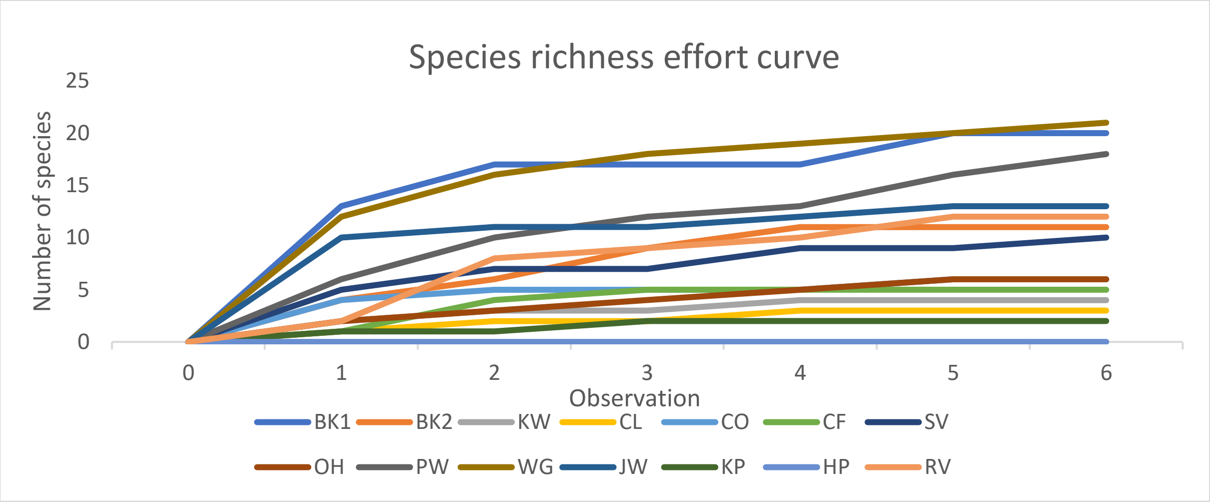

Figure 4. An species effort curve over the observational period of 17th of August till the 14th of December (2022). The number of species is cumulative with each observation and mostly shows a stabilisation of species richness. Each line represents a lake used as observation site. BK1&2 is in the Blauwe Kamer, KW is Kwintelooie Plassen, CL is Campus Lumen, CO is Campus Orion, CF is Campus Forum, SV is Surfvijver, OH the lake south of Ouwehands in Rhenen, PW is in the Palmerswaard, WG is the Wageningse Geul, JW is in the Jufferswaard, KP is Kreelsche Plas, HP is Heidebloem Plas and RV is in the Rijnvallei.

The island biogeography theory

The IBT is divided in 3 main parameters, namely lake size, lake isolation and river distance. Lake size is represented only by the coastal length (circumvention) of the lake due to the high correlation with lake surface area ($R^2 = 0.919$, $p < 0.001$). A backwards selection procedure of Generalized Linear Models (with Poisson distribution) converged upon a model with two explanatory variables: species richness was positively influenced by increasing lake circumvention (figure 5A, $p < 0.001$, df = 12, $f^2 = 3.14$) and negatively influenced by increasing distance from the river (figure 5B, $p < 0.001$ df = 12, $f^2 = 0.76$). However, the species richness was not significantly influenced by the degree of isolation which was measured by average lake distance ($p = 0.418$, df 12, $f^2 = 0.058$) and the nearest neighbour ($p = 0.589$, df = 12, $f^2 = 0.026$).

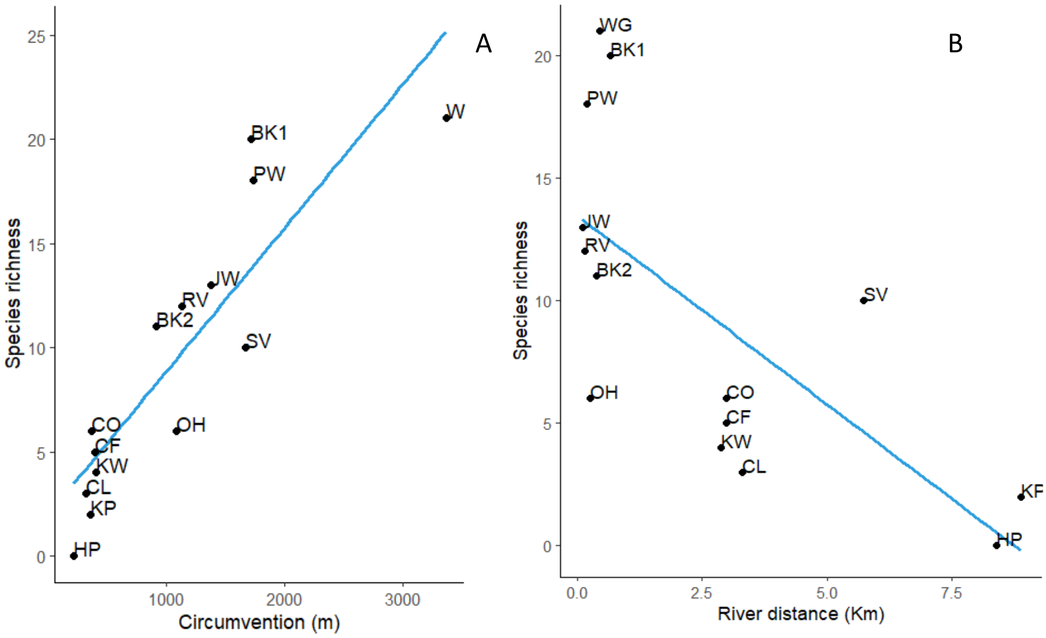

Figure 5. Graphs showing the effect of river distance (A)and lake size (B). The markers are the lakes used for observation sites. Abbreviations are the same as Figure 1.

Lake habitat diversity

The positive effect of island size in the IBT might be related to the habitat diversity (MacArthur & Wilson 1967). I quantified habitat diversity be calculating the Simpsons Diversity Index for the habitat types of the lake coasts. Contrary to the prediction of the IBT, the Simpsons diversity of the coastal habitats was not correlated with the lake circumvention ($R = 0.037$, $p = 0.909$). The Simpsons diversity index alone was also not significantly correlated with the species richness of the lakes ($p = 0.962$, df = 12, $f^2 < 0.001$).

Multivariate habitat analysis

A Principal Component Analysis (PCA) confirmed the results of the generalized linear models (variation explained by PC1 = 33% and by PC2 = 28%, figure 6.A), showing a strong positive relationship between species richness and the circumvention of the lakes and a strong negative relation between the species richness and the lake distance from the river. The PCA also confirmed the weak relation of the lake circumvention with the Simpsons diversity. Additionally, I included the effect of each habitat type. Larger reed coverage (Preeds) had a positive relation with species richness and sandy and muddy coasts (Psand.mud) showed a negative relation. Grassy coast coverage (Pgrass), however, did not influence the species richness (figure 6.B).

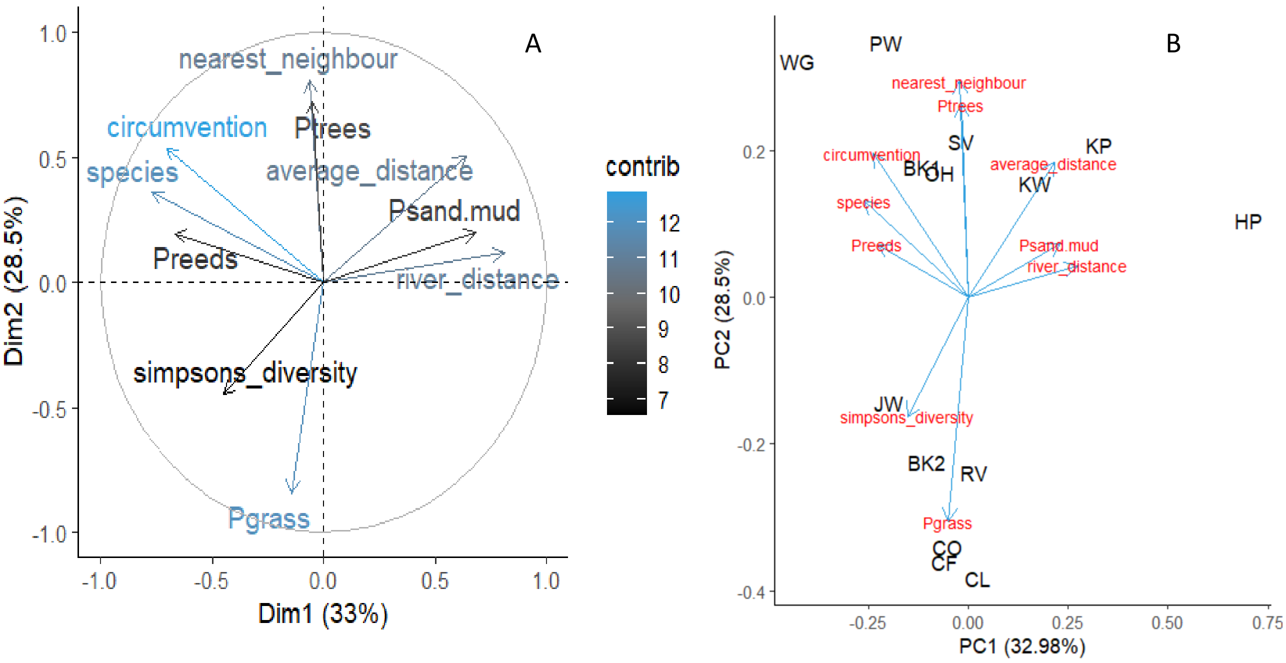

Figure 6. (A) A variable PCA plot containing both IBT and habitat variables. The contrib scale explains the contribution of a parameter for the PCA. The more blue colour is a higher contribution. (B) A PCA biplot showing the individual lakes in relation to the IBT and habitat variables. The percentage of habitat coverage is represented by the P(Habitat), e.g., Preeds = Percentage of coast covered with reeds.

Bird characteristics for lake selection

To analyse whether the applicability of the IBT depends on the migration status and feeding clade (table 1), I used GLM on the respective feeding clade and migration status groups for the IBT characteristics used in the general analysis, namely terrestrial herbivores, aquatic herbivores, aquatic predators and omnivores for the feeding clade, and resident, resident/wintering and wintering for the migration status. For migration status, the species richness of all three groups was significantly correlated with lake size: resident ($p < 0.001$, df = 12, $R^2 = 0.783$), resident/wintering ($p = 0.010$, df = 12, $R^2 = 0.440$) and wintering ($p = 0.012$, df = 12, $R^2 = 0.668$). However, while both resident and resident/wintering negatively correlated with distance from river: resident ($p = 0.015$, df = 12, $R^2 =$

0.401) and resident/wintering ($p = 0.009$, df = 12, $R^2 = 0.440$), the species richness of pure wintering group did not ($p = 0.087$, df = 12, $R^2 = 0.224$).

For the feeding clade, the species richness distribution was significantly correlated with both lake size and river distance for aquatic herbivores, aquatic predators and omnivores, with lake size: aquatic herbivore ($p = 0.018$, df = 12, $R^2 = 0.387$), aquatic predator ($p < 0.001$, df = 12, $R^2 =0.797$) and omnivores ($p < 0.001$, df = 12, $R^2 =0.841$). And river distance: aquatic herbivore ($p = 0.008$, df = 12, $R^2 = 0.452$), aquatic predator ($p = 0.024$, df = 12, $R^2 =0.356$) and omnivores ($p =0.033$, df = 12, $R^2 =0.326$). However, the species richness of terrestrial herbivores was not significantly correlated with lake size ($p = 0.260$, df = 12, $R^2 = 0.093$) or distance from river ($p = 0.137$, df = 12, $R^2 = 0.174$).

Lastly, both nearest neighbour and average lake distance did not correlate significantly for all groups of the feeding clade and the migration status (appendix 2).

Lake	Resident	Resident/ Wintering	Wintering	Exote	Aquatic Herbivore	Aquatic Predator	Omnivore	Terrestrial Herbivore	Total Species
WG	13	6	1	1	6	10	4	1	20
PW	12	4	2	0	7	9	2	0	11
BK1	12	5	2	1	6	10	3	1	3
SV	8	0	1	0	3	4	2	0	12
JW	8	2	2	0	5	5	2	0	3
RV	7	2	1	2	4	4	1	3	6
OH	4	1	0	1	1	4	1	0	5
BK2	6	4	0	1	5	4	1	1	9
KW	2	0	0	1	1	1	1	0	6
CF	4	1	0	0	4	0	1	0	18
CO	5	1	0	0	5	0	1	0	21
KP	2	0	0	0	1	1	0	0	12
CL	3	0	0	0	2	0	1	0	2
HP	0	0	0	0	0	0	0	0	0

Table1. A table Containing the Species richness of each lake with the proportion species richness of corresponding migration status and feeding clade. Lakes are ordered in decreasing circumvention (appendix 1). The Wintering column contain species with only stopover or wintering populations in The Netherlands. The Resident/Wintering column count species with both resident, stopover and wintering populations in The Netherlands.

To further examine the lake preference for specific bird groups, I performed a Redundancy Analysis (RDA) to constrain the ecological characteristics of the waterbirds with the lakes. The axes of the RDA (figure 7) had constrained parameter values of RDA1 = 23.6% and RDA2 = 14.6%. RDA1 was strongly positively influenced by waterbird tail length (RDA1 = 91.8%) and wing length (RDA1 = 90.4%), and moderately influenced by the mass (RDA1 = 47.7%), which signify larger birds. While RDA2 was positively influenced by the hand wing index (RDA2 = 41.0%) and negatively influenced by mass (RDA2 = -48.4%). Lakes which are larger and closer to the river (figure 5) show a divide in species size where larger species prefer Rijnvallei and Blauwe Kamer 1&2, and smaller species prefer Jufferswaard, Wageningse Geul and Palmerswaard. Additionally, wintering species and species which are wintering or resident are mostly found in the lakes closer to the river (figure 7A) while resident species do not have a specific preference. Aquatic predators, which are mostly smaller species, are more often found in larger lakes which are closer to the river (figure 7B) such as Wageningse Geul. Aquatic herbivore species distribution followed the IBT distribution with a more widespread distribution but a higher species richness on lakes near the river. And lastly, terrestrial herbivores and omnivores do show preference to lakes closer to the river.

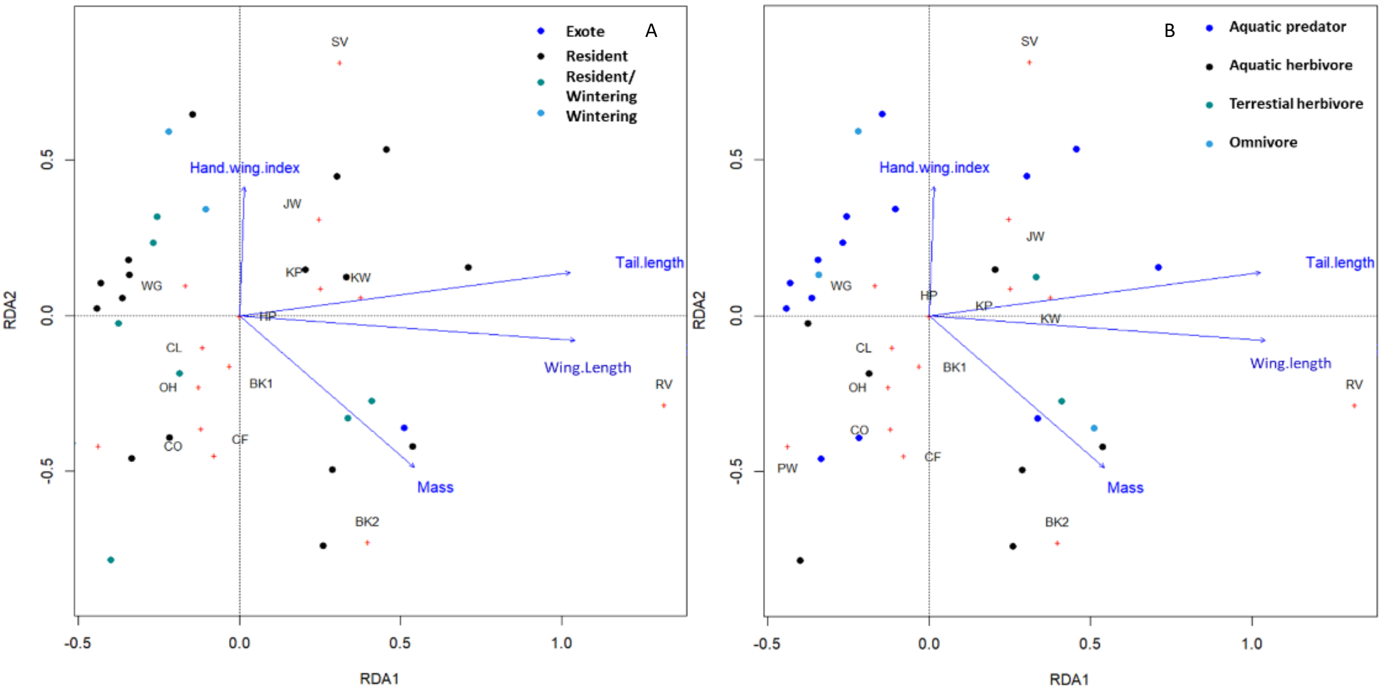

Figure 7. Graphs showing the lake preference of waterbirds based on waterbird characteristics. The RDA plots are created with RDA1 = 23.6% and RDA2 = 14.6%. The red dots represent the lakes, with the abbreviations used in figure 4., and the coloured dots represent a species. A. Individual species are marked with the migratory status during the winter migration period from 14 September to 17 December in 2022. Resident/wintering classified species both stay in the Netherlands and come from other populations during the migration. B. The same RDA but the individual species are marked with the feeding clade.

Discussion

This study was aimed to determine the applicability of the island biogeographic theory (MacArthur & Wilson, 1967) on the species richness distribution of Dutch lakes, ponds and fens in a period of biodiversity shift during the winter migratory period. First, I analysed the general applicability of the theory with regard to the lake size, distance to the river and degree of isolation. I found a positive influence of lake size, a negative effect of distance from the river and no significant effect of degree of isolation with both nearest neighbour and average distance to other lakes. Secondly, I analysed the influence of habitat diversity on the species diversity and its relation to the lake size, where habitat diversity was not correlated with lake size or species richness. However, larger reed coverage was positively correlated with species richness and muddy or sandy beaches were negatively correlated. Next, I analysed the characteristics of the waterbird species and the influence of these characteristics on the confirmed IBT parameters lake size and distance from the river. I found that wintering species generally resided more in the larger lakes and lakes closer to the river. In contrast, species with resident populations were spread more widely. Lastly, I found that terrestrial herbivores were found more closer to the river while aquatic herbivores, aquatic predators and omnivores were found more generally following the IBT distribution.

Island biogeography theory

Of the three main characteristics of the island biogeography theory as described by MacArthur and Wilson (island size, island isolation and mainland distance), only lake size and distance from the river significantly influenced the waterbird species richness in my study. The positive effect of lake size on waterbird species richness has been reported for other waterbird populations (Zhao & Zhou 2018, Elmberg et al. 1994, Eadie et al. 1986). However, the use of a hypothetical mainland is not often used in similar studies due to the size of the study area, which in most studies encompass complete wetland ranges and river deltas (Eadie et al. 1986, Bengtsson et al. 2014, Ma et al. 2010). Although, the distance from major water features, like major lakes and rivers, is sometimes used (Beatty et al., 2014). I chose the Nederrijn as a mainland substitute as it serves as a geographical barrier and the northmost river in the Maas-Waal delta in combination with the fact that migratory birds use landmarks like rivers to determine the routes and stopover site selection (Aurbach et al., 2020). The nearest river distance would in hindsight better fit as another measure of lake isolation instead of a hypothetical mainland. The IBT as described by MacArthur & Wilson uses mainland as the principal source area from where the species originate and migrate from. However, the species of migratory waterbird in my study originate from the Scandinavia, Siberia and freshwater bodies in the north of the Netherlands (Sluis et al., 2004). Furthermore, with the migration route following the river, it is logical that most species are found in the floodplains near the river.

To determine the degree of isolation I used the nearest neighbour and the average distance from other lakes, which both did not have a significant effect on the species richness. This is most likely due to the smaller study area and the fact that the ability to fly lessens the restraint of lake isolation in comparison to animals that cannot fly. This reduces the possible effect of lake isolation on the species richness (Barreto et al., 1965). However, other studies reported that nearby lakes with more natural connectivity experience an increased waterbird species richness and diversity (Xia et al., 2016). Besides, the nearest neighbour parameter was too local to determine the general lake isolation while average lake distance would favour the lakes in the middle of the study area and not general connectivity. To further calculate the lake isolation could have put more emphasis on the direct neighbours of the lakes and include the distance from the river. Other studies used different parameters for isolation such as distance to nearest source pool (Zhao & Zhou 2018) or a binary classification of isolation, i.e. isolated or not (Sebastián-González & Green, 2014). Another useful analysis for the degree of isolation was described by Weigelt and Kreft (2013). They captured the most important degrees of isolation as the mainland distance and stepping stone distance, both modified by wind current and surrounding landmass. In my study, the wind current modification would not be possible due to time constraints but the addition of stepping stone routes and surrounding lake area could have explained the lake isolation better. In addition, my study area is portrayed as if the lakes are the only lakes in the “archipelago”. However, there are a lot of fresh waterbodies, like small lakes, ditches and lakes close to urban areas, which I excluded from the study due to lake selection specification or time constraints. This could reduce the isolation of most of the study lakes, especially the floodplains which had a lot of lakes that were inaccessible. Only the lakes on the Uterechtse Heuvelrug and the Ginkelse Heide did not have much neighbouring water. Thus better analysis of neighbouring water will be needed for future research.

Habitat diversity

The habitat diversity hypothesis (Williams, 1964) states that there is a positive relationship between habitat heterogeneity and increasing the size of an area. More habitat diversity in large lakes is thus expected to result in higher levels of species richness (Ma et al., 2010, Hart & Horwitz, 1991). Therefore, I expected that a lake with a larger habitat diversity score could support a larger species richness. However, the Simpsons diversity index of the coastal habitats was not correlated with species richness and coastal length. In combination with the results of the general IBT analysis, these results imply that lake size is more important than habitat diversity for a larger species richness. Ultimately, these results are supported by a number of other studies (Roach & Griffith, 2015, Elmberg et al., 1994), which suggest that the importance of a bigger habitat diversity is outweighed by a larger presence of a favourable habitat which could support more species (Hortal et al., 2009, Elmberg et al., 1994). Kadmon & Allouche, (2007) suggest that islands with a high habitat diversity and niche differentiation are more vulnerable to stochastic extinction due to the lower number of individuals that can be supported by the available resources. Which shifts the importance from habitat diversity to island size due to the direct habitat abundance (Roach & Griffith, 2015). Especially during the winter migratory period for wintering location and stopover site selection of waterbirds, where direct food and water availability is the most important (Hutto, 1998, Sillén & Solbreck, 1977). Which explains the importance of lake size compared to habitat diversity for a larger waterbird species richness.

Of the four habitat types tested, only the number of reeds and sandy or muddy shores significantly influenced the species richness, where reeds had a positive influence and muddy or sandy shores a negative influence. Muddy and sandy shores are mostly used as roosting ground and foraging grounds for waders, which mostly leave during the winter migration. Additionally, the amount of muddy shores could also be an indicator for the water reduction due to droughts, which is an increasing problem in wetlands around the world (Canepuccia et al., 2007, Wen et al., 2016). And this was reflected by the state of the Heidebloem Plas which had a severely reduced water level even following a period of rain. On the contrary, reeds are one of the most important defining features of wetland habitats (Ionescu et al., 2020), which was reflected by the dominance of reed coverage in lakes with the largest species richness (Appendix 1). Of the 28 species recorded, 23 are designated with wetland as their primary habitat by AVONET. This explains the positive effect of reed coverage on the recorded species richness.

Feeding clades

For the feeding clades, I expected to find aquatic predators and terrestrial herbivores closer to the river while aquatic herbivores and omnivores would follow the IBT distribution. However, while the terrestrial herbivore species distribution was not correlated with both lake size and distance from the river, the species distribution of aquatic herbivores, aquatic predators and omnivores were positively correlated with lake size and negatively correlated with distance from the river.

The analysis for the terrestrial herbivores was mostly aimed at the large populations of goose species that winter stopover in the Netherlands (Koffijberg et al., 2017), and the only terrestrial herbivores recorded were indeed goose species. Notably, the graylag goose *(Anser Anser)* was found at 4 different lakes close to the river and only Rijnvallei and Blauwe kamer 2, which had the largest grassy coast of the lakes. However, there were flocks of geese nearby the other lakes but not close enough to be included in calculations of lake species richness. This observation suggests that most goose species prefer larger grassy pastures instead of foraging grounds near water bodies due to their large food requirement (Ebbinge et al., 1975, Voslamber et al., 2010).

I expected aquatic predators to be concentrated near the rivers. Most recorded piscivores, like the Great Egret (*Ardea alba*) and the common kingfisher (*Alcedo atthis*), were indeed found only in the river floodplain lakes. Most likely due to the important role of these lakes in the fish lifecycle which increase the abundance of fish in these waters (Buijse et al., 2002, King et al., 2003). However, the aquatic predators clade included predators for all aquatic prey animals. Reeds provide shelter during the winter for not only the waterbirds, but also for many invertebrates that serve as the main food source for several waterbirds (Ditlhogo et al., 1992). The lakes in the river floodplain generally contain large amount of reed coverage, which also increases the amount of aquatic predator species found closer to the river. However, many lakes outside the floodplain area still had a considerable coastal reed coverage, which was reflected by the amount of aquatic carnivorous species found further from the river. Altogether, the abundance of reeds and fish in more inland lakes caused the feeding clade of aquatic predator to still follow the IBT in distribution and be correlated by both lake size and river distance.

Lastly, the omnivorous and aquatic herbivore waterbirds species richness followed the IBT model. The flexibility in food choice and the extended availability of aquatic plants in colder climates, as long as the water does not freeze over (Mitchell & Rogers, 1985), allows for a wider dispersal of species due to the large habitat availability in the Dutch fresh waters (Ten Cate et al., 1991).

Migration

For the different migration strategies, I expected that species with wintering populations in the Netherlands would be found mostly close to the river and resident species a species distribution more akin to the IBT. In line with these expectations, I found that species with only wintering populations did only significantly correlate with lake size and not with river distance. This result signifies that wintering species are predominantly found in lakes close to the river when combining the observation data in table 1. This distribution suggests that rivers serve as migration landmarks for populations moving southward (Aurbach et al., 2020) and the importance of the wetlands as connective habitat for the flyway of long-distance migrating species (Stroud et al., 2004, Aurbach et al., 2020).

On the other hand, species classified with both resident and wintering populations and species with only resident populations were found to follow the IBT on lake size and distance from the river. Although, the wintering individuals gravitate more to the river like the wintering species, I did expect resident species would be spread more widely according to the IBT because these species stay year-round in the same area and might migrate only short distances to congregate (Severcan & Yamaç ,2011). So if a population consists of both wintering and resident individuals, the counted resident individuals more land inward will cause the species richness pattern to follow like it is a resident species. Additionally, the floodplains near the river still has a larger species richness of resident birds because of the general resource abundance (Ditlhogo et al., 1992), causing the IBT distribution with river distance.

These results are mostly in line with my hypotheses and explain the importance of the river during the winter migratory period of waterbirds. However, the migration status of the waterbirds is difficult to classify. A lot of species found during the observational period have resident populations, breeding populations, stopover populations and wintering populations (SOVON, 2023), which complicates the analysis on the effect of the migration status of the species, as it is hard to determine the place of origin of each individual. Future research could classify the waterbirds in breeding and non-breeding groups, which would indicate a possible origin in the Netherlands and group wintering and stopover species under non-breeder (Aarts & Bruinzeel, 2009)

Conclusion

In conclusion, lake size was the best biogeographic characteristic to determine waterbird species richness. In all cases, except for the terrestrial herbivores, larger lakes have a larger species richness. And although river distance was not a good parameter for IBT mainland distance, it was still useful as an isolation factor and an important parameter for lake selection in waterbirds. Further research could expanded to include the spring migration period to analyse the species richness distribution and investigate if certain lake characteristics are more important during the breeding period. Additionally, the effect of climate change on the waterbird habitat and species assemblage should also be studied in more detail as the summers are getting warmer and dryer with reduced water levels as result (Wantzen et al., 2008). A dry and hot summer could have negative impacts on the state of the lake or the floodplain during the winter migratory period (Bond et al., 2008), such as the Heidebloem Plas which had severely reduced banks and had no waterbird presence. Additionally, a warmer winter period might cause certain waterbird species to delay their winter migration, stay longer at stopover locations or migrate shorter distances (Lehikoinen & Jaatinen, 2012). Analyses of these phenomena could help accommodate the many migratory species that visit during the migration period and contribute to the preservation of the waterbird species in the Netherlands. So the land of water could keep serving as the crossroads for the winter migration.

References

Aarts B. & Bruinzeel L. (2009). *De nationale windmolenrisicokaart voor vogels. SOVON*

Aurbach, A., Schmid, B., Liechti, F., Chokani, N., & Abhari, R. (2020). Simulation of broad front bird migration across Western Europe. *Ecological Modelling*, *415*, 108879.

Beatty, W. S., Webb, E. B., Kesler, D. C., Raedeke, A. H., Naylor, L. W., & Humburg, D. D. (2014). Landscape effects on mallard habitat selection at multiple spatial scales during the non-breeding period. *Landscape ecology*, *29*, 989-1000.

Bengtsson, D., Avril, A., Gunnarsson, G., Elmberg, J., Söderquist, P., Norevik, G., ... & Waldenström, J. (2014). Movements, home-range size and habitat selection of mallards during autumn migration. *PloS one*, *9*(6), e100764.

Bond, N. R., Lake, P. S., & Arthington, A. H. (2008). The impacts of drought on freshwater ecosystems: an Australian perspective. *Hydrobiologia*, *600*, 3-16.

Browne, R. A. (1981). Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *Journal of Biogeography*, 75-83.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., Van Geest, G. J., Grift, R. E., ... & Roozen, F. C. (2002). Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater biology*, *47*(4), 889-907

Canepuccia, A. D., Isacch, J. P., Gagliardini, D. A., Escalante, A. H., & Iribarne, O. O. (2007). Waterbird response to changes in habitat area and diversity generated by rainfall in a SW Atlantic coastal lagoon. *Waterbirds*, *30*(4), 541-553.

Ditlhogo, M. K., James, R., Laurence, B. R., & Sutherland, W. J. (1992). The effects of conservation management of reed beds. I. The invertebrates. *Journal of Applied Ecology*, 265-276.

Eadie, J. M., Hurly, T. A., Montgomerie, R. D., & Teather, K. L. (1986). Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Environmental Biology of Fishes*, *15*, 81-89.

Ebbinge, B., Canters, K., & Drent, R. (1975). Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl*, *26*(26), 5-19.

Elmberg, J., Nummi, P., Poysa, H., & Sjoberg, K. (1994). Relationships between species number, lake size and resource diversity in assemblages of breeding waterfowl. *Journal of biogeography*, 75-84.

Hart, D. D., & Horwitz, R. J. (1991). Habitat diversity and the species—area relationship: alternative models and tests. *Habitat structure: the physical arrangement of objects in space*, 47-68.

Hortal, J., Triantis, K. A., Meiri, S., Thébault, E., & Sfenthourakis, S. (2009). Island species richness increases with habitat diversity. *The American Naturalist*, *174*(6), E205-E217.

Hutto, R. L. (1998). On the importance of stopover sites to migrating birds. *The Auk*, *115*(4), 823-825.

Ionescu, D. T., Hodor, C. V., & Petritan, I. C. (2020). Artificial wetlands as breeding habitats for colonial waterbirds within Central Romania. *Diversity*, *12*(10), 371.

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1467-1471.

Jeong, H. J., YOO, Y. D., Kim, J. S., KIM, T. H., Kim, J. H., Kang, N. S., & Yih, W. (2004). Mixotrophy in the phototrophic harmful alga Cochlodinium polykrikoides (Dinophycean): prey species, the effects of prey concentration, and grazing impact. *Journal of Eukaryotic Microbiology*, *51*(5), 563-569.

Kadmon, R., & Allouche, O. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *The American Naturalist*, *170*(3), 443-454.

Kersten, M., Britton, R. H., Dugan, P. J., & Hafner, H. (1991). Flock feeding and food intake in little egrets: the effects of prey distribution and behaviour. *The Journal of Animal Ecology*, 241-252.

King, A. J., Humphries, P., & Lake, P. S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(7), 773-786.

Koffijberg, K., Schekkerman, H., van der Jeugd, H., Hornman, M., & van Winden, E. (2017). Responses of wintering geese to the designation of goose foraging areas in The Netherlands. *Ambio*, *46*, 241-250.

Lehikoinen, A., & Jaatinen, K. (2012). Delayed autumn migration in northern European waterfowl. *Journal of Ornithology*, *153*, 563-570.

Ma, Z., Cai, Y., Li, B., & Chen, J. (2010). Managing wetland habitats for waterbirds: an international perspective. *Wetlands*, *30*, 15-27.

Mitchell, D. S., & Rogers, K. H. (1985). Seasonality/aseasonality of aquatic macrophytes in Southern Hemisphere inland water. In *Perspectives in Southern Hemisphere Limnology: Proceedings of a Symposium, held in Wilderness, South Africa, July 3–13, 1984* (pp. 137-150). Springer Netherlands..

Moyle, J. B. (1949). Some indices of lake productivity. *Transactions of the American Fisheries Society*, *76*(1), 322-334.

Navedo, J. G., & Herrera, A. G. (2012). Effects of recreational disturbance on tidal wetlands: supporting the importance of undisturbed roosting sites for waterbird conservation. *Journal of Coastal Conservation*, *16*, 373-381.

Osborn, J. M., Hagy, H. M., Mcclanahan, M. D., Davis, J. B., & Gray, M. J. (2017). Habitat selection and activities of dabbling ducks during non-breeding periods. *The Journal of Wildlife Management*, *81*(8), 1482-1493.

Paracuellos, M. (2006). How can habitat selection affect the use of a wetland complex by waterbirds?. *Biodiversity & Conservation*, *15*(14), 4569-4582.

Paracuellos, M., & Tellería, J. L. (2004). Factors affecting the distribution of a waterbird community: the role of habitat configuration and bird abundance. *Waterbirds*, *27*(4), 446-453.

Peterson, R. T., Mountfort, G., & Hollom, P. A. D. (1993). *A field guide to the birds of Britain and Europe* (Vol. 8). Houghton Mifflin Harcourt.

Pöysä, H., Holopainen, S., Elmberg, J., Gunnarsson, G., Nummi, P., & Sjöberg, K. (2019). Changes in species richness and composition of boreal waterbird communities: a comparison between two time periods 25 years apart. *Scientific reports*, *9*(1), 1-10.

Rajpar, M. N., & Zakaria, M. (2010). Density and diversity of water birds and terrestrial birds at Paya Indah Wetland Reserve, Selangor Peninsular Malaysia. *Journal of Biological Sciences*, *10*(7), 658-666.

Ricklefs, R. E., & Lovette, I. J. (1999). The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, *68*(6), 1142-1160.

Roach, J. K., & Griffith, B. (2015). Climate-induced lake drying causes heterogeneous reductions in waterfowl species richness. *Landscape Ecology*, *30*, 1005-1022.

Schaub, M., Pradel, R., Jenni, L., & Lebreton, J. D. (2001). Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. *Ecology*, *82*(3), 852-859.

Scheffer, M., Van Geest, G. J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M. G., ... & De Meester, A. L. (2006). Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos*, *112*(1), 227-231.

Sebastián-González, E., & Green, A. J. (2014). Habitat use by waterbirds in relation to pond size, water depth, and isolation: lessons from a restoration in southern Spain. *Restoration Ecology*, *22*(3), 311-318.

Severcan, Ç., & Yamaç, E. (2011). The effects of flock size and human presence on vigilance and feeding behavior in the Eurasian Coot (Fulica atra L.) during breeding season. *Acta ethologica*, *14*, 51-56.

Sillén, B., & Solbreck, C. (1977). Effects of area and habitat diversity on bird species richness in lakes. *Ornis Scandinavica*, 185-192.

Simberloff, D. S. (1974). Equilibrium theory of island biogeography and ecology. *Annual review of Ecology and Systematics*, *5*(1), 161-182.

Stroud, D. A., Davidson, N. C., West, R., Scott, D. A., Haanstra, L., Thorup, O., ... & Delany, S. (2004). *Status of migratory wader populations in Africa and Western Eurasia in the 1990s*. Thetford, UK: International Wader Study Group.

Suter, W. (1994). Overwintering waterfowl on Swiss lakes: how are abundance and species richness influenced by trophic status and lake morphology?. In *Aquatic Birds in the Trophic Web of Lakes: Proceedings of a symposium held in Sackville, New Brunswick, Canada, in August 1991* (pp. 1-14). Springer Netherlands.

Ten Cate, J. H., Simons, J., & Schreurs, H. (1991). Periphytic macro-and microalgae in dutch freshwater ditches and their significance as ecological indicators of water quality. *Archiv für Hydrobiologie*, 275-296.

Uden, D. R., Allen, C. R., Bishop, A. A., Grosse, R., Jorgensen, C. F., LaGrange, T. G., ... & Vrtiska, M. P. (2015). Predictions of future ephemeral springtime waterbird stopover habitat availability under global change. *Ecosphere*, *6*(11), 1-26.

Van der Graaf, A. J., Stahl, J., Klimkowska, A., Bakker, J. P., & Drent, R. H. (2006). Surfing on a green wave-how plant growth drives spring migration in the Barnacle Goose Branta leucopsis. *Ardea-Wageningen-*, *94*(3), 567.

Van der Sluis, T., Bloemmen, M., & Bouwma, I. M. (2004). European corridors: Strategies for corridor development for target species. *ECNC, Tilburg, the Netherlands & Alterra*.

van Eerden, M. R., Lenselink, G., & Zijlstra, M. (2010). Long-term changes in wetland area and composition in The Netherlands affecting the carrying capacity for wintering waterbirds. *Ardea*, *98*(3), 265-282.

Viana, D. S., Santamaría, L., & Figuerola, J. (2016). Migratory birds as global dispersal vectors. *Trends in ecology & evolution*, *31*(10), 763-775.

Voslamber, B., Knecht, E., & Kleijn, D. A. V. I. D. (2010). Dutch greylag geese Anser answer: migrants or residents. *Ornis Svecica*, *20*(3–4), 207-214.

Wantzen, K. M., Rothhaupt, K. O., Mörtl, M., Cantonati, M., Tóth, L. G., & Fischer, P. (2008). *Ecological effects of water-level fluctuations in lakes: an urgent issue* (pp. 1-4). Springer Netherlands.

Weerstatistieken de Bilt - 2023. Weerstatistieken KNMI - Actuele weergegevens. (n.d.). Retrieved April 4, 2023, from https://weerstatistieken.nl/

Weigelt, P., & Kreft, H. (2013). Quantifying island isolation–insights from global patterns of insular plant species richness. *Ecography*, *36*(4), 417-429.

Wen, L., Saintilan, N., Reid, J. R., & Colloff, M. J. (2016). Changes in distribution of waterbirds following prolonged drought reflect habitat availability in coastal and inland regions. *Ecology and evolution*, *6*(18), 6672-6689.

Xia, S., Liu, Y., Wang, Y., Chen, B., Jia, Y., Liu, G., ... & Wen, L. (2016). Wintering waterbirds in a large river floodplain: Hydrological connectivity is the key for reconciling development and conservation. *Science of the Total Environment*, *573*, 645-660.

Zhao, J. M., & Zhou, L. Z. (2018): IBT with waterbirds in China. Isolation, area and agricultural disturbance.

Zou, Y. A., Zhang, P. Y., Zhang, S. Q., Chen, X. S., Li, F., Deng, Z. M., ... & Xie, Y. H. (2019). Crucial sites and environmental variables for wintering migratory waterbird population distributions in the natural wetlands in East Dongting Lake, China. *Science of the Total Environment*, *655*, 147-157.

Appendix 1

	area (m²)	river distance (km)	Coastal length (m)	reeds (m)	sand/mud (m)	trees (m)	grass (m)	simpsons diversity	eveness	average distance (m)	nearest neighbour (m)	total species
BK1	49654	0,672	1715	129	0	1593	193	1,134933721	0,28373343	6799	396	20
BK2	22857	0,391	910	306	47	195	566	1,823101276	0,455775319	6924,076923	396	11
KW	8451	2,873	402	115	71	276	140	1,417056874	0,354264218	8768,307692	2846	4
RV	7361	0,155	1128	111	0	0	1017	1,215719322	0,303929831	8788,769231	491	12
CL	5009	3,304	317	107	0	0	210	1,809015464	0,452253866	5671,384615	367	3
CO	3701	2,99	364	160	0	31	204	1,943412001	0,485853	5578,769231	170	6
CF	6045	2,994	391	180	0	0	200	2,111616022	0,527904006	5561,076923	170	5
SV	39505	5,725	1669	702	0	850	390	2,037116317	0,509279079	8891,846154	2846	10
OH	53406	0,268	1088	504	24	704	0	1,577887732	0,394471933	7331,153846	1986	6
PW	34368	0,191	1739	1036	48	1096	80	1,324500617	0,331125154	8578,692308	2348	18
WG	88370	0,448	3366	2457	643	730	258	1,607140213	0,401785053	6233,846154	2670	21
JW	38442	0,112	1379	678	183	124	409	2,813786011	0,703446503	8405,307692	491	13
KP	9216	8,875	356	148	11	270	0	1,335117198	0,333779299	10245,69231	1246	2
HP	2179	8,381	217	0	217	0	0	1	0,25	10562,46154	1246	0

Apendix 2

	River distance	**Coastal Length**	**Nearest neighbour**	**Average distance**
General	< 0.001	< 0.001	0.589	0.418
Aquatic predator	0.024	< 0.001	0.289	0.798
Aquatic herbivore	0.008	0.018	0.581	0.101
Terrestrial herbivore	0.137	0.260	0.439	0.984
Omnivore	0.033	< 0.001	0.306	0.178
Resident	0.015	< 0.001	0.527	0.350
Resident/Wintering	0.009	0.010	0.957	0.248
Wintering	0.087	0.009	0.743	0.734

P values of the Generalized lineair model