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# BATS & WETLANDS

Unveiling the role of humid  
habitats for bat conservation

Maria Mas Navarro

All the drawings of this thesis were provided by Ramon Mas and Lucía Gómez

# Bats and Wetlands: Unveiling the role of humid habitats for bat conservation

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*“The truth is: the natural world is changing.  
And we are totally dependent on that world. It provides our food, water and  
air. It is the most precious thing we have and we need to defend it”*

*David Attenborough*

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## Abstract


Mediterranean wetlands account for 1.5% of global wetlands and represent one of the 25 Biodiversity Hotspots in the world. Humid habitats have been managed and exploited for centuries for human benefit, jeopardising the conservation of their associated fauna and flora. Understanding the role of these habitats for animal conservation is essential for developing appropriate management plans and minimising the effects of human activities and climate change. While the study of bats in wide open areas, such as wetlands, has not always been feasible due to the low efficiency of traditional methods (e.g. mist nets), the recent development of acoustic passive bat detectors has opened new research opportunities in wetlands that were totally unimaginable a few decades ago. However, the relationship between bats and wetlands and how the conservation of wetlands might increase the resilience of bat populations in new scenarios of global change remained widely unknown.

This thesis aims to broaden the understanding of the relationship between bats and wetlands and assess the importance of humid habitats for bat conservation. The work includes a first systematic literature review to identify knowledge gaps and biases in bat research studies globally, followed by two ecological field studies using bioacoustics in one of the largest deltas in the Mediterranean Sea, the Ebro Delta, to understand the environmental factors imperilling their conservation.

The Ebro Delta contains large expanses of protected wetlands (Natura 2000 network), surrounded by vast areas of rice fields, providing an excellent field laboratory with relatively stable environmental features and habitat to evaluate the responses of bats towards a broad range of stressors. Due to the use of passive acoustic monitoring, it was possible to continuously monitor, for the first time, bat populations in a temperate delta for a whole year and gather one of the largest acoustic datasets in bat research in the Mediterranean region.

With the results of this project, I show the essential role that wetlands play during the wintertime for hibernating bats and provide a temperature threshold that triggers a significant increase in bat arousal bouts during winter. According to this, and considering the future climate scenarios, I predict a potential end of bat hibernation in the Mediterranean coastal regions in 60-80 years. Finally, I also demonstrate that rice paddies could never replace the role of well-preserved wetlands to protect bat populations in highly degraded areas. The presence of Natura 2000 areas and their connection through the territory significantly contribute to the conservation of bat species of priority concern and their resilience under new environmental scenarios, but might not be enough to sustain the diverse bat assemblage that would be expected in such humid areas.

The results of this study provide new tools for policymakers, researchers, and other organisations to help them define new conservation plans for endangered species and habitats and create holistic management plans for bats and wetlands, as they can benefit each other. Bats could act as umbrella species to protect new wetlands sites, and wetlands could represent the last remaining natural habitats in those areas, essential for bats as they provide unlimited resources in a rapidly changing world.



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*Per mi i per tots vosaltres:*

*"Happiness is only real when shared"*  
*Christopher McCandless*









Chapter 1  
General introduction

## General Introduction

### 1.1. WETLANDS. ROLES AND THREATS

Wetlands are defined as any *area where water is the primary factor controlling the environment and the associated plant and animal life, with water is at or near the surface of the land, static or flowing and where the depth of which at low tide does not exceed six metres* (Ramsar-Secretariat, 2014). However, the term “wetland” does not include only one specific type of humid habitat but many forms depending on their location (coastal or inland) and several other structural traits. Wetlands on the coast include marshes, coastal lagoons, rocky shores, coral reefs, mangroves and swamps, whereas inland wetlands include lakes, rivers, streams, peatlands, swamps, vernal pools, bogs, fens or sloughs (RAMSAR-Secretariat, 2014; Gibbens, 2023) (Fig. 1.1). Additionally, these humid habitats are also divided into two categories depending on how long the water table remains on the surface: temporary wetlands, characterised by frequent drying, and permanent wetlands, which contain standing water throughout the year.

Wetlands are found in all biomes and account for 1-6% of the world’s terrestrial area, being more abundant in tropical regions, and varying in size from less than one hectare to about 120,000 km<sup>2</sup> in Rio Negro (Brazil) (RAMSAR-Secretaria, 2014). In general terms, Asia and North America have some of the largest areas of wetlands (Mas, et al., 2021), yet these wetlands are generally less protected (excepting for some countries, i.e. China or India) than those in other areas, according to Ramsar-Secretariat, (2014). Conversely, the countries with less extensive wetlands have more sites protected under the Ramsar Convention; for example, the United Kingdom with more than 175 protected sites, followed by Mexico with 142, China with 82 and Spain with 76 ([www.ramsar.org](http://www.ramsar.org)).

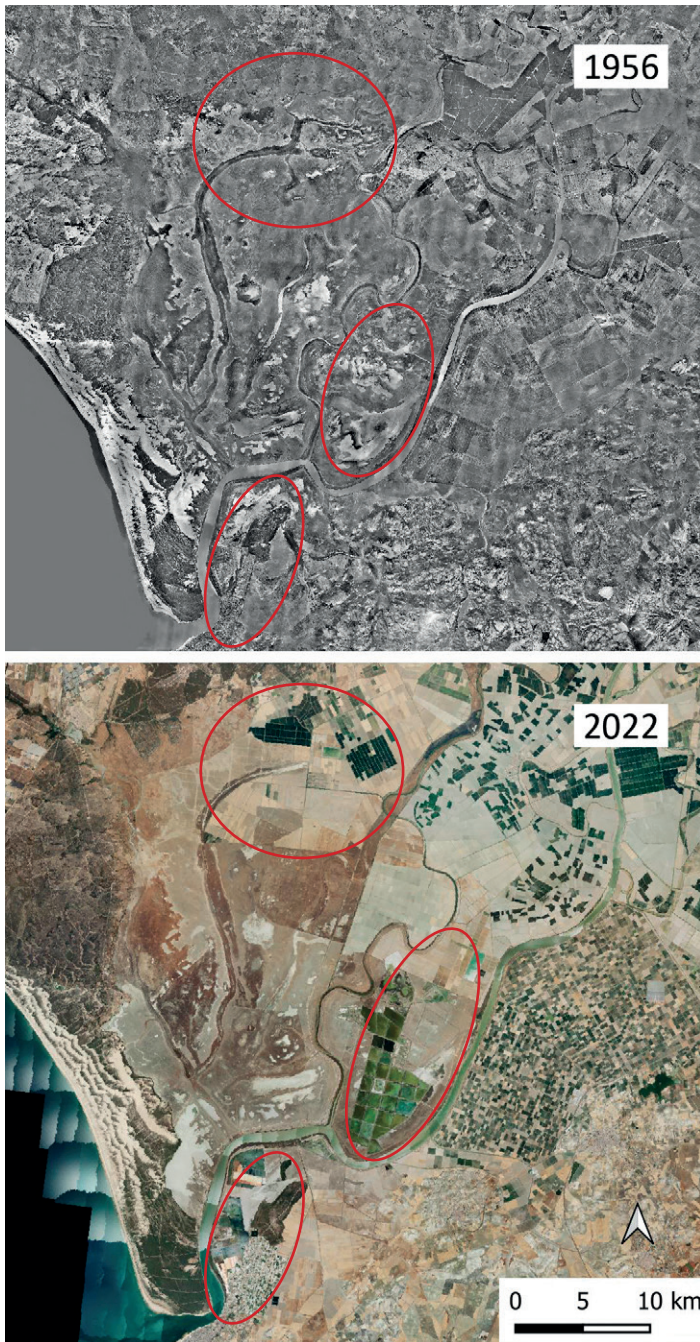
Despite their small global coverage, wetlands play an essential role for human settlements due to the provision of natural resources such as fresh water and food, as well as considerable non-material resources and services such as the biological control of pests and diseases, flood regulation or socialcultural and spiritual values (RAMSAR-Secretariat, 2014; Sharma & Singh, 2022). In fact, the economic value of wetlands per hectare/year has been suggested to range from \$14 to \$492 (depending on the type of wetlands and its function), rising to a total of \$70 billion per year for all wetlands globally (Schuyt & Brander, 2004). However, most of these ecosystem services do not seem to be widely recognised by policymakers or stakeholders as reasons to preserve wetlands, and their destruction or complete disappearance could result in a considerable threat to humans.



**Figure 1.1:** Wide variety of wetlands including forested wetlands, saltmarshes, floodplains, lagoons and peatlands. Pictures by Klye Glenn, Claudio Carrozzo, Transly Translation Agency and Stelios Triantafyllidis from Unsplash.

Since the 1970s, wetlands have been decreasing in terms of size and quality at an alarming rate (Ramsar-Secretariat, 201; Xu et al., 2019). In recent years, the media has recognised how rapidly wetlands are perishing due to overexploitation and climate change. For example, The Guardian newspaper recently highlighted a scientific article reporting the loss of more than half of European wetlands in 300 years (Weston, 2023), and the same publication revealed the dramatic situation that one of the UNESCO World Heritage Sites in Spain (i.e. Doñana National Park) is currently experiencing (Jones, 2022) (Fig. 1.2). According to Fluet-Chouinard et al. (2023), the world has lost 16-23% of its wetlands since 1700, primarily due to their conversion to fields for cultivation. The main driver for wetland loss has been the complete drainage to create croplands (61.7% of the total loss), followed by rice paddies (18.2%) or urban settlements (8%). With a closer look, the United States of America, Central Asia, India and Europe account for more than 50% of the global loss of wetlands. One of the most worrying scenarios was recently reported in Europe, as Ireland leads the list of extant wetlands loss, with 90% of its wetlands gone (Fluet-Chouinard et al., 2023).

Humid habitats are threatened by natural drivers, such as droughts, reduction of precipitation events or the increase of sea level, and also by anthropogenic processes, such as water pollution by pesticides or wastewater (Xu et al., 2019). Fortunately, to protect these habitats, relatively new international and national policies and laws have been developed, encouraging a balanced coexistence of natural habitats with human exploitation, slowing down habitat degradation and increasing their conservation. The most broadly recognised and global directive is the Ramsar Convention (Ramsar-Secretariat, 2014). However, some continental or country-specific initiatives, such as



**Figure 1.2:** Aerial view of wetlands's reduction between 1956 and 2022 period because their conversion into croplands, low water supply and climate change in National Park of Doñana, Andalucía, Spain. Red circles show the loss of wetlands. Source: Orto-AMS-1956-1957 1956-1957 CC-BY 4.0 [scne.es](https://scne.es) and OrtoPNOA 2022 CC-BY 4.0 [scne.es](https://scne.es).

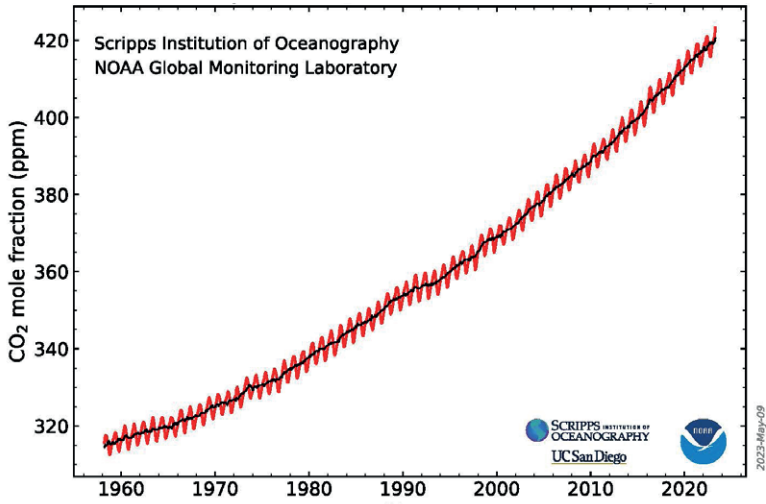
the Birds Directive (2009/147/CE), Habitats Directive (92/43/CEE), Water Directive (2000/60/CE) and the Nature 2000 network in European Union, also protect wetlands ([www.eionet.europa.eu](http://www.eionet.europa.eu)). The Nature 2000 network in European Union is one of the main tools to guarantee nature and biodiversity conservation ([www.miteco.gob.es/es/biodiversidad/temas/](http://www.miteco.gob.es/es/biodiversidad/temas/)) and includes several wetland areas. Moreover, this network also has an ambitious long-term plan to protect and reverse the degradation of these habitats through the Biodiversity Strategy for 2030, including the first-ever European Nature Restoration Law (<https://environment.ec.europa.eu/>).

## 1.2. USING WETLANDS TO TACKLE CLIMATE CHANGE

Throughout the Earth's history, global temperature fluctuations have occurred as cyclical phenomena, mainly associated with greenhouse gas concentrations, that provoke periods of colder or warmer temperatures (Petit et al., 1999). These fluctuations have been associated with the rise and reduction of greenhouse gases, such as CO<sub>2</sub> and CH<sub>4</sub> (Petit et al., 1999; Sigman & Boyle, 2000). However, the recurrent and unstoppable emissions from human activities and natural environmental changes have increased carbon dioxide concentrations, reaching new records each year (NOAA, 2023) (Fig. 1.3 and Fig. 1.4).

The rise in greenhouse gas concentrations subsequently affects and causes significant impacts on ecosystems, such as increased droughts or biodiversity loss due to warmer global temperatures (Allen et al., 2018). For example, the increase in air temperatures, along with the decline in vegetation productivity and over-extraction of groundwater, exacerbates the process of desertification (IPCC, 2019). Aquatic ecosystems are not free from these effects, and the increase in ocean temperatures produces an intensification of meteorological extreme phenomena such as storms or a significant increase of the global cyclone activity (NOAA, 2023). Prakash, (2021) states that climate change is producing changes in aquatic environments and reports that marine ecosystems are becoming more acidic due to the increase of CO<sub>2</sub>, which kills non-mobile animals, such as coral reefs. Similarly, freshwater ecosystems, such as wetlands, are suffering profound alterations in their hydrological cycle (Prakash, 2021).

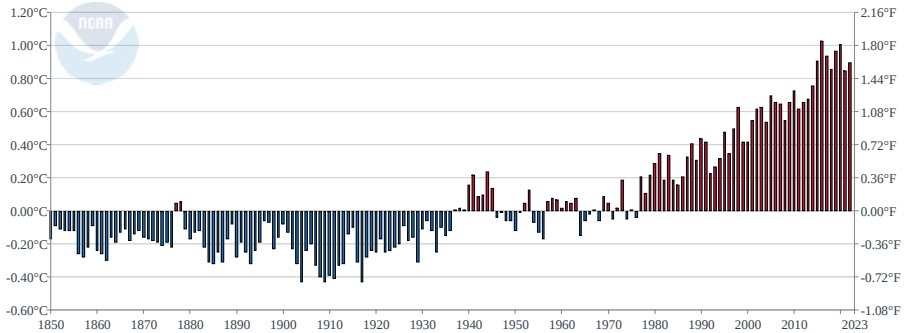
Although the unique primary solution to cope with climate change would be a drastic reduction of natural resource consumption and significantly decrease our societies' direct impacts on the globe (e.g. overpopulation, habitat loss, resource over-consumption), some natural environments such as forests or wetlands could also help store and reduce large concentrations of greenhouse gases. The carbon sequestered by oceans and vegetated coastal habitats is known as "Blue Carbon" (Nellemann et al., 2009). Wetlands, such as mangroves, salt marshes or lagoons, act as natural



**Figure 1.3:** Changes in Global atmospheric CO<sub>2</sub> concentrations in a 53-year-period. Source: NOAA National Centers for Environmental Information. Accessed May 2023.

**Global Land and Ocean**

January-December Temperature Anomalies



**Figure 1.4:** Changes in Global Temperatures in a 173-year-period. Source: NOAA National Centers for Environmental Information. Accessed July 2023.

carbon sinks thanks to their associated dense vegetation. For example, a systematic review by Duarte et al., (2013) reported that salt marshes could bury between 4.8 to 87.3 teragrams of carbon per year (Tg C yr<sup>-1</sup>), storing the carbon over millennia. Wetlands conservation could help humanity to mitigate or reduce climate change's effects. On the other hand, according to Zou et al., (2022) the degradation of 46% of global wetlands in the last ~70 years has released approximately 276,4 Gigatonnes of CO<sub>2</sub> eq. Their study suggests that rewetting and restoring global wetlands could reduce an equivalent volume of 10% of anthropogenic emissions.

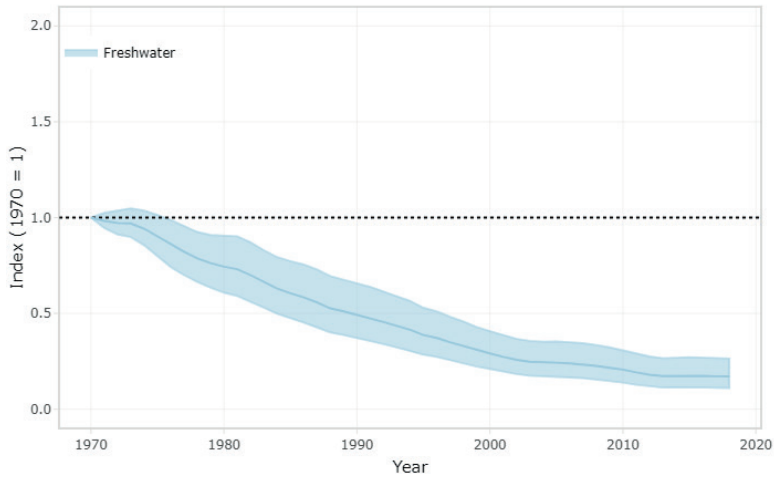
### 1.3. MEDITERRANEAN WETLANDS

Mediterranean wetlands represent 1.1 to 1.5% of global wetlands. The largest areas are found in Egypt, France, Turkey and Algeria, representing two-thirds of these habitats (Geijzendorffer et al., 2018). Most of these humid habitats are coastal wetlands widely used for educational and tourism activities (Geijzendorffer et al., 2018). Economically speaking, these wetlands provide an estimated value between 2-45 million euros per year (depending on the wetland size) due to their ecosystem services, such as flood control or carbon sequestration (Plan Bleu, 2016). However, the conservation status of Mediterranean wetlands is still poor, and many conservation indicators, like wetland size or water surface cover, have been decreasing since 1970 (Geijzendorffer et al., 2018).

One of the indicators used to determine wetlands conservation status is the Living Planet Index (LPI) defined as “*a measure of the state of the world's biological diversity based on population trends of vertebrate species from terrestrial, freshwater and marine habitats*” ([www.livingplanetindex.org](http://www.livingplanetindex.org)). This index increases or decreases depending on the progress of its indicators resulting in a single average trend. The LPI for Mediterranean wetlands declined continuously for 28 years from 1990 (e.g. freshwater populations, Fig. 1.5). Fortunately, as a result of recent political and conservation measures, this trend has changed, and since the start of the 21<sup>st</sup> century, it seems to be slowly reversing. According to some authors, such as Galewski et al. (2011) and Geijzendorffer et al. (2018), the general increase of the LPI for Mediterranean wetlands was related to the recovery of some bird species that were positively affected by some national and international laws, such as the Habitat Directive in Europe. However, when it comes to freshwater ecosystems, a major decrease in amphibians, reptiles, mammals and fishes was consistently reported (ca. 34-35%) due to pollution, rising temperatures or reduction of precipitation events (Geijzendorffer et al., 2018).

According to Taylor et al., (2021), many questions remain unanswered regarding the conservation and the future of Mediterranean wetlands. In a systematic review encompassing a wide diversity of expert assessors, the authors highlighted the need





**Figure 1.5:** Living Planet Index (LPI) for the global freshwater populations of vertebrate species in the period 1970-2018. The bold line shows the index values and the shaded areas represent the statistical certainty surrounding the trend (95%). Source: Living Planet Index Report 2022, WWF/ZSL.

to fill a long list of knowledge gaps in order to improve the conservation of these humid habitats in the coming decades. For instance, it is vital to understand the impacts of increasing aquacultural production on freshwater, the relationship between Mediterranean wetlands and antimicrobial resistance (Taylor et al., 2021), and the effects of the establishment of new alien species in these habitats due to trade links and world transportation (Kourantidou et al., 2021).

The Mediterranean region is among the 25 Global Biodiversity Hotspots, hosting 4.3% of global endemic plants and 0.9% of vertebrate species (Myers et al., 2000). Moreover, 30% of the total Mediterranean vertebrate species are endemic, thanks to the vast diversity of landscapes such as mountains, deserts, forests or islands (Myers et al., 2000; Vié et al., 2008). Of all the mammals, 26% of the species are endemic (87/330), and 20% are considered threatened with extinction, according to the IUCN RedList (Vié et al., 2008). As pointed out by Perennou et al., (2018), “natural wetlands” are rare (primarily because of strong human modification), but keeping these habitats unharmed could efficiently guarantee the resilience and conservation of many species.

## 1.4. EUROPEAN BATS

Bats are one of the most diverse orders of mammals, following rodents, with more than 1,456 bat species, representing a quarter of mammal species worldwide, grouped into 21 families (Wilson & Mittermeier, 2019). Amongst them, the Vespertilionidae family is the largest bat family, with 528 described species and it is widespread throughout the globe, from arid to tropical regions (Lynx Nature Books, 2023; Wilson & Mittermeier, 2019). Bats have conquered the nocturnal niche exploiting many resources and feeding upon fruits, pollen, nectar, insects, and other vertebrates such as fishes, amphibians, and some mammals, including blood (Altringham, 2011). Their flying ability and large movements result in a considerable capacity to provide ecosystem services in more than one region (Kunz et al., 2011). For example, in Europe, all 45 bat species are insectivorous (Fig. 1.6) and provide some of the most valued ecosystem services: the suppression of agricultural pests such as the rice borer moth (*Chilo suppressalis*) (Puig-Montserrat et al. 2021; Puig-Montserrat et al., 2015) or *Lobesia botrana* (Baroja et al., 2021; Charbonnier et al., 2021), the suppression of agroforestry pests (Ancillotto et al., 2022) and the suppression of disease vectors (Kunz et al., 2011; Puig-Montserrat et al., 2020).



**Figure 1.6:** Insectivorous bat species from the Vespertilionidae and Molossidae families. From left to right top line: *Pipistrellus pygmaeus*, *Plecotus austriacus*, *Myotis myotis*; middle line: *Eptesicus serotinus*, *Myotis emarginatus*, *Pipistrellus nathusii*; bottom line: *Rhinolophus ferrumequinum*, *Barbastella barbastellus* and *Tadarida teniotis*. Photos courtesy of Oriol Massana and Adrià López-Baucells.

Insectivorous bats are excellent insect suppressors in agricultural lands due to their intense prey consumption to compensate for the energy demands of flying activity (Voigt et al., 2010). More than ten years ago, Cleveland et al. (2006) and Wanger et al. (2014) assessed the economic value of bats in different croplands, estimating savings ranging from \$1.2 million to \$6.4 million per year. In Europe, the monetary value of bats in agriculture has not been studied in depth; only Puig-Montserrat et al. (2015) estimated that bats could save an average of 21€ per hectare in rice paddies.

However, these ecosystem services could be at risk since bat populations are still declining in most European regions due to several environmental changes and anthropogenic factors (Jones et al., 2009). Bats are considered good bioindicators to study habitat changes due to their slow reproduction rate, rich trophic diversity and predictable ways of responding to stress factors such as climate change or human-induced changes (Jones et al., 2009, 2012; Russo et al., 2021). The study of bat population changes could be used as an ecological indicator to monitor environmental changes such as climate change, habitat fragmentation or habitat quality (Russo et al., 2021). For example, López-Baucells et al. (2017) reported that the presence and activity of the trawling bat *Myotis daubentonii* was significantly related to the quality of riparian habitats in some specific regions. Bats could act as natural samplers of heavy metals in the environment due to their bioaccumulation rate and ability to forage in different habitats (Zukal et al., 2015). One of the most recent studies about bats as bioindicators pointed out that long-term surveys of bat populations can be used to detect different climatic and land-cover changes under current global changes (Tuneu-Corral et al., 2020) since each bat species responded differently to land-cover changes.

## 1.5. BATS, WETLANDS, AND GLOBAL CHANGE

Bat populations have been declining worldwide mainly due to four major drivers: logging activities, conversion of natural habitats to croplands, hunting and collection of animals, and human disturbances (Browning et al., 2021; Frick et al., 2019). In Europe, both Browning et al., (2021) and O'Shea et al., (2016) reported that one of the main drivers of bat mortality has been the new and recent massive development of wind farms. However, the loss of underground habitats (e.g. caves or mines) and changes in foraging grounds are also considered some of the critical declining forces for many species (e.g. *Rhinolophus mehelyi* across Spain, whose five largest known colonies have decreased by 85% in the last 20 years due to habitat and roost destruction – unpublished data from SECEMU). Kerth & Melber, (2009) also reported that roads, such as motorways, forced a reduction of movements and habitat use of two threatened forest-dwelling species. Moreover, the decrease of some bat populations

is also influenced by the recent increase in urbanisation, the use of artificial lights or light pollution, and climate change (Browning et al., 2021; [www.eurobats.com](http://www.eurobats.com)).

In terms of climate, bats respond differently towards different environmental effects depending on the stressors they face, such as increased temperatures, reduced rainfall, or extreme events (heatwaves). For example, Festa et al., (2022) reported that while some species expanded their distribution ranges to cope with new environmental changes, others advanced their migration or parturition timing due to the increase in temperatures during the end of spring. However, although some species seem to be rather plastic and adaptable, others might not be capable of coping with these new extreme environmental changes. The recent increase in temperatures are causing some fatal effects on bats. Bats are temporal heterothermic animals that are capable of dropping their body temperature until it is equalised with the environment to save energy expenses (Altringham, 2011). Thus, during their daily torpor, bats suffer from a passive rewarming keeping their body temperature high (Turbill & Geiser, 2008). However, during some climate events, such as in heatwaves, bats see their survival compromised because they, as well as their roosts, suffer from overheating (i.e. Flaquer et al., 2014; Martin-Bideguren et al., 2019), resulting in high mortality events (Mo et al., 2022; O'Shea et al., 2016).

Temperatures are one of the major stressors to induce changes in bat behaviour, specifically during hibernation. However, according to Festa et al., (2022) the capacity of hibernators to respond to new climate change scenarios is poorly studied, and it is, therefore, difficult to foresee the consequences that climate change will have on European bat populations. When bats hibernate, they need steady roost temperatures and high humidity to maintain deep torpor (Klüg-Baerwald & Brigham, 2017). Changes in roost temperatures are related to bat arousal bouts with intrinsic energy consumption that is more likely to dehydrate or kill them (Park et al., 2000; Zahn & Kriner, 2014; Festa et al., 2022).

Winter bat activity is well-studied in North America, where bats have been reported to fly out from their roosts during mild winter nights (Park et al., 1999; Lausen & Barclay, 2006). However, there is still a remarkable lack of information in the Mediterranean region, where it is generally assumed that bats continuously hibernate during the whole winter in most regions (Barros et al., 2017). Also, in the face of climate change, we do not know which Mediterranean habitats will be essential for their resilience during new winter scenarios. In the case of bats awakening from hibernation, stored fats and water loss must be replenished every time they awaken so that they are able to continue with their hibernation. Therefore, insectivorous bats must find large areas with high concentrations of insects and also freshwater availability during winter. Humid habitats, such as lagoons or saltmarshes, would be the perfect ecosystems for



that since they remain highly productive in terms of insects and freshwater accessibility during periods of low temperatures, providing the necessary resources for bats to cope with their energy and water loss (Lookingbill et al., 2010; Lindsay et al., 2015).

These habitats are not only essential for hibernating bat survival, but also for bat migration and species of conservation priority. It is well-known that some European bats use wetlands as stopover locations during their migration routes. This is the case for *Pipistrellus nathusii*, a bat species that has a record on distance migration flying of more than 2,400 km (Šuba et al., 2012; Vasenkov et al., 2022). This bat species has been described as following the coastal line of Europe during its migration route and using the so-called “fly-and-forage” strategy to recover its fats en route, mainly in wetlands (Flaquer et al., 2009; Šuba et al., 2012). Other bat species have been associated with humid habitats, such as the threatened *Rhinolophus mehelyi*, where the proximity of bat colonies to water sources like wetlands increases the carrying capacity of these species (Salsamendi et al., 2012). However, the importance of wetlands, usually under the Natura 2000 network, is not fully understood and they could be essential in highly degraded regions, providing a large amount of resources for these flying mammals.



**Figure 1.7:** Rice paddy in the Buda Island (Ebro Delta, Spain) during summer as an example of artificial wetlands and their vegetation coverage. Photo courtesy of Adrià López-Baucells.

The role of wetlands in sustaining bat populations could be jeopardised due to their decreasing trends, in terms of conservation status, and their conversion to agricultural fields (Xu et al., 2019). The principal loss of wetlands is related to their complete drainage for many human benefits, such as human settlements or peat extraction (Fluet-Chouinard et al., 2023). Some authors have suggested that artificial wetlands, such as irrigated fields (Fig. 1.7) with controlled water levels, could supply the ecosystem services that “natural” wetlands provide (i.e. flood control or overwintering grounds for many migratory animals). However, due to their strict water management cycle of irrigated fields, such as rice paddies, they show reduced availability of aquatic insects, consequently reducing foraging predator activity (Hagen & Sabo, 2012). In general, more research is needed to understand the role of wetlands in bat conservation and the ecosystem services that could vanish with their replacement and loss.

## 1.6. THE GOLDEN CENTURY: STUDYING BATS USING THEIR CALLS

Surveying bats in vast, open, challenging areas such as wetlands has not always been as feasible as it might be today (Kunz & Brock, 1975; Duffy et al., 2000). The absence of well-defined flying paths or corridors has hindered the study of bat communities using traditional methods (i.e. mist nets or harp traps) for decades (Duffy et al., 2000). These methods are generally used in bat roosts (hand nets, funnel traps or bucket traps) or foraging areas (mist nets and harp traps) (Kunz & Kurta, 1988). By directly capturing bats, researchers can identify bat species and gather information on the sex, age, and body condition of each individual. However, mist nets or harp traps always need corridors to place them, are time-consuming, and, generally, few animals and species are captured; and even if one is successful with them, they are still invasive, causing stress to the captured animals. Setting a mist net is not always achievable by a single person; they constantly need monitoring, and their efficiency depends on the capacity of bats to detect it. On the other hand, harp traps are more efficient when placed near natural structures and are partially hidden, such as on trails covered by branches or in front of cave entrances where mist nets could not be placed (Kunz & Kurta, 1988).

During recent decades, some authors have highlighted the importance of combining different methodologies, such as captures and acoustic surveys (Duffy et al., 2000; Flaquer et al., 2007). Acoustic ultrasound detectors are a non-invasive technique to study bat communities in their habitats. The first ultrasound detector appeared on the market at the beginning of the 20<sup>th</sup> century (MacDonald & Brudzynski, 2018; Noyes & Pierce, 1938; Pierce & Griffin, 1938). But only recently, thanks to technological advances, bat detectors have become more affordable for scientists, low-income institutions, and countries (Zamora-Gutierrez et al., 2021) (Fig. 1.8).



**Figure 1.8:** Two different ultrasonic devices used to monitor bat populations. **A)** Batlure placed near mist nets to improve the capture ratio in alpine meadows. **B)** Ultrasonic bat detectors placed in a lagoon to record the bat activity in open wide areas. Upper photo courtesy of Adrià López-Baucells; bottom photo courtesy of Maria Mas.

Moreover, acoustic detectors have been proven to be more suitable for studying aerial insectivorous bats, detecting 30% more species than mist nets (Flaquer et al., 2007; MacSwiney et al., 2008). In Europe, bioacoustics have improved to be suitable for all bat species ([www.eurobats.org](http://www.eurobats.org)). The development of this new cost-effective method to study bat communities in Europe has opened many opportunities for research and conservation in new, previously unexplored habitats (Ochoa et al., 2000; Meyer et al., 2011; Zamora-Gutierrez et al., 2021).

However, studying bats through acoustic recordings is not perfect; it has pros and cons. Weller & Zielinski, (2006) reported that some bat researchers prefer sampling bats using captures since bioacoustics require much more experience and training to identify the recordings at species level. Some bat species emit highly similar echolocation calls hindering the discrimination between two or more bat species (Russ, 2012). And most importantly, it is still impossible to calculate their absolute abundances and determine sexes or ages, and sometimes species could be misidentified (López-Baucells et al., 2019). On the other hand, automatic detectors can be used in passive acoustic monitoring (PAM), implying that surveys could be carried out without the observer's presence and simultaneously at multiple points (Britzke et al., 2013). Due to the new autonomous bat detectors, it is now possible to record the nocturnal behaviour of bats and gather a large amount of data on bat communities in places where it was rather difficult in the past.

The use of bioacoustics has also been of great importance in describing new species. In Europe, one of the most common bat species *Pipistrellus pipistrellus* was split into two phonic types: one emitting at 45kHz and the other at 55kHz (Jones & Parijs, 1993). Later, these groups were designated as two separate species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* (Jones & Barratt, 1999). The coexistence of different species with similar echolocation patterns is not rare, as it also happens in *Myotis myotis* and *Myotis blythii* or in *Pipistrellus kuhlii* and *Pipistrellus nathusii*, among others. Over the last decade, software and algorithms have been developed to classify bat species automatically, such as the Kaleidoscope software (Wildlife Acoustics) or the Tadaria software (Bas et al., 2017), and supercomputing services have been set up to analyse larger datasets remotely and much more efficiently.

## 1.7. BAT RESEARCH IN THE EBRO DELTA: TRANSFERRING SCIENCE TO SOCIETY

The Ebro Delta is an ancient delta located in the northeastern part of Spain with the last sediments dating back 3.5 million years, and suggesting that the delta had a similar or even larger area than now (Curcó, 2006). The shape of the delta has changed from the glacial periods until the XX-XXI centuries, as the hydrology management of the river from the last century (ca. 1923) forced the stabilisation of the delta morphology (Curcó, 2006). However, the construction of dams during the 21st century has reduced the sediment supply by 99% resulting in a progressive reduction of the Ebro Delta (Curcó, 2006; Fig. 1.9). Despite this significant reduction in sediments, it is still one of the most extensive deltas of southwestern Europe, being the third most important after the National Park of Doñana (Spain) and the Regional Park of Camargue (France).



In the Mediterranean region, it is one of the largest deltas with vast coastal wetlands. The delta is mostly flat, ranging from zero to four m.a.s.l., with few vertical structures (trees or buildings), and, thanks to its proximity to the sea, it has mild and stable temperatures throughout the seasons (ranging from ca. 9°C in winter to 27°C in summer) ([www.meteo.cat](http://www.meteo.cat)). Its temperate climate and size have favoured rice cultivation, one of the world's most widely-cultivated crops. Rice fields cover almost 60% of the Ebro Delta, providing a substantial economic income for many local inhabitants (CEDEX, 2021). Wetlands, which cover approximately 20% of the delta and present different degrees of salinity depending on their proximity to the sea, have favoured the presence of more than 100 species of fish, including freshwater and marine species (López et al., 2012), and it is considered one of the most important places within Catalonia, in terms of biodiversity. In fact, the humid habitats of the Ebro Delta were listed as a Euro-African area of international concern (1962), resulting in the declaration of the Ebro Delta Natural Park in 1986 to protect the wetlands and associated habitats and fauna (DECREE 332/1986).

Despite being a protected natural park, the Ebro Delta is shrinking due to the decrease of water flow and sediments being supplied by the river. The increasing number of alien species also affects the ecosystem's functions and reduces autochthonous fauna (Gallardo et al., 2019). Some of them are endemic to Spain with decreasing trends in their populations, such as the critically endangered "samaruc" (*Valencia hispanica*) or the endangered European sturgeon (*Acipenser sturio*) (Crivelli, 2006; López et al., 2012; DECREE 172/2022). Up to 60% of European bird species have been recorded in the Ebro Delta either during wintertime, the breeding season or resting during their annual migrations (CEDEX, 2021). For instance, it has the world's largest Audouin's Gull (*Ichthyaetus audouinii*) breeding colony and the second largest colony of greater flamingos (*Phoenicopterus roseus*) in the Iberian Peninsula. Additionally, its ecosystems have some singular natural elements, highly sensitive to human activities, such as moving dunes, essential for many breeding colonies of threatened and vulnerable European birds (i.e. greater flamingos or Audouin's Gull). All these characteristics and scenarios have turned the Ebro Delta into a perfect field-laboratory or biological station to study one of the most unknown and diverse groups of flying vertebrates: bats.

Thus, in 2006, the BiBio Research Group from the Natural Sciences Museum of Granollers established several synergies with other institutions, such as IRTA and ADV, to reduce the usage of pesticides in rice fields and assess the power of bats as rice pest suppressors (i.e. against the rice borer moth). The enthusiastic team of Natural Park (directors, technicians, and rangers) have consistently helped, provided, and facilitated the resources and motivation needed to carry out bat research in the area since the beginning of the project. The Natural Park team has helped researchers



**Figure 1.9:** Evolution of the aerial morphology of Ebro Delta (Catalonia, Spain) from 1945 to 2022. The Ebro Delta goes into the sea for 25 km. Source: ICGC©, Institut Cartogràfic i Geològic de Catalunya.

efficiently communicate with the irrigation community to raise their awareness of bat conservation. Thanks to that, and because of the numerous awareness and education actions carried out in the territory, the study of bats has always been welcomed by all these communities and farmers. Many endeavours in terms of knowledge transfer by all researchers (e.g. European Bat Night, public talks, news published in local newspapers or naturalists' meetings such as the Delta Birding Festival) have also taken place in the Ebro Delta.

Due to the above-mentioned reasons, bats have been widely and intensively studied in the Ebro Delta for more than 20 years (Flaquer et al., 2020), resulting in three doctoral theses (including this one), two master theses and five bachelors' internships. Since 2000, a large amount of scientific bat research has been published, from conservation and transversal studies (Flaquer & Jarillo, 2002; Flaquer et al., 2006; Tuneu-Corral et al., 2020) to specific studies assessing the role of bats as pest suppressors (Montauban et al., 2020; Puig-Montserrat et al., 2015), the effects of climate change in bat boxes (Flaquer et al., 2014; Martin-Bideguren et al., 2019), the role of natural humid habitats for bat conservation (Mas et al., 2022) and the influence of bat assemblage composition and density on their echolocation (Montauban et al., 2021), amongst many others. Also, thanks to the Bat Monitoring Programme coordinated by the Natural Sciences Museum of Granollers, the southernmost resident colony of Nathusius' Pipistrelle (*Pipistrellus nathusii*) was discovered and studied (Flaquer et al., 2005).

This has led to the monitoring of one of the largest densities of soprano pipistrelle (*Pipistrellus pygmaeus*) ever reported (Fig. 1.10 and Fig. 1.11). One of the most relevant studies considering bats and wetlands found the Ebro Delta wetlands to be vital habitats for one of the farthest travelling migrant bats in Europe: the Nathusius pipistrelle (*Pipistrellus nathusii*) (Flaquer et al., 2009). Additionally, for the first time, and thanks to passive acoustic monitoring, I present the results of the first project using bioacoustics to study the entire bat community of Ebro Delta for two consecutive years, gathering information on bats in different habitats and seasons, being the most extensive dataset of bat activity in wetlands.

This thesis was born with the aim to forge a baseline knowledge to better understand bat responses to different climatic conditions and predict their behaviour under future scenarios. The lack of knowledge about the importance of wetlands for bat conservation made the Ebro Delta a perfect scenario to evaluate the role of these humid habitats for bat resilience in a Mediterranean region that has barely changed throughout time but is suffering the ravages of climate change. With this thesis, I contribute with helpful information for policymakers, technicians and stakeholders to develop new holistic management plans for wetlands.



**Figure 1.10:** *Pipistrellus pygmaeus* in an artificial bat roost from the Ebro Delta that can host more than 1000 bats. The Ebro Delta count with an extensive network including more than 500 bat boxes ([www.batmonitoring.org](http://www.batmonitoring.org)) spread across all habitats. Photo courtesy of Joan de la Malla.



**Figure 1.11:** Leucistic *Pipistrellus pygmaeus* from Buda Island in Ebro Delta. Photo courtesy of Adrià López-Baucells. Source: López-Baucells et al., 2013.

## 1.8. MAIN AIMS AND OUTLINE OF THE THESIS

The general aim of this PhD thesis was to assess and improve our understanding of the role of wetlands in the Mediterranean region in conserving one of the most unknown and elusive vertebrate taxa: bats. I specifically aimed to:

1. Compile and summarise research scientific literature about the relationship between bats and wetlands and describe which knowledge gaps need to be filled in the future to apply proper conservation measures. Moreover, I also aimed to create a quantitative method or indicator to easily identify which regions need more attention regarding bat-wetland studies.
2. Identify which habitats within the Mediterranean coastal regions are essential for hibernating bats and how humid habitats could favour the resilience of overwintering bats under future climate change scenarios.
3. Evaluate the effectiveness of Natura 2000 areas in a highly degraded delta to protect and conserve bat species of conservation priority, and assess whether artificial humid habitats such as rice fields could supply the ecosystem services that wetlands provide for bats.



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*Chapter 2*  
*Bats and wetlands: synthesising gaps in current  
knowledge and future opportunities for conservation*



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## Chapter 2

### Bats and wetlands: synthesising gaps in current knowledge and future opportunities for conservation

#### ABSTRACT

Worldwide, wetland area has decreased by up to 33% in the past ten years. Despite their relatively small coverage, wetlands provide essential ecosystem services. However, the importance of wetlands for bat conservation and the consequences of losing these habitats are not comprehensively understood. Through a systematic literature review, we quantified the knowledge gaps regarding bats in wetlands by: 1) assessing research trends over time; 2) evaluating research biases in geography, themes, species, seasons and methodology; 3) creating the 'bat Knowledge Index' (bKI), a standard indicator for measuring how well-studied bats in wetlands are per country; 4) summarising ecological responses of bats to wetlands; and 5) assessing how bat researchers perceive the role of wetlands for bat conservation. We found strong similarities between the reviewed studies and the bat researchers' perceptions. However, although 75% of respondents considered wetlands important for bat conservation, they rarely studied these habitats. Most of the studies of wetlands took place in developed countries, leaving critical gaps in countries where wetlands are rapidly decreasing. The bKI can be used as a tool for land managers to prioritise conservation actions and resources for the protection of bats in wetlands. Research topics were found to be biased towards habitat selection and species inventory, with many topics only superficially explored. There was also an important seasonal bias, resulting in many unanswered questions during energetically demanding periods for bats (e.g. migration). However, constantly evolving technological developments, such as bat lures and tracking devices, might aid new studies in these habitats. Up to 66% of studies reported that wetlands benefit bat activity or species richness, mainly because of high prey densities and the availability of fresh water. However, the low number of studies and all the research gaps make 'bats and wetlands' a largely underexplored ecological interaction between a poorly studied animal taxon and an increasingly threatened habitat.

**Keywords:** chiroptera, conservation, hibernation, lagoons, marsh, migration, water ecosystems



## 2.1. INTRODUCTION

Changes in the landscape caused by natural factors result in a mosaic of several habitats of unequal surface areas (Chape et al., 2005; UNEP-WCMC & IUCN, 2019). Oceans represent 70% of the Earth's surface area, whereas land represents 30% (Eakins & Sharman, 2010), and, on land, forests cover 30%, while wetlands only comprise around an estimated 1–6% (Loveland et al., 2000; Bartholomé & Belward, 2005; Junk et al., 2013). Most forest and wetland habitats currently face numerous anthropogenic pressures, such as deforestation or the expansion of agricultural croplands (Foley et al., 2005; Williams-Guillén et al., 2016), that modify habitats and affect their provision of ecosystem services. Despite their proportionally small worldwide cover, wetlands are regarded as key components in the landscape providing essential regulating, provisioning and supporting ecosystem services, such as flood mitigation (Watson et al., 2016) and carbon sequestration (Barbier et al., 2011; Junk et al., 2013), as well as social and cultural ecosystem services such as places for birdwatching and a beneficial 'sense of peace' (Millennium Ecosystem Assessment, 2005; Barbier et al., 2011).

These ecosystem services are at risk due to the 30–50% reported decrease in global wetland cover since 1900 (Russi et al., 2013; Davidson, 2014; RAMSAR-Secretariat, 2014; Hu et al., 2017). The loss of wetlands is, in general, directly related to human activities such as increased pressure from agriculture (Hu et al., 2017). Due to the decreasing trend in wetland cover, and given the need to improve the protection of wetlands, several guidelines on wetland management and protection (e.g. Working for Wetlands 2002 in South Africa, Environmental Protection Agency in the USA) and new International agreements (e.g. RAMSAR-Secretariat, 2014 and Natura 2000 in Europe) have recently been developed. Current protection guidelines and management plans are mainly designed to protect wetlands as important feeding and/or wintering grounds for migratory animals (Altringham, 2011; Yetter et al., 2018); they are mostly focused on birds, and rarely on bats.

Several studies report that bats have a preference for foraging in wetlands (Fukui et al., 2006; Flaquer et al., 2009; Lookingbill et al., 2010; Šuba et al., 2012). However, the specific role and significance of wetlands for bat conservation is complex. It varies greatly depending on species, season and region, and has not been comprehensively assessed. For example, although ponds and wetlands are essential for bats in arid regions since they provide water and high insect availability (Razgour et al., 2010; Korine et al., 2015; Blakey et al., 2018), the pollution of these water bodies may in fact affect some bat populations negatively (Korine et al., 2015). In warmer winter nights in temperate zones, bats can come out of hibernation and sometimes forage to refuel or rehydrate themselves (Avery, 1985, 1986; Padgett & Rose, 1991; Soszynska-Maj, 2015; Zahn & Kriner, 2016). In these situations, wetlands could play an essential role

in bat survival due to the food resources and fresh water they provide. Long-distance migratory bat species may also take advantage of wetlands as stopover areas for the same reasons (Fleming et al., 2003; Petersons, 2004; Webb et al., 2010; McGuire et al., 2012). For instance, insectivorous bat species that perform long-distance migrations, such as *Tadarida brasiliensis* and *Pipistrellus nathusii*, need to replenish their fat reserves *en route* (O'Shea, 1976; Glass, 1982; McGuire et al., 2012; Voigt et al., 2012).

The review of bats in aquatic habitats carried out by Salvarina, (2016) reported that studies of bats in areas of open water or lentic systems (including wetlands) were largely lacking, and only represented 7% of the studies reviewed. Wetlands are ecologically and functionally very different from lakes, which are usually found at higher elevations and have different vegetation cover and ecosystem dynamics. Rivers and streams are also markedly distinct from wetlands, as they frequently have turbulent waters that can impair the foraging ability of bats (Frenckell & Barclay, 1987), and they tend to serve a stronger function as commuting corridors because of their long and linear dimensions.

Due to the vulnerability of wetlands in the face of increasing anthropogenic threats and climate change (Erwin, 2009; Xu et al., 2019), it is essential to tackle the extensive knowledge gaps concerning bats and wetlands in order to effectively conserve the bats. Therefore, the main goal of this study was to highlight key areas for further research in these threatened ecosystems by reviewing, detecting and describing gaps within the existing literature, and by investigating the perceptions of bat researchers in terms of the importance of wetlands for bats. To achieve this, we carried out a systematic review based on all published scientific literature, and interviewed bat researchers in all continents via an online questionnaire about bats, wetlands, and their current research.

Our specific aims were to: 1) explore and describe the evolution of research on bats and wetlands over time, and compare it with available literature for other habitats and a similar taxon (i.e. forests and birds); 2) quantify the focal points of those studies (i.e. geographical range, research aims, and target bat species or assemblages), and document any seasonal and methodology biases; 3) create a new 'bat Knowledge Index' (bKI) to quantify the research needs per country (taking into account both the country's wetland area and the existing research carried out); 4) summarise the reported responses of bats to wetland habitats, thus assessing the main benefits these habitats provide for bats; and 5) evaluate how bat researchers perceive the role of wetlands in bat research and conservation, and compare their perception with the publication trends through time.

## 2.2. METHODS

### Systematic literature review

We systematically compiled and reviewed scientific publications focused on bats in wetlands that were published in the period of 1900–2019 using the ISI Web of Knowledge online database (WOS – [www.webofknowledge.com](http://www.webofknowledge.com)), following the procedure of Khan et al., (2003) and Siddaway et al., (2019). Grey literature was not included. The review was performed using the following word clusters in English to search publication titles, abstracts and keywords: ‘bat or bats’ or ‘Chiroptera’ and ‘wetland\*’, ‘lagoon\*’, ‘bog\*’, ‘marsh\*’, ‘fen\*’, ‘saltmarsh\*’, ‘peatland\*’, ‘mangrove\*’, ‘vernal pool\*’, ‘woodland pool\*’, ‘brackish\*’, ‘estuarine\*’, ‘lacustrine\*’, ‘riverine\*’, ‘swamp\*’, ‘vereda\*’, ‘floodplain\*’ and ‘water\*’. An asterisk (\*) indicates that plural forms and variations of the marked words were also considered in the online searches. The outputs were all sorted and filtered using the following WOS categories: acoustic, behavioural science, biodiversity conservation, ecology, environmental studies, forestry and zoology. We only took into account studies that were directly carried out in wetland areas or those that included wetland cover in their analyses. We used the definition of wetland provided by the RAMSAR-Secretariat, (2014) as aquatic habitats where the water table is at or near the surface of the land, or where the land is covered by shallow water, and amended it to include forested wetlands also. Our definition therefore includes areas of marsh, fen, peatland or shallow water – either permanent or temporary - with water that is static or flowing, fresh, brackish or salt, including areas covered with shallow sea water such as coastal lagoons, and forested wetlands. We excluded studies in which the study area was not mentioned or described, and studies that were focused only on agricultural land, dams, ponds, rivers, streams, and lakes. References cited in each publication were also meticulously checked to locate any overlooked published scientific publications that matched our criteria.

All search results were screened and information for the following fields was extracted from each study: 1) methodology; 2) country and continent where the study was performed; 3) main study topics; 4) sampling seasons; 5) bat assemblage, ensemble, guild or species; 6) International Union for Conservation of Nature (IUCN) Red List category for each species, when available; and 7) bat assemblage or species responses to wetlands, in terms of species richness, diversity or bat activity (responses were classified as positive, negative, neutral or not applicable, compared to other habitats). We also classified the topics covered in studies, based on the classification proposed by Tanalgo and Hughes, (2018), with some extra categories extracted from Westgate et al., (2015) and Lisón et al., (2019; see Appendix S2.1 for the definition criteria). A single publication could contain a combination of different methodologies, countries, continents, topics, seasons and target species, so each study was classified

independently in more than one category and our sample unit is the study, not the publication.

To compare the evolution of publications of bats in wetlands with the total number of scientific publications on bats in forests, we performed a similar search over the same period with the following combination of search terms: ‘bat or bats’ or ‘Chiroptera’ and ‘forest\*’. Forests were selected as a habitat category comparable to wetlands, as forests are commonly sampled in bat research (Altringham, 2011). The results were filtered using the same WOS categories that were used for wetland habitats, and all the retrieved publications were individually checked to ensure that they were focused on bats in forests.

To compare trends in bat publications with those focused on other flying animals in wetlands, we performed searches using the same word clusters, but including ‘bird or birds’. The output of publications was filtered with the same previously used WOS categories (with the addition of the category ‘ornithology’).

### Bat Knowledge Index (bKI)

We created a ‘bat Knowledge Index’ (bKI) in order to quantify how well-investigated bat-wetland relationships are in each country. The index takes into account the total area (extent) of wetland cover in each country and the research that has been carried out about bats in these habitats. The index can therefore be used to prioritise conservation actions and financial investment by policymakers and land managers. The index is calculated using the following formula:

$$\text{Bat Knowledge Index} = (Pw) + (1-Aw)$$

where  $Pw$  is the total number of bat publications in wetlands in the country and  $Aw$  is the total area of wetlands in the country. Both  $Pw$  and  $Aw$  have been scaled from 0-1. The index oscillates from 0 to 2, with 0 indicating countries where wetlands have been proportionally studied the least, and 2 denoting countries where wetlands have been studied the most. The results obtained with the bKI were plotted with the function *mapCountryData* from the *rworldmap* R package (South, 2011). All the analyses were carried out using QGIS software v.3.10.4 (QGIS.org, 2019) and R v.3.5 (R Core Team, 2019).

## Questionnaire

To assess bat researchers' perceptions of the role of wetlands in bat research and conservation, and how this is reflected in their research projects, a short online multiple-choice questionnaire was circulated amongst bat researchers between 2017 and 2019. The survey was sent to bat researchers, naturalists and ecologists, including MSc and PhD students as well as professors, across a wide range of disciplines, which ensured good coverage of bat researchers from many regions. The questionnaire was distributed via e-mail, delivered in person during international bat conferences and shared through bat research networks on social media. It included 19 short questions (Appendix S2.2) related to the topics of the literature review (e.g. main topics of bat research projects, target habitats, methodology, and opinions regarding the role of wetlands in bat conservation) as well as additional information about the respondents (e.g. gender, age and research position). All responses representing <5% of the overall answers were pooled together into an 'other' category. A total of 217 completed questionnaires were gathered from researchers in 52 countries (Appendix S2.3), mostly from Europe and North America.

## 2.3. RESULTS AND DISCUSSION

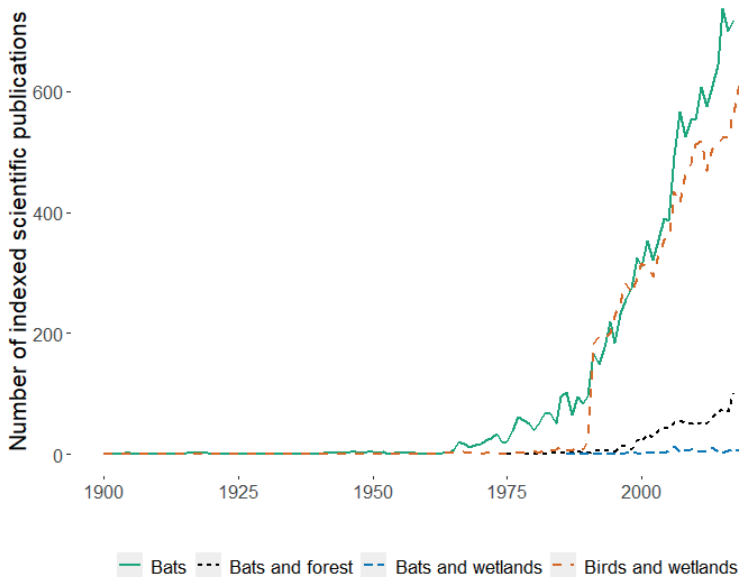
### Bats in wetlands: current state of knowledge

After screening all retrieved scientific publications, we compiled a total of 116 focused on bats and wetlands (Appendix S2.4), while 941 were excluded based on our inclusion criteria (see Methods). Whereas the first scientific publication on 'bats and forests' in our search dates from 1975, the first study of bats and wetlands was not published until 1986 (Fig. 2.1). Publications on bats in forests have undergone a notable exponential increase in numbers since 1990, while studies on bats in wetlands do not follow this trend (Fig. 2.1). Indeed, the maximum detected annual number of publications on bats in wetlands occurred in 2006 with just 14 publications (Fig. 2.1). Compared to the trends for birds, which show a notable increase since 1990, the number of publications about bats in wetlands has barely increased: there have been only a few publications each year since 2005, with an average of six publications annually (Fig. 2.1).

Studies on birds in wetlands represent a major topic in ornithology. Wetlands are the primary habitat used by waterbirds during overwintering or migration periods, due to the high concentration of insects and fish found there (Tiner Jr, 1984). Unlike bats, a large number of bird species are strictly freshwater-dependent (~567 of the ~10000 bird species and ~17 of ~1300 bat species; Dehorter & Guillemain, 2008; Aizpurua & Alberdi, 2018), which makes this taxon especially sensitive to wetland

cover reduction and water pollution. In fact, waterbirds are used in Ramsar criteria to identify wetlands of international importance (Criterion 5 and 6 of the Ramsar Sites Criteria [www.ramsar.org](http://www.ramsar.org); RAMSAR-Secretariat 2014).

Although 75% of the questionnaire respondents considered wetlands to be high-priority habitats for bat conservation, 24% of respondents focused their studies on forests, followed by wetlands, urban areas, and underground roost sites (Appendix S2.5A). Overall, forest habitats were considered to be far more important than wetlands in terms of conservation priorities (Fig. 2.1). The low detectability of bats in wetlands using capture methods (e.g. mist nets or harp traps, generally not appropriate for surveying areas without delimited flyways; Thomas & West, 1989; Duffy et al., 2000), and the general lack of natural roosts for bats to establish maternity or resident colonies (Flaquer et al., 2005, 2007; Lookingbill et al., 2010; Puig-Montserrat et al., 2015), might have discouraged researchers from working in wetland habitats. Also, their location and reduced global cover compared to forests (1–6% vs 30%, respectively) may affect the accessibility and feasibility of carrying out bat studies in wetlands (Bartholomé & Belward, 2005; Keenan et al., 2015; Appendices S2.6-S2.13). The low number of bat publications in wetlands could be also associated with the fact that there are very few strictly water-dependent bat species, and due to the fact that many conservation plans for bats prioritise forest habitats or caves as they can host large bat populations (Mickleburgh et al., 2002).



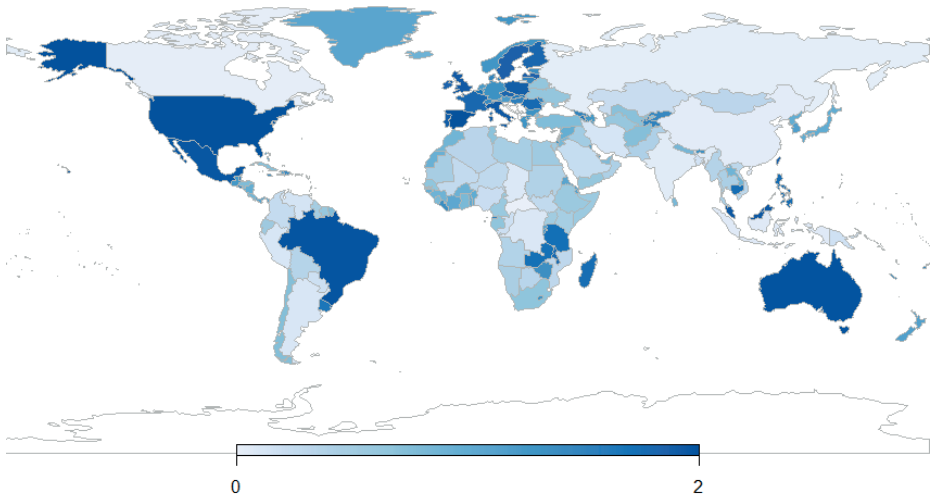
**Figure 2.1:** Evolution of indexed scientific publications on bats in wetlands and a comparative habitat (forests) and taxon (birds) published since 1900, obtained from the ISI Web of Knowledge. Each line represents the clusters of keywords used for the systematic review.

## Geographical distribution of the studies

Although the total number of publications on bats in wetlands is extremely low, we found that studies had taken place in all six continents (Fig. 2.2). However, more than 56% were carried out in the Americas (39% in North America and 17% in South America), while the remaining 44% were carried out in Europe (20%), Oceania (11%, all in Australia), Asia (8%, mostly in Malaysia) and Africa (5%; Figs. 2.2 and 2.3). Africa and Asia stand out for their low number of studies, despite the vast areas of wetlands present in these areas (Appendices S2.6, S2.10 and S2.12) and the high bat diversity that they host (Procheş, 2005). In general, even with the recent increase of bat research in Africa and Asia, these regions are still poorly surveyed (Fig. 2.2), probably due to financial limitations and ongoing social and political challenges (Racey, 2013; Salvarina, 2016). Lisón et al., (2019) reported similar results, highlighting knowledge gaps in Africa, Asia and Oceania with regards to bats in semi-arid and arid landscapes. For some countries (e.g. China), we might have underestimated the number of publications since there is a large body of scientific literature published in local non-English journals which, due to their inaccessibility, were not included in this review (Gates, 2002).

The bKI that we developed to quantify the existing level of study of bats and wetlands in each country (Fig. 2.2) can be used to aid research and funding prioritisation regarding studies of bats in wetlands. Countries with critical knowledge gaps are those with large areas of wetlands but a low number of studies of bats in wetlands (Fig. 2.2). For example, Canada has the lowest index value: more than 33% of its territory is covered by wetlands, but we found only one study on bats and wetlands. Similarly, Russia has extensive areas of wetlands, but only one study was focused on the interaction of bats and wetlands (Appendices S2.11 and S2.12). Most of the reviewed studies from Oceania report higher richness and bat activity in wetlands (Korine et al., 2016; Blakey et al., 2018). However, for example the lack of studies from New Zealand is a cause for concern, given the reported annual wetland habitat loss in the south of New Zealand of between 0.5 and 1% (Robertson et al., 2019). On the other hand, we found a series of countries with relatively low wetland cover, but many studies focused on bats in them (e.g. the USA, with 39 studies and only 23% of wetland cover, Fig. 2 and Appendix S2.8).

This is the first map that attempts to prioritise which countries need to increase their research efforts on bats and wetlands (e.g. Canada, Russia, China, India and Congo; Fig. 2.2) while acknowledging those that seem to have better scientific coverage (e.g. USA, Brazil, and Australia; Fig. 2.2).



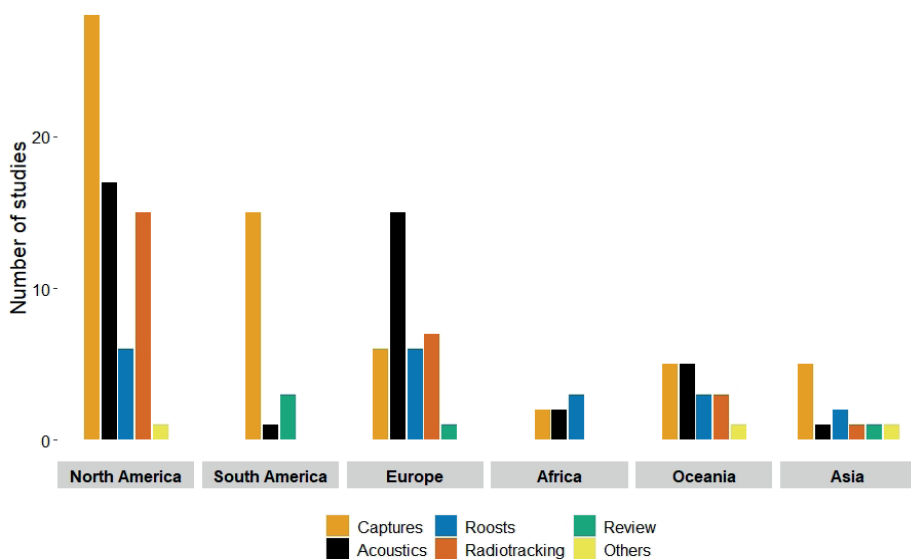
**Figure 2.2:** Bat Knowledge Index (bKI) worldwide map. This index takes into account the total cover of wetlands in each country and the research that has been carried out on bats in these habitats, and can be used to prioritise conservation actions and financial investment by policy makers, researchers and land managers. The index oscillates from 0-2, with the lowest values representing countries where bats in wetlands are understudied (per unit of wetland area), and the highest values representing countries where wetlands have been extensively studied (per unit of wetland area).

### Methodological approach

We observed that both trapping (with mist nets or harp traps) and acoustics were most frequently used as sampling methods for bats in wetlands worldwide (Fig. 2.3). Radiotracking, roost surveys and other techniques were only occasionally used. In Europe, studies were mainly carried out with acoustic methods; these methods are suitable for all the bat species present in the continent, which are insectivorous and easily recorded. In Africa, Oceania and Asia, studies were equally often carried out by acoustic methods and captures, due to the presence of both insectivorous and frugivorous/nectarivorous/carnivorous bats, some of which do not echolocate or have ‘whispering’ calls that are often undersampled with acoustics (Yoh et al., 2020; Fig. 2.3, Table 2.1). In North America, although most bat species are insectivorous, mist netting was the most popular technique. Weller and Zielinski, (2006) reported that more than half of American bat researchers prefer mist netting, since bioacoustics generally requires much more experience for accurate identification of bat calls. In South America, the majority of studies reviewed were carried out in areas where phyllostomid bats are abundant, and mist netting is the most appropriate method for sampling them due to their quiet echolocation calls (MacSwiney et al., 2008; Meyer et al., 2011).



Ultrasound detectors appeared on the market in the early 20<sup>th</sup> Century (Noyes & Pierce, 1938; Pierce & Griffin, 1938; MacDonald & Brudzynski, 2018) and have proven to be highly efficient for studying aerial insectivorous bats in open spaces, detecting 30% more species than mist nets (MacSwiney et al., 2008). However, we found no increase in acoustic studies over the years, perhaps due to accessibility and financial constraints of costly acoustic detectors. The difficulty of sampling bats in wide open areas like wetlands with mist nets or harp traps has probably hindered the study of these challenging ecosystems (Kunz & Brock, 1975; Duffy et al., 2000; MacSwiney et al., 2008; Bruckner, 2016). The two most common methodologies used by questionnaire respondents were reported in similar proportions to those revealed by the literature review, with mist netting and bioacoustics used by 34% and 30% respectively. However, the lack of respondents from Africa, Asia and Oceania make our results highly biased towards research practices in Europe and North America.



**Figure 2.3:** The total number of studies on bats and wetlands performed in each continent, grouped according to the methodology used. Methodologies were classified as: acoustics (bat detectors), captures (mist nets, harp traps and hand nets), roosts (roost inspection), radiotracking (global positioning system tags or VHF radio tags), review (literature reviews), others (video or camera recordings, number of bat fatalities).

Given that bat lures are now being widely developed to help improve trapping rates, and are increasingly more accessible in price, the use of mist nets and harp traps in wetland habitats is likely to increase (Samoray et al., 2019). Also, three-dimensional flight studies are increasingly being used in open areas, and wetlands are a good target for this type of research (Grodzinski et al., 2009; Hristov et al., 2013).

Population genetics (e.g. Budinski et al., 2019) and the use of soundscape exploration (e.g. Paraskevas & Rangoussi, 2010; Krause, 2016) are also new methods that are highly suitable for wetland ecosystems, and their use is likely to increase in the near future. Finally, ongoing reductions in the size and weight of global positioning system tags (e.g. Conenna et al., 2019) are progressively enabling the use of these methods to track smaller species, including most insectivorous bats; this may result in their increased use to study bats in wetlands.

### Topics of studies and species/assemblage targets

We found that 42% of studies on bats in wetlands assessed habitat selection, 15% included species inventories, and 15% were focused on roost-site selection. The remaining 28% included studies of diet, habitat fragmentation, natural history, or pollutants (Fig. 2.4A; see Appendix S2.1 for the full breakdown of topics assigned). Similar results were reported by Lisón et al., (2019) in semi-arid and arid landscapes, where the majority of studies were focused on habitat use and species inventories. Most of the studies were strongly biased towards insectivorous bats and were performed in temperate areas (Fig. 2.3). In total, 26 out of 116 publications were focused on full bat assemblages, 30 on insectivorous species, three on nectarivorous bats, one on frugivorous bats and 56 on specific target species. In terms of species-specific studies, we retrieved studies focused on a total of 34 different species, of which 22 were insectivorous (Table 2.1). Most insectivorous bat species are closely tied to wetlands due to the high insect availability and water supply in wetlands (Menzel et al., 2005b; Lookingbill et al., 2010; Ciechanowski, 2015). In contrast, nectarivorous bats obtain water and energy partially from nectar (water and sugar), and frugivorous species obtain them from fruit (Morrison, 1980; Rocas et al., 1993).

Our questionnaire results coincided with the literature review results. Bat researchers that were undertaking studies in wetlands mainly focused on habitat selection (almost 30%), closely followed by species inventories (Appendix S2.5B). Most studies were focused on insectivorous bats (46%) or full bat assemblages (36%; Appendix S2.14). However, studies focused on insectivorous bats could be overrepresented due to the high number of responses gathered from Europe and North America, where insectivorous bats represent the highest number of species (see Appendix S2.3).

The review carried out by Salvarina, (2016) encompassed rivers, streams, ponds, canals and wetlands, and identified the five most frequently studied bat species in these habitats, of which *Myotis daubentonii* was the most representative. However, *Myotis daubentonii*, a river-dependent trawling species that is highly influenced by water quality and the health of riparian ecosystems (López-Baucells et al., 2017), was

not specifically studied in any of our reviewed publications, probably due to the lack of riparian forests in many wetlands. We found that the most studied species were *Corynorhinus rafinesquii*, a forest-dwelling bat associated with forested wetlands (Johnson & Lacki, 2013), followed by *Pipistrellus pygmaeus* and *Myotis sodalis* (Table 2.1). *Pipistrellus pygmaeus* is common in temperate areas and forages over riparian and humid habitats (Davidson-Watts et al., 2006; Table 2.1), and *Myotis sodalis*, present in the USA, is a cave-dwelling bat that also forages over riparian habitats and forests (Menzel et al., 2005a; Arroyo-Cabrales & Ospina-Garces, 2016). These species are closely linked to inland wetlands, and none of them is currently threatened (Critically Endangered, Endangered, or Vulnerable) according to the IUCN. In terms of conservation status, only two studies were focused on Critically Endangered species, five on Endangered species and nine on Near Threatened species (Table 2.1). Many migratory species (e.g. *Pipistrellus nathusii*) and short-distance fliers rely on wetlands but are rarely targeted by scientific studies. The number of threatened bat species in wetlands is probably widely underestimated due to the lack of studies of these ecosystems. Besides, information about bat species' natural history and behaviour is largely deficient, presumably as a result of the current lack of interest in descriptive studies in academia (Agnarsson & Kuntner, 2007). The low number of studies on threatened species could be attributed to the vast understudied tropical regions that host an elevated number of threatened, Data Deficient or even unknown bat species (Frick et al. 2020).

**Table 2.1:** Numbers of studies that included each species, classified according to their International Union for Conservation of Nature (IUCN) Red List category.

Continent	Family	Species	Least Concern	Near Threatened	Vulnerable	Endangered	Critically Endangered	Data Deficient
Africa	Emballunoridae	<i>Coleura seychellensis</i>					2	
		<i>Eidolon helvum</i>		1				
		<i>Pteropus voeltzkowi</i>			1			
Asia	Pteropodidae	<i>Acerodon jubatus</i>				1		
		<i>Eonycteris spelaea</i>	1					
		<i>Pteropus vampyrus</i>		1				
		<i>Pteropus vampyrus lanensis</i>			1			
	Vespertilionidae	<i>Kerivoula krauensis</i>						1

Table 2.1: Continuation.

Continent	Family	Species	Least Concern	Near Threatened	Vulnerable	Endangered	Critically Endangered	Data Deficient
Europe	Rhinolophidae	<i>Rhinolophus mehelyi</i>			1			
		<i>Eptesicus nilssonii</i>	2					
	Vespertilionidae	<i>Pipistrellus kuhlii</i>	1					
		<i>Pipistrellus nathusii</i>	2					
		<i>Pipistrellus pipistrellus</i>	3					
		<i>Pipistrellus pygmaeus</i>	5					
North America	Phyllostomidae	<i>Artibeus intermedius</i>	1					
		<i>Artibeus jamaicensis</i>	2					
		<i>Dermanura phaeotis</i>	1					
	Vespertilionidae	<i>Corynorhinus rafinesquii</i>	8					
		<i>Lasiurus borealis</i>	2					
		<i>Lasiurus cinereus</i>	1					
		<i>Myotis austroriparius</i>	3					
		<i>Myotis evotis</i>	1					
		<i>Myotis grisescens</i>			1			
		<i>Myotis lucifugus</i>				4		
<i>Myotis septentrionalis</i>			1					
<i>Myotis sodalis</i>			5					
South America	Noctilionidae	<i>Noctilio albiventris</i>	1					
		<i>Noctilio leporinus</i>	2					
	Phyllostomidae	<i>Artibeus jamaicensis</i>	1					
		<i>Vampyrum spectrum</i>			1			
Oceania	Molossidae	<i>Mormopterus norfolkensis</i>			1			
	Vespertilionidae	<i>Chalinolobus gouldii</i>	1					
		<i>Nyctophilus geoffroyi</i>	1					
	Pteropodidae	<i>Pteropus alecto</i>	3					
		<i>Pteropus scapulatus</i>	2					
<b>Total</b>			<b>45</b>	<b>9</b>	<b>5</b>	<b>5</b>	<b>2</b>	<b>1</b>

## Seasonality

We found an uneven seasonal coverage in studies of bats and wetlands in temperate areas: 60% of them were conducted in summer, while the migration seasons (spring and autumn) and winter were underrepresented (15%, 15% and 10% of studies respectively; Fig. 2.4C). Bats are most active in spring, summer and autumn in temperate regions; these are also the best seasons for fieldwork. During summer, water resources are more intensively used by lactating females due to their higher risk of dehydration (Adams & Hayes, 2008). Also, due to reduced mobility when bats are still carrying pups, they tend to fly shorter distances and remain close to aquatic ecosystems, in order to access the high abundance of insects and water they provide (Kipson et al., 2019).

These results match our questionnaire results, where most bat researchers reported that their studies were carried out in summer (36%), spring and autumn (both 26%), and far fewer in winter (12%). In fact, most researchers agreed that wetlands are important feeding sites for bats, especially during summer (37% of respondents), spring (30%) and autumn (26%). In terms of bat migration, 91% of respondents acknowledged that wetlands could be used as stopover areas due to insect concentrations (50%), large amounts of water (27%) and the absence of extreme temperatures (16%). By contrast, only 5% of respondents focused their studies on migration (Appendix S2.5B).

Some bat species perform seasonal migrations during the night (Alerstam, 2009; McGuire et al., 2014), and, therefore, they need to find areas with high concentrations of insects, such as wetlands, to be able to refuel (McGuire et al., 2014). However, although wetlands may represent important stopovers during migration periods (Petersons, 2004; Flaquer et al., 2009), we did not retrieve any studies addressing the relationship between bat migration and wetlands (Fig. 2.4A).

The lack of studies during the winter (Fig. 2.4C) results from the seasonal reduction in bat activity due to the absence of insects at low temperatures (Mellanby, 1939; Fukui et al., 2006). Only 6% of the respondents considered wetlands to be important feeding spots in winter and high-priority habitats for bat conservation during this season (8%). However, Lindsay et al., (2015) showed that the production of Diptera and Hemiptera in wetlands during cold winters is an essential resource for small insectivorous passerine birds. Some bat studies in temperate regions report that bats wake up and emerge early at night or even during the day (above 10°C) to forage or drink, specifically in humid areas such as wetlands (Avery, 1986; Brigham, 1987; Padgett & Rose, 1991). Nevertheless, the importance of wetlands as winter feeding resources to bats has never been proved, so the role of wetlands for bat conservation in winter remains unanswered.

In the tropics, the dry and wet seasons were equally represented in all studies (55% and 45% respectively; Fig. 2.4C), in line with our questionnaire results where both seasons were well represented in respondents' studies (59 vs 41%, respectively). Tropical areas tend to have two markedly different seasons (dry and wet) defined by rainfall. Depending on the climatic region, the annual dry period may vary in length from three to eight months (Murphy & Lugo, 1986). A study carried out in the Amazonian forests demonstrates that some bat guilds exhibit marked seasonality since their food resources vary between dry and wet seasons (e.g. nectarivorous species), while others do not (carnivorous and insectivorous species; Ferreira et al., 2017). However, no references to seasonal differences in aquatic ecosystems have been reported, leaving unexplored questions about how seasonality in these habitats can affect tropical bat communities (Bader et al., 2015; Torrent et al., 2018).

### Ecological responses of bats to wetlands

In this study, we have collected and summarised in a single document for the first time all the published evidence of the effects of wetland cover on bat richness, activity and diversity (Appendix S2.15). About 70% of the studies reported that wetland cover had a positive effect on bat assemblage richness, diversity or activity (including foraging activity and time spent over a habitat type) compared to other habitats (Fig. 2.4B; e.g. Flaquer et al., 2009; Lookingbill et al., 2010; Salsamendi et al., 2012; Ciechanowski, 2015; Straka et al., 2016; Blakey et al., 2018; see Appendix S2.15 for the complete list). Some bat species, such as *Nyctalus noctula*, were reported to select, at least brackish waters for foraging and drinking (Ciechanowski, 2015). Wetlands were also found to be important for insectivorous bats in urban environments, supporting higher activity and species richness than non-wetland habitats (Straka et al. 2016). In fact, in this last study, the proximity of wetlands to patches of natural bushland was the strongest landscape-scale predictor of both bat species richness and bat activity (Straka et al., 2016). Lookingbill et al., (2010) suggested that the management of a wetland network as foraging sites was critical for the success of bat populations, primarily benefitting bats with small to moderate home ranges that preferred to forage on wetlands. Furthermore, Salsamendi et al., (2012) concluded that networks of wetlands and water bodies would increase the carrying capacity of an area for the vulnerable species *Rhinolophus mehelyi*, due to the increase of water and insect availability.

In contrast, a few studies reported a negative (13%) or neutral (17%) effect of wetlands on bat assemblages (e.g. Zimmerman & Glanz, 2000; Vindigni et al., 2009; Barros et al., 2014; see Appendix S2.15). Vindigni et al., (2009) reported that total bat activity was lower in natural wetlands than over artificial water bodies (small artificial ponds and ditches). The authors concluded that these artificial ponds were critical structures within managed pine forests, as they provided water and insect prey

(as wetlands do), but had little overhanging vegetation. Moreover, Zimmerman and Glanz, (2000) found that bat activity in wetlands was remarkably low, especially during summer and early autumn. A negative correlation between bat passes and wetland cover was linked to low temperatures and reduced insect biomass (Zimmerman & Glanz, 2000).

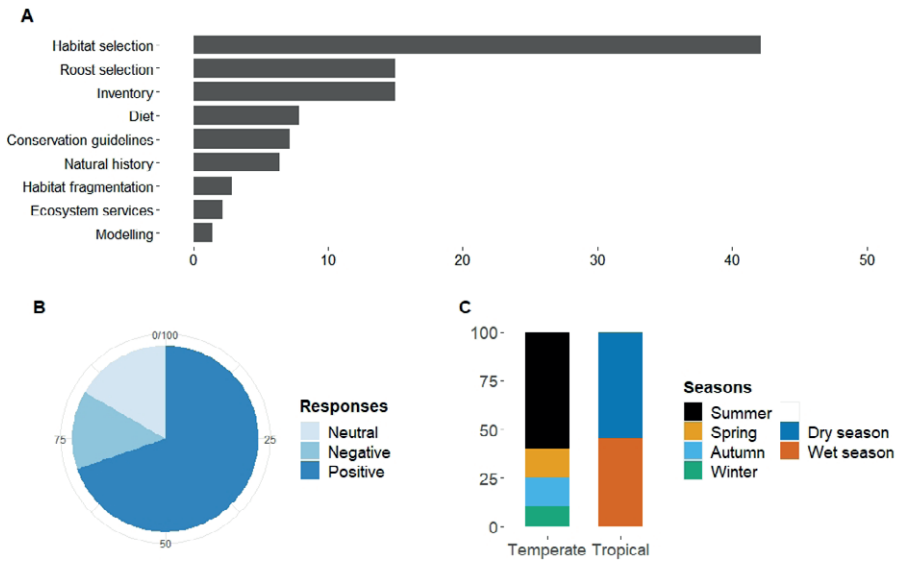
The positive responses of bats to wetland cover are strongly related to the availability of fresh water and the high concentration of insects. However, these results could be slightly biased due to the fact that most studies were carried out in temperate areas (Fig. 2.2 and 2.3) and during hot seasons (summer; Fig. 2.4C), and many of them were focused on insectivorous bats (Table 2.1).

## 2.4. KNOWLEDGE GAPS AND OPPORTUNITIES FOR FUTURE RESEARCH

Our results show that there is still a lack of information on bats and wetlands, above all regarding habitat use during migration periods in autumn and in winter. Bat researchers' perceptions are shaped by a notable bias towards the use of wetlands based on the season. During cold seasons, temperate bats typically hibernate (Hock, 1951; Eklöf & Rydell, 2017), but they can awaken to feed or drink fresh water (Ben-Hamo et al., 2013). Wetlands therefore probably increase the resilience of bat populations by providing freshwater resources during their most sensitive periods, such as during hibernation, although this remains underexplored.

Most questionnaire respondents did not undervalue the importance of wetlands, as most consider these ecosystems to be high priority habitats for bat conservation. However, we showed that, despite the positive effects of wetlands on bat conservation, there are several knowledge gaps in specific topics. We can identify as potential research topics to be addressed in future research in wetlands those that have either been poorly addressed or not addressed at all in previous research.

Despite the fact that some studies have been focused on the effects of water quality or wastewater treatment on bats and their foraging activity (Korine et al., 2016; Salvarina, 2016), the effects of pollutants in wetlands on bat activity or bat populations is poorly studied (Straka et al., 2016). Research is also needed to explore the effects of wetland habitat fragmentation on ecosystem services provided by bats. There are also important knowledge gaps regarding the diet and population genetics of bats in wetlands, the role of wetlands as stopovers during migration, and the importance of wetlands during warm winter nights for periodic foraging of hibernating bats (Avery, 1986; Brigham, 1987; Arlettaz et al., 2000).



**Figure 2.4:** **A)** Percentages of the studies (140) on bats and wetlands that covered each of the main topics (see Appendix S1 for more information). **B)** Summary of ecological responses of bats and bat assemblages to wetlands (66 studies), in terms of richness, selection and preference (when applicable). **C)** Seasonal distribution of 167 studies conducted in temperate and tropical regions. Each publication could contain a combination of different topics, seasons and bat responses to wetlands, so each study was classified independently in more than one category.

Some countries in Africa (e.g. Congo, Chad), Asia (e.g. Bangladesh, Vietnam), Oceania (e.g. Papua New Guinea, Solomon Islands) and South America (e.g. Paraguay, Venezuela and French Guiana), where rates of wetland loss are the highest (Appendices S2.9, S2.10 and S2.12; Racey, 2013; Hu et al., 2017), should prioritise research efforts in wetland areas. We foresee an increase of studies in Asia, where the recent development and implementation of new technologies and the establishment of bat conservationist groups may provide a stimulus (Pei-Chun & Hsin-Ning, 2015; Kingston et al., 2016). In order to increase the effectiveness of bat studies and overcome methodological constraints in these open areas, a combination of established methods (captures and bat assemblages to wetlands) and new techniques (e.g. three-dimensional flight detection, LiDAR, global positioning system tags and soundscape) may prove decisive.

Bats do not have borders, and the establishment of a well-connected network of researchers would increase our consciousness of how they use the landscape. As reported in some bird studies (e.g. Fletcher & Koford, 2003), the use of management programs in wetlands, such as the European Union's Birds Directive and the Natura 2000 protected area network, has contributed to the conservation of some bird populations. As reported by Popov et al., (2019), bats could be included in Criterion



9 of Ramsar Sites Criteria (RAMSAR-Secretariat 2014) to identify wetlands of international importance. Also, in Latin America and the Caribbean, bat researchers and conservationists have declared protected 'AICOM' and 'SICOM' areas (Important Areas and Sites for Bat Conservation, RELCOM; [www.relcomlatinoamerica.net](http://www.relcomlatinoamerica.net)) to describe and categorise areas or sites that play an important role in bat conservation (Bichuette et al., 2018). Building on these existing network structures to include wetlands in habitat assessments for bat conservation would be an excellent way of increasing and improving their management and protection.

## 2.5. CONCLUSIONS

1. There is a strong correlation between the research carried out over recent decades and the perceptions of current bat researchers and conservationists. However, although 75% of bat researchers consider wetlands important for bat conservation, the majority of research efforts are still focused on other hotspots of biodiversity such as forests, and we lack adequate coverage of wetland habitats that may host understudied species.
2. Most of the studies were carried out in more developed continents, leaving important knowledge gaps in Africa, Asia, Oceania and South America, where wetland areas are rapidly decreasing. We propose the 'bat Knowledge Index', a useful tool for land managers, scientists and policymakers to prioritise conservation actions and funding resources to protect bats in wetlands worldwide.
3. Research topics related to bats in wetlands are strongly biased towards habitat selection and inventories of species, while other conservation-relevant topics such as wetland fragmentation or pollution remain largely unexplored.
4. Recent advances of new technologies, such as the development of bat lures to improve trapping rates, could lead to increases in the number of bat studies carried out in open habitats such as wetlands in future.
5. There is an important seasonal bias in research in temperate areas that leaves big information gaps during highly energetically demanding periods for bats (migration and hibernation). These periods are likely to be crucial for the conservation of bats.
6. The majority of the studies we reviewed (66%) reported that wetlands benefit bat activity or species richness. This positive ecological response of bats to wetlands is driven by the presence of large amounts of water and high concentrations of insect prey.



7. The overall low number of studies and the research biases and gaps identified within them clearly reveal that bats and wetlands constitute an underexplored ecological interaction between a poorly studied animal taxon and a highly threatened habitat.

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## 2.8. APPENDIX

**Appendix S2.1:** Categories used to classify the topics studied in the reviewed studies, based on Tanalgo & Hughes (2018), Westgate et al. (2015) and Lisón et al. (2019).

<b>Topics used</b>	<b>Scope and description</b>	<b>Source</b>
Habitat fragmentation	Studies focused on bats and habitat fragmentation.	Westgate et al. 2015
Pollution	Studies focused on the effects of heavy metals concentration/pollution/contamination or other elements on bats.	Lisón et al. 2019
Seasonality (migration/hibernation/...)	Studies focused on the knowledge of bat phenology and seasonality.	Lisón et al. 2019
Phylogenetics	Studies using principles of molecular biology to assess evolutionary processes to understand bat taxonomy and systematics.	Tanalgo & Hughes 2018
Roosting	Studies that include the observation of bat roosting habits, habitat selection for roosting.	Tanalgo & Hughes 2018
Diet	Studies focused on diet analyses and foraging habits.	Tanalgo & Hughes 2018
Ecosystem services	Studies focused on the ecological services of bats such as pest control, pollination or seed dispersal.	Tanalgo & Hughes 2018
Inventories	Findings resulting from species inventories, rapid-assessments, biodiversity surveys, results of observations and sightings	Tanalgo & Hughes 2018
Conservation guidelines	Studies focused on bat species/populations or habitat management. Studies designed to understand the human-bat conflicts and threats that directly leads to the conservation of the species or population. Diversity surveys that focus on endemism and the conservation status patterns of bats	Tanalgo & Hughes 2018
Bat Health	Studies focused on ecto- and endoparasite of bats, including those focused on bat-parasite relationships including parasite taxonomy and distribution. Also, studies focused on bat-borne diseases or emerging diseases (virus, bacteria and fungi).	Tanalgo & Hughes 2018
Natural history	Studies focused on the reproductive biology, phenology patterns of bats. It may also include anatomical and physiological studies relating to bat reproduction or reproductive parts. Also, studies that describe new species.	Tanalgo & Hughes 2018

## Appendix S2.2. Questionnaire

**Definition of wetlands:** We considered wetlands those aquatic habitats where water table is at or near the surface of the land, or where the land is covered by shallow water. This definition includes areas of marsh, fen, peatland or water, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas covered with shallow sea water such as coastal lagoons, and forested wetlands. Agricultural lands, dams, ponds, rivers, streams and lakes have been excluded.

1. Research position
  - a) Bachelor
  - b) Master
  - c) PhD
  - d) Post-Doc
  - e) Independent researcher
  - f) Lecturer/Professor
  - g) Other
2. Age
  - b) <20
  - c) 20-30
  - d) 31-40
  - e) 41-50
  - f) 51-65
  - g) >65
3. Gender
  - a) Female
  - b) Male
  - c) Other
4. Country
5. Research center/institution
6. Are you carrying out any fieldwork at the moment?
  - a) Yes
  - b) No
7. Which are your principal habitats of study?
  - a) Agricultural lands
  - b) Coastlines
  - c) Deserts/Semi-deserts
  - d) Forests
  - e) Grasslands
  - f) High mountains
  - g) Mines and caves
  - h) Riparian habitats
  - i) Urban areas
  - j) Wetlands
  - k) Other
8. Do you consider wetlands....
  - a) Not relevant for bat conservation
  - b) Important for bat conservation but not a priority
  - c) A high priority habitat for bat conservation
- 8.1. If so... during which periods?
  - a) Spring
  - b) Summer
  - c) Autumn
  - d) Winter
  - e) Dry season
  - f) Wet season
9. Have you ever carried out any study analysing the relationship between wetlands and bats?
  - a) Yes
  - b) No
- 9.1. If so, could you indicate the main aims of the study?
  - a) Conservation guidelines
  - b) Diet
  - c) Ecosystem services
  - d) Habitat fragmentation
  - e) Habitat selection
  - f) Hibernation
  - g) Migration
  - h) Natural history
  - i) Roost selection

- j) Toxicology
- k) Species inventory
- l) Other

9.2. Which methods did you use?

- a) Acoustics
- b) Captures
- c) Radiotracking
- d) Literature review
- e) Roosting inspection/video tapping...
- f) Other

9.3. Was it focused on...

- a) Full bat assemblage
- b) Insectivorous bats
- c) Nectarivorous bats
- d) Frugivorous bats
- e) Carnivorous bats
- f) Sanguinivorous bats
- g) Specific species (if so, please add the species in "Other")
- h) Other

9.4. When?

- a) Spring
- b) Summer
- c) Autumn
- d) Winter
- e) Dry season
- f) Wet season

10. Do you consider that wetlands could be important as feeding hotspots for bats?

- a) Yes
- b) No

10.1. During Which periods?

- a) Spring
- b) Summer
- c) Autumn
- d) Winter
- e) Dry season
- f) Wet season

11. Do you think that wetlands are used as stopover sites for bats as well as for birds?

- a) Yes
- b) No

11.1. If so, why?

- a) There are a huge concentration of insects
- b) Temperate climate (no extreme temperatures)
- c) Large water bodies
- d) Other

11.2. If not, why?

- a) Forest, rocky or urban areas (where they might roost) are far from wetlands
- b) Many predators inhabit these areas
- c) Wetlands do not usually present natural roost for bats
- d) Other



**Appendix S2.3:** Total number of questionnaires obtained from bat researchers by country.

Continent	Country	Total	Continent	Country	Total
<b>Africa</b>	Algeria	2	<b>Europe</b>	Albania	1
	Kenya	1		Belgium	4
	Madagascar	2		Bosnia and Herzegovina	1
	Mozambique	1		Bulgaria	1
	Nigeria	1		Croatia	1
	Swaziland	1		Czech Republic	2
	Turkey	2		Denmark	2
<b>Asia</b>	India	5		Finland	1
	Indonesia	3		France	4
	Israel	1		Germany	5
	Malaysia	7		Gibraltar	1
	Nepal	2		Greece	1
	Pakistan	2		Italy	7
	Sri Lanka	3		Netherlands	9
	Taiwan	2		Poland	2
<b>North America</b>	Belize	1		Portugal	8
	Canada	3		Romania	1
	Costa Rica	2		Russia	1
	Grenada	1		Slovenia	1
	Mexico	5	Spain	35	
	United States	23	Sweden	1	
<b>South America</b>	Bolivia	1	Switzerland	1	
	Brazil	9	United Kingdom	30	
	Chile	3	<b>Oceania</b>	Australia	6
	Colombia	2			
	Guatemala	2			
	Nicaragua	1			
	Peru	2			

**Appendix S2.4:** Reference list of reviewed publications

1. Adams RA, Simmons JA (2002) Directionality of drinking passes by bats at water holes: is there cooperation? *Acta Chiropterologica* 4: 195-199. doi:<https://doi.org/10.3161/001.004.0211>.
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5. Barros MA, Pessoa D, Rui AM (2014) Habitat use and seasonal activity of insectivorous bats (Mammalia: Chiroptera) in the grasslands of southern Brazil. *Zoologia (Curitiba)* 31: 153-161. doi:<https://doi.org/10.1590/S1984-46702014000200006>
6. Bartonička T, Řehák Z (2007) Influence of the microclimate of bat boxes on their occupation by the soprano pipistrelle *Pipistrellus pygmaeus*: possible cause of roost switching. *Acta Chiropterologica* 9: 517-526. doi:<https://doi.org/10.3161/150811007783528022>.
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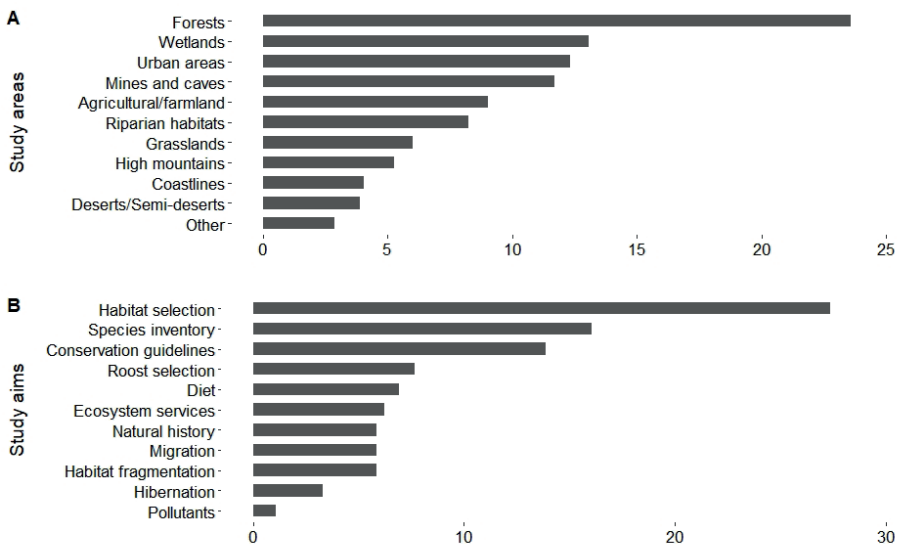
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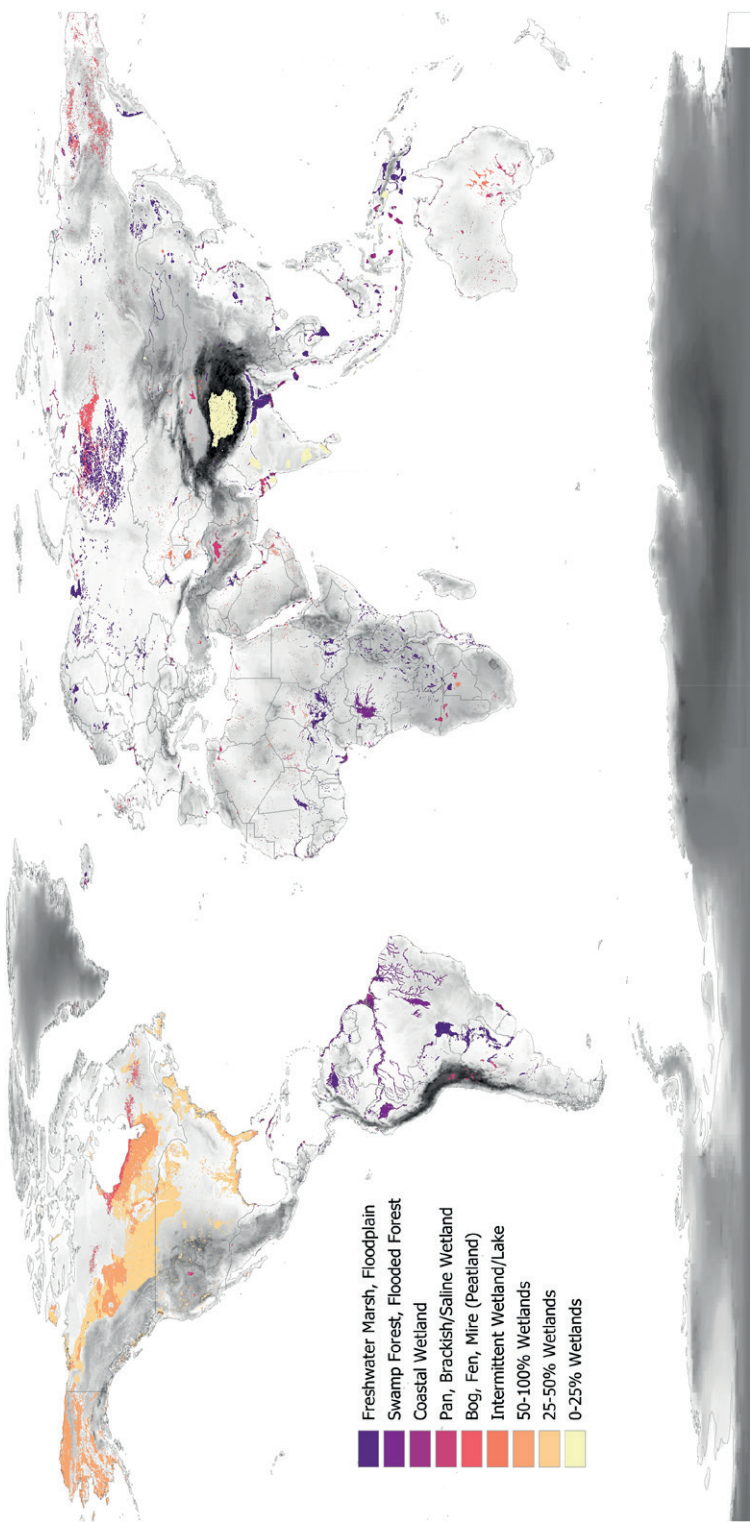


**Appendix S2.5:** Results obtained through the questionnaire: **A)** Main habitats surveyed by the participants of the questionnaire (%) and **B)** Main research aims reported for their studies.

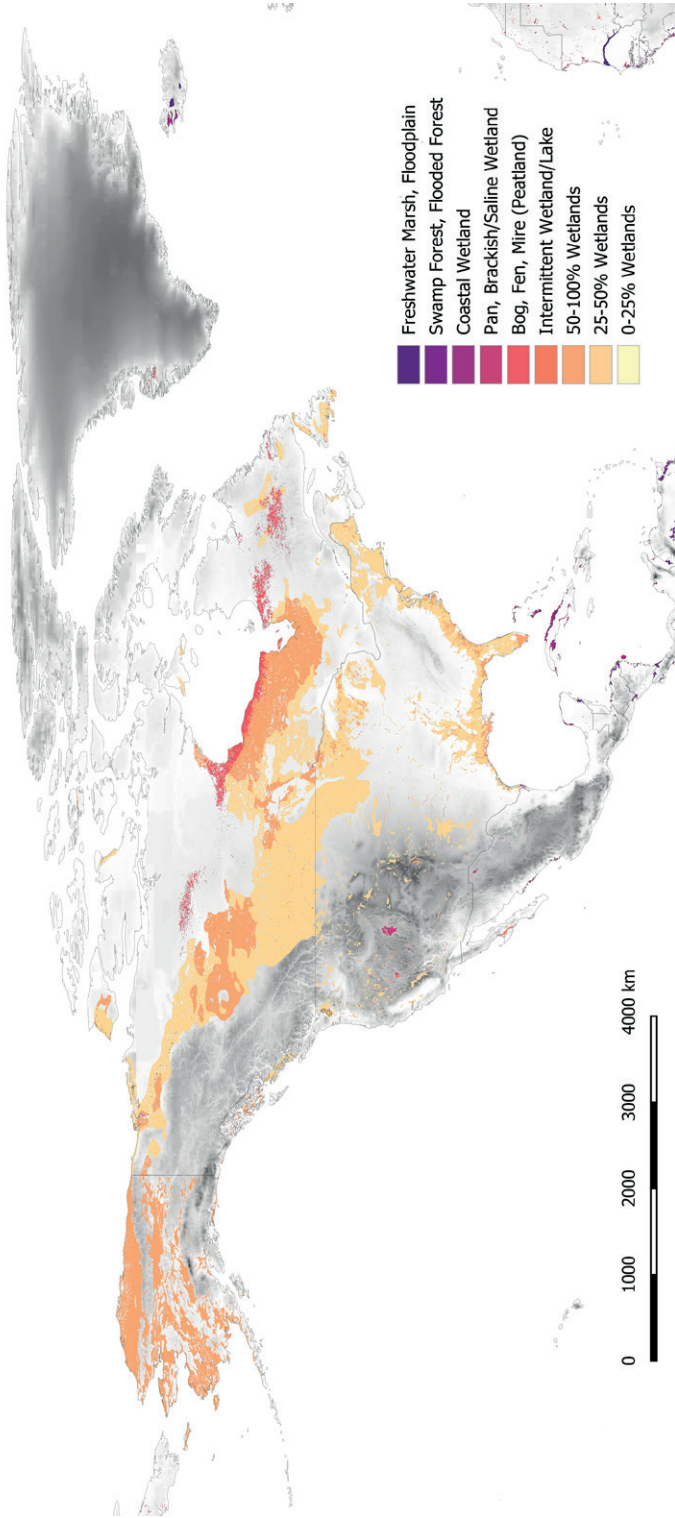
**Appendix S2.6:** Distribution of wetland cover by continents. All data is expressed in km<sup>2</sup> and has been calculated using the GLWD-3 package from Lehner and Döll (2004). Three categories (lakes, rivers and water reservoirs) have been excluded for our analysis. The numbers could slightly differ between the global extension and continents wetlands extension due to the specific shape files used to calculate the extension by continent. Calculations have been carried out with QGIS Software (V.3.4 Madeira). The percentage of wetlands (e.g. 50-100% wetlands) reflects their maximum extent when seasonal variations are applied.

<b>Wetland Types</b>	<b>Global</b>	<b>Africa</b>	<b>Asia</b>	<b>Europe</b>	<b>North America</b>	<b>South America</b>	<b>Oceania</b>
Freshwater marsh, floodplain	2487749	694281	1183656	164349	13115	427022	5326
Swamp forest, Flooded forest	1148466	179067	56329		4469	908332	269
Coastal wetlands	392358	59492	178379	25280	30266	50683	48258
Plan, brackish/saline wetlands	433287	114121	151457	382	13051	58044	96232
Bog, fen, mire (peatland)	708931		484472	19010	205449		
Intermittent wetlands/lakes	688337	200709	341293	4925	26014	2806	112591
50-100% wetlands	1755143				1755143		
25-50% wetlands	3152360				3152360		
0-25% wetlands	898796		898364				431
<b>Total</b>	<b>11665427</b>	<b>1247670</b>	<b>3293950</b>	<b>213945</b>	<b>5199867</b>	<b>1446888</b>	<b>263106</b>



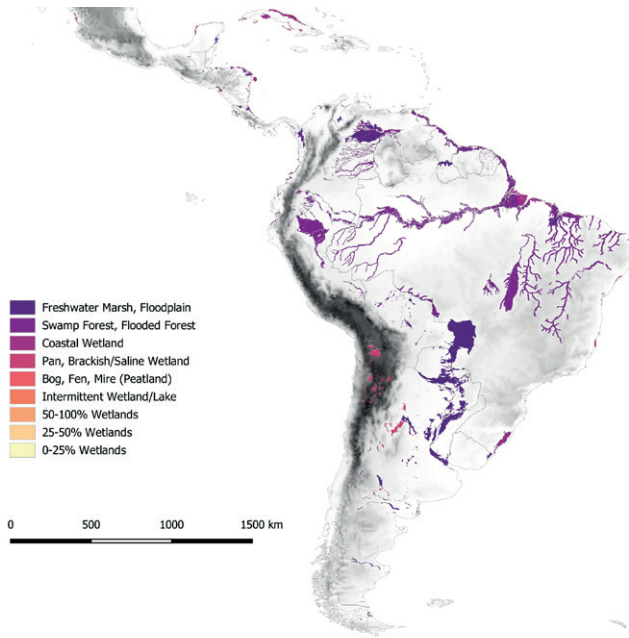


**Appendix S2.7.** Wetlands distribution worldwide classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS software (V.3.4 Madeira).

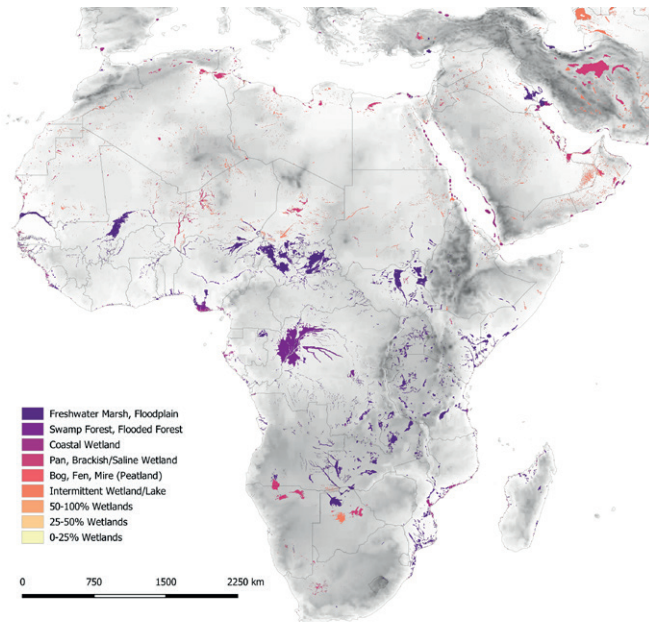


**Appendix S2.8.** Wetlands distribution in North America classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).

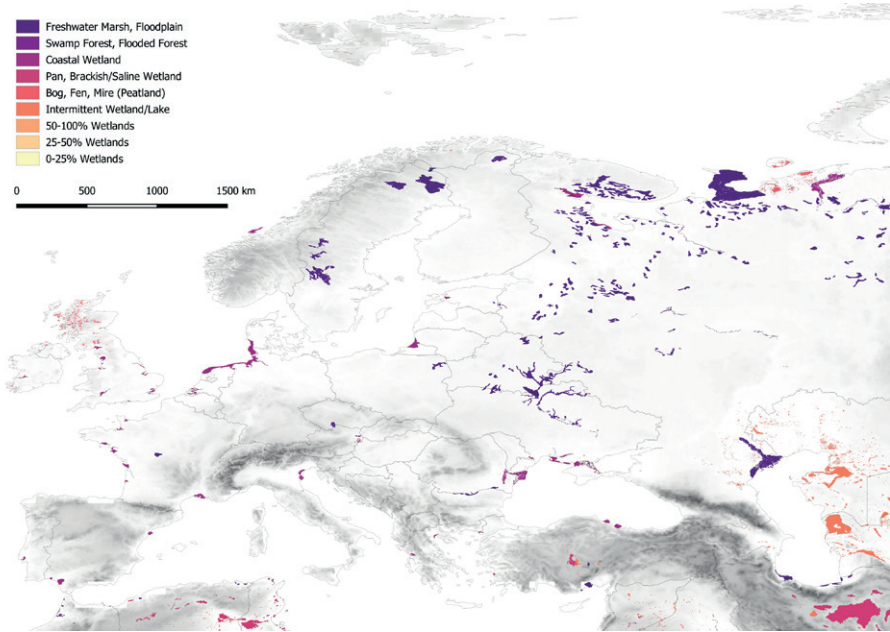




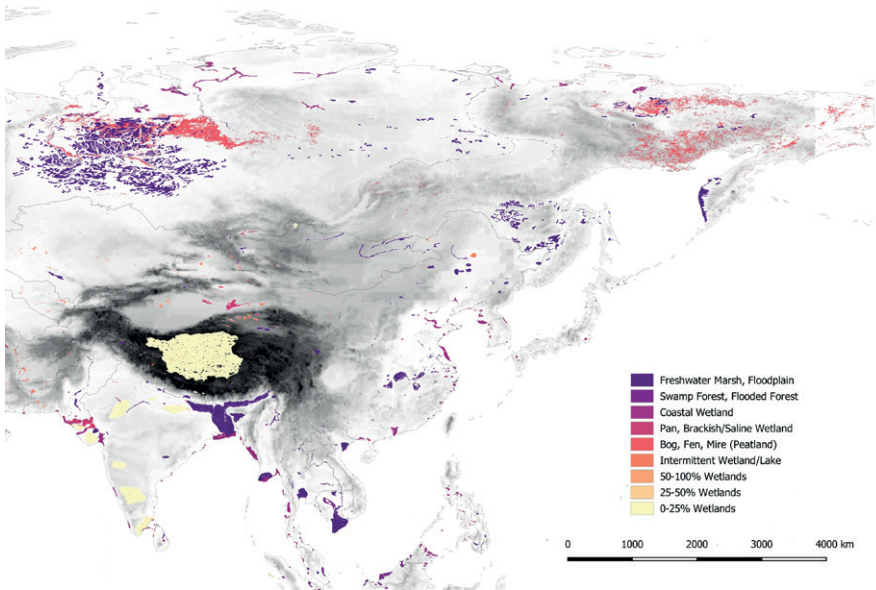
**Appendix S2.9:** Wetlands distribution in South America classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).



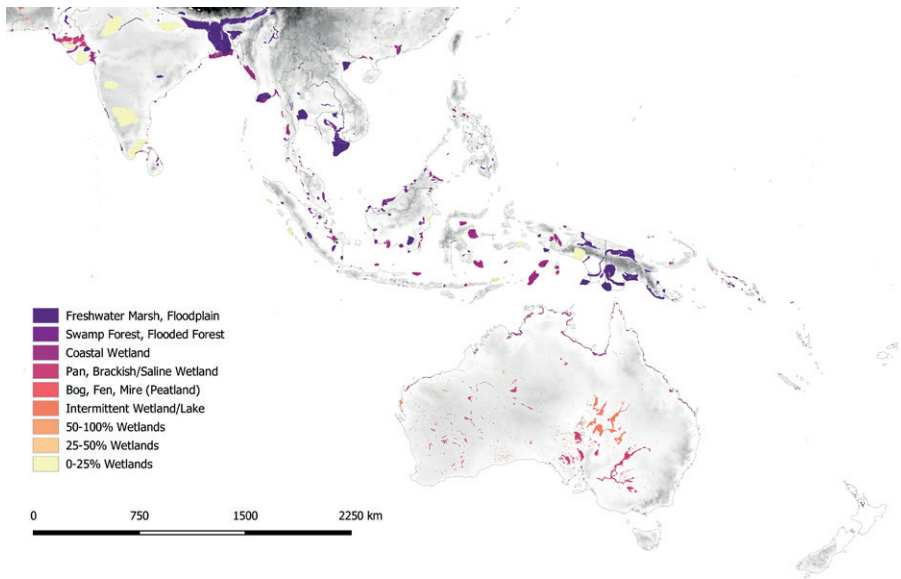
**Appendix S2.10:** Wetlands distribution in Africa classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).



**Appendix S2.11:** Wetlands distribution in Europe classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).



**Appendix S2.12:** Wetlands distribution in Asia classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).



**Appendix S2.13:** Wetlands distribution in Oceania classified by humid habitat categories (excluding lakes, rivers and water reservoirs). Data has been obtained from GLWD-3 package from Lehner and Döll (2004). Maps have been prepared with QGIS Software (V.3.4 Madeira).

**Appendix S2.14:** Species or bat guilds identified through the questionnaire (Appendix S2).

Bat guilds	Total
Full assemblage	47
Carnivorous	1
Frugivorous	10
Insectivorous	57
Nectarivorous	4

Family	Species	Endangered	Near threatened	Least concern
Phyllostomidae	<i>Artibeus</i> spp.			1
	<i>Uroderma</i> spp.			1
Molossidae	<i>Molossus molossus</i>			1
	<i>Myotis dasycneme</i>		2	
	<i>Myotis daubentonii</i>			1
Vespertilionidae	<i>Myotis lucifugus</i>	1		
	<i>Myotis sodalis</i>		2	
	<i>Noctilio</i> sp			1
	<i>Nyctalus noctula</i>			1
	<i>Pipistrellus nathusii</i>			1

**Appendix S2.15:** Summary of all the ecological bat responses towards wetlands reported in the reviewed studies in terms of bat activity.

<b>BAT ACTIVITY</b>	<b>Response</b>	<b>References</b>	<b>Results</b>
		Williams et al. 2006	More than one-half (51%) of all bat activity was detected in riparian woodland habitat whereas riparian marshes were the least used habitat.
		Vindigni et al. 2009	Heliponds and ditches had the highest bat activity as they provided similar food resources than natural wetlands, were easily accessible and also were use as conduits.
		Wermundsen & Siivonen 2008	Wetlands were not positively selected. 10% of the total area of Finland is covered by water, so bats do not need to use riparian habitats like it is in arid conditions.
Negative		Nicholls & Racey 2006	<i>Pipistrellus pipistrellus</i> spent more time foraging in woodland edges than other habitats (e.g. grasslands, agricultural lands or water).
		Zimmerman & Glanz 2000	Wetlands had low bat activity during all seasons, especially during the early autumn due to cold temperatures reducing insect biomass and activity.
		Gerlach & Taylor 2006	Bat foraging was detected in gaps in woodland, but not in open areas (fringes of marsh or littoral habitats).
		Russ & Montgomery 2002	Bats selected rivers, canals and lake/reservoir margins because these habitats provided a rich source of food (aquatic larval stages). Bats avoided habitats with open areas (e.g. grasslands or marshlands).
Neutral		Moore & Best 2018	Freshwater habitats presented higher bat activity than saltwater and brackish waters, yet saltwater habitats had most insects than freshwater and wetlands areas.
		Rogers et al. 2006	Riparian edges, riparian wetlands, wetlands and edges had the highest bat activities.

## Appendix S2.15: Continuation

## BAT ACTIVITY

Response	References	Results
	Palmer & Woinarski 1999	<i>Pteropus alecto</i> roosted in three distinct habitats: during the dry season males and females roosted in bamboo and mangroves; while during the wet season the rainforest was the dominant roosting habitat for both sexes.
Neutral	Davidson et al. 2006	<i>Pipistrellus pygmaeus</i> selected riparian habitats as feeding zones (including swamps, fens, marshlands, lakes). <i>Pipistrellus pipistrellus</i> selected significantly deciduous woodland above all other habitats except for riparian habitats and grasslands.
	Womack et al. 2013	A colony of Indiana bats presented a strong relationship between habitat selection and canopy cover, distance to water and land cover. All bat locations were <1.5 km of water, so no individuals were ever truly distant from water.
	Nelson & Gillam 2016	Bats selected marsh, mixed forest, shrubs, and stream habitat.
	Brooks & Ford 2005	The northern myotis was recorded (+ feeding-buzz sequences) significantly more often in closed-canopy vernal pool and stream habitats than in open-canopy habitats.
	Walsh & Harris 1996	Bats showed a stronger preference for woodland edges and all water bodies than for any other habitat type. Sandy, shingle or rocky beaches and estuarine coastal marshes were significantly selected as foraging areas.
Positive	Toffoli & Rughetti 2017	<i>Myotis sp.</i> , <i>Eptesicus serotinus</i> and <i>Hypsugo savii</i> were recorded hunting only in natural wetlands. <i>Rhinolophus ferrumequinum</i> was detected only in natural wetlands. The importance of natural wetlands is underlined.
	Mildenstein et al. 2005	<i>Pteropus vampyrus</i> and <i>Acerodon jubatus</i> used both disturbed and non-disturbed areas but both positively selected lowland dipterocarp forests, beaches and mangroves.

## Appendix S2.15: Continuation

## BAT ACTIVITY

Response	References	Results
	Menzel et al. 2005	Forest locations in the absence of water (wetlands) presented extremely low bat activity (both above and below the canopy). The absence of water was related to low levels of insects.
	Coleman et al. 2014	Females of <i>Myotis lucifugus</i> selected riparian forests and woodlands, followed by open waters and wetlands.
	Gonsalves et al. 2013	All bat species were recorded in forest habitats, whereas 12 and 11 species were present in saltmarshes and urban habitats. Forests habitats presented more feeding-buzzes followed by saltmarshes and urban habitats.
Positive	de Jong 1994	Most of the time the bats hunted close to lakes and wetlands. These habitats cover only a small part of the total area but were positively selected.
	Lisón & Calvo 2013	Three bat species showed a strong preference for watercourses and wetlands, reflecting the importance of aquatic habitats as critical resources for bats in semi-arid landscapes.
	Popov et al. 2019	Sorokaoziorki wetlands were considered of high ecological-value due to its highest bat activity and richness according to the Ramsar criterion.
	Blakey et al. 2017	Flooded habitats supported higher bat activity and richness than dry habitats across a large river basin. The importance of wet habitats during dry periods was linked to the emergent aquatic insects in water sources.
	Šuba et al. 2012	<i>Pipistrellus nathusii</i> was more frequently recorded (more feeding-buzzes) in wetland habitats than in the meadows and forest habitats.





## Appendix S2.15: Continuation

## BAT ACTIVITY

Response	References	Results
Positive	Popa-Lisseanu et al. 2009	Bat activity was highest in riparian and marsh areas, possibly because of higher density of insects. The Doñana marshlands were considered of high importance as foraging grounds for the giant noctule populations.
	Johnson & Lacki 2013	Both wetlands and deciduous forests were essential habitats for the Rafinesque bat big-eared. Reproductive females generally had their home ranges close to the wetlands.
	Flaquer et al. 2009	Wetland habitats, along with riparian vegetation were found to provide key foraging sites for <i>Pipistrellus nathusii</i> species. This species avoided rice paddies and preferred natural wetlands during the study period.
	Blakey et al. 2018	Bats were more active over wetlands than surrounding dry habitats. Wetland importance increased with increasing aridity, likely reflecting the importance of wetlands as drinking and foraging habitats.
	Lookingbill et al. 2010	Bats with moderate or small home ranges preferred to forage near wetlands. A network of well-connected wetlands for these bat species provided both roosting and foraging sites.
	Veilleux et al 2009	Bat foraging activity occurred in forest, with 17 and 15% of foraging activity observed in open habitats and wetland habitats (including an 18-ha pond).
	Kerbiriou et al. 2018	Bat activity average on quarries had the same order of magnitude than in numerous habitats but appears to be lower in gravel-sand pit stages (restoration process) than in bodies of water (wetlands)
	Ford et al. 2006	The study confirms the importance of riparian and wetland areas as foraging habitats for most species of bats in the Savannah River Site, except for southeastern myotis.

## Appendix S2.15: Continuation

## BAT ACTIVITY

Response	References	Results
	Limpert et al. 2007	Red bat roosts are close to open waters, such as wetlands or streams. These results indicate that both streams and wetlands represent optimal habitat for red bats, presumably for foraging.
	Moore et al. 2017	Bats foraging activity along the Illinois River may have been over adjacent wetlands or riparian forests. Results on the habitat use by gray bats highlighted the need to manage the landscape with emphasis on water bodies.
	Ciechanowski 2015	Bats strongly selected water bodies (both stagnant and running) used as either foraging habitat or as drinking sites. <i>N. noctula</i> strongly selected only lakes and ponds, rivers and canals and coastal lagoons.
Positive	Salsamendi et al. 2012	Foraging bat activity increased considerably at distances below 500 m from water bodies. A network of small wetlands and water bodies around the colonies of major importance would likely translate into a greater carrying capacity for <i>Rhinolophus mehelyi</i> increasing insect abundance and drinking spots.
	Thomas & Jung 2019	The presence of water had a stronger influence on bat activity than forest cover, developed land cover, nor edge density. Little brown bat activity was higher at sites associated with water (wetlands, lakes, and rivers).
	de Jong & Ahlén 1991	Bat foraging activity was close to lakes and wetlands. Within the coniferous area, lakes and wetlands were used the most. These habitats cover only a small part of the total area but were positively selected.



## Appendix S2.15: Continuation

## BAT ACTIVITY

Response	References	Results
	Bergeson et al. 2013	<i>Myotis sodalis</i> selected hydric habitats for foraging (i.e. wetlands and bottomland hardwood forests) and open water (i.e., temporal pools). <i>Myotis lucifugus</i> typically also selected hydric habitats and open water.
	Parker et al. 2019	After a wetland construction, total bat activity was significantly higher at the wetland sites than the control sites (no wetlands). <i>Lasiurus borealis</i> , <i>Lasiurus cinereus</i> and <i>Pipistrellus subflavus</i> increased their activity.
Positive	Joshua & Gates 2008	Total bat activity and eastern red bat activity were similar among forested areas, freshwater pools and bayside marshes. In shrublands, total bat activity and eastern red bat activity were higher than at beach areas, lower than in forested areas and similar at freshwater pools and bayside marshes.
	Oprea et al. 2009	Habitats having higher bat richness were Caraís lagoon and <i>Clusia</i> shrubs.
	Straka et al. 2016	Bat activity and species richness were higher in wetlands than in non-wetland habitats in urban environments.
	Bucci et al. 2010	Nine bat species were detected most often in the marsh vegetational association. Riparian and marsh vegetational associations had the highest overall activity, possibly because of higher density of insects.
	Nicholls & Racey 2006	Foraging time of <i>Pipistrellus pygmaeus</i> was recorded principally in riparian woodland, natural grassland and over water.

## Appendix S2.15: Continuation

## DIVERSITY

Responses	References	Results
Neutral	Andrade et al. 2008	Woodlands and mangrove forests were relatively similar according to both Jaccard's CJ (64.28%) and Sørensen's CS (78.26%) indices. <i>Terra firme</i> forest: 217 individuals and 14 species; mangrove forest: 221 individuals and 18 species.
Positive	Parker et al. 2019	Richness and diversity increased after wetlands construction. Species diversity and species richness were also higher at wetland sites compared to control sites (non-wetland).

## PRESENCE/ABSENCE

Responses	References	Results
Negative	Silveira et al. 2018	<i>Artibeus planirostris</i> mostly occupies the Pantanal habitats (> 80% of occupancy probability), areas with around 16 or more trees per hectare. The pristine habitats with low probability of occupancy mainly include permanent ponds and the surrounding grassland areas seasonally submitted to deep and long floods.
Neutral	Rancourt et al. 2005	<i>Myotis evotis</i> selected relatively open, rocky habitats in close proximity to forest edges and water was not a limiting factor. Like in other studies with bats in the Pacific Northwest, distance to permanent water did not appear to be a driver in roost-site selection.
Positive	Lucas et al. 2015	Most roosts (67.4%) were in water tupelo ( <i>Nyssa aquatica</i> ) in semi-permanently flooded and saturated areas. The majority of roosts were in semi-permanently flooded areas followed by seasonally flooded areas. Few roosts were in saturated, temporarily flooded, or upland sites.



## Appendix S2.15: Continuation

## PRESENCE/ABSENCE

Responses	References	Results
	McConville et al. 2013	All roost trees, except for three, were located on the Hunter River in two patches of mangrove forest. Mangrove forests provide benefits as roosting habitat for bats such as a high abundance of hollow-bearing trees, stable microclimate and potentially fewer predators and competitors
	Lumsden et al. 2002	Only 17% of roosts were in remnant vegetation in the farmland mosaic with 83% in the floodplain forest. All maternity roosts were in the extensive floodplain forest, between 4–10 km from foraging areas. The extra water available in floodplain forests may provide productive environments for invertebrates.
Positive	Trousdale & Beckett 2005	Bat roosts were usually located closer to permanent sources of water. Five trees were located beside depressions within the floodplain where water seasonally pooled. Over most of their study area <i>Nyssa</i> and <i>Magnolia grandiflora</i> were restricted to creek bottoms and floodplains.
	Gooding & Langford 2004	The swamp forest represented 32.2 to 87.2% of the habitat used by radiotagged bats. Roost trees of <i>Corynorhinus rafinesquii</i> found in their study also were located in swamp forest habitat
	Cruz & Ward 2016	Absence of permanent water (>200 m away) was the best predictor of habitat suitability. Steep slopes may accelerate roost loss, prevent the formation of preferred foraging areas such as wetlands, and alter microclimatic conditions.
	Limpert et al. 2007	Red bats select roosts in mature riparian forests near trails, open water, and wetlands. These results may indicate that open areas over streams and wetlands represent optimal habitat for them, presumably for foraging.







### Chapter 3

*Winter bat activity: the role of wetlands as food and drinking reservoirs under climate change*





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## Chapter 3

### Winter bat activity: The role of wetlands as food and drinking reservoirs under climate change

#### ABSTRACT

Bat arousals during hibernation are related to rises in environmental temperature, body water loss and increasing body heat. Therefore, bats either hibernate in cold places or migrate to areas with mild winters to find water and insects to intake. During winter, insects are abundant in wetlands with mild climates when low temperatures hamper insect activity in other places. However, the role of wetlands to sustain winter bat activity has never been fully assessed. To further understand bat behaviour during hibernation, we evaluated how the weather influenced hibernating bats, assessed the temperature threshold that increased bat arousals, and discussed how winter temperatures could affect bat activity under future climate change scenarios. The effects of weather and landscape composition on winter bat activity were assessed by acoustically sampling four different habitats (wetlands, rice paddies, urban areas and salt marshes) in the Ebro Delta (Spain). Our results show one of the highest winter bat foraging activities ever reported, with significantly higher activity in wetlands and urban areas. Most importantly, we found a substantial increase in bat activity triggered when nocturnal temperatures reached ca. 11°C. By contrasting historical weather datasets, we show that, since the 1940s, there has been an increase by ca. 1.5°C in winter maximum temperatures and a 180% increase in the number of nights with mean temperatures above 11°C in the Ebro Delta. Temperature trends suggest that in 60-80 years, winter months will reach average temperatures of 11°C (except maybe in January), which suggest a potential coming interruption or disappearance of bat hibernation in coastal Mediterranean habitats. This study highlights the significant role of wetlands in bat conservation under a climate change scenario as these humid areas represent one of the few remaining winter foraging habitats.

**Keywords:** bioacoustics, bat activity, climate change, echolocation, habitat use, hibernation, wetlands



### 3.1. INTRODUCTION

Since the Industrial Revolution, human activities have given rise to an exponential increase in greenhouse gas concentrations, which have led to environmental changes, including a rise in global temperatures (Trenberth, 2018) and a greater recurrence of extreme weather events such as heatwaves (Lhotka et al., 2018). These alterations – known collectively as climate change (Trenberth, 2018) – affect the dynamics of many habitats and their fauna, examples including a reduction in habitat suitability for drought-sensitive tree species (Morán-Ordóñez et al., 2021) and an increase in the severity of droughts (Schlaepfer et al., 2017).

Habitat loss has led to a generalised global decline in biodiversity, epitomised by the 45–75% decrease in insect biomass (Hallmann et al., 2017; Wagner, 2020) and a 30–40% decrease in terrestrial vertebrate populations (Ceballos et al., 2017). Indeed, these rates of decline could even speed up due to rising temperatures linked to climate change. It has been suggested that droughts will be the primary drivers of extinction in non-dispersing species such as amphibians due partly to their limited dispersal capacity and the loss of aquatic environments (Araújo et al., 2006). Conversely, other taxa, such as certain mammals, which as endotherms can generally acclimatise to new habitats by adjusting their body temperatures (Huey et al., 2012), will be obliged to change their behaviour or shift their distribution ranges to cope with novel environmental conditions (Ancillotto et al., 2016; Root & Schneider, 2002, Smeraldo et al., 2021).

Thermoregulation in mammals is defined as the regulation of the core internal temperature to compensate for changes in environmental temperatures and maintain the equilibrium of internal homeostasis by metabolic and physiological changes (Terrien et al., 2011). Mammals such as bats employ thermoregulation adaptations known as ‘torpor’ or ‘thermo-conforming’ (Barclay et al., 2001; Geiser & Baudinette, 1990) to maintain their body temperatures near or at the environmental temperature. Torpor is an energy-saving strategy used by bats either during the daytime or during long periods of low temperatures during hibernation (deep torpor) (Baloun & Guglielmo, 2019; Speakman & Rowland, 1999). To survive harsh environmental conditions (e.g. cold winter) with low prey availability, insectivorous bats in temperate latitudes tend to overwinter during the cold season (Dunbar & Brigham, 2010; McNab, 1982; Wojciechowski et al., 2007), and it is generally assumed that, except for a few bat species (e.g. *Tadarida teniotis*), bats remain completely passive during the winter. However, some studies have reported that on warm winter nights, insectivorous bats in temperate regions awake and forage (Avery, 1986; Barros et al., 2017, 2021; Lausen & Barclay, 2006; Zahn & Kriner, 2014), observations that underline the general lack of knowledge about winter bat activity.

Arousal periods result from abrupt rises in environmental temperatures, a fall to freezing temperatures, or human disturbance (Davis, 1970; Speakman et al., 1991; Thomas, 1995). When a bat awakes from hibernation, its increase in body heat implies energy consumption, so insectivorous bats need to forage in areas with a high concentration of insects (Avery, 1986; Hope et al., 2014; Turbill, 2008). Recent studies suggest that arousal bouts are mainly related to water loss and dehydration and that bats with greater water evaporation rates awake more often than ones with lower rates (Ben-Hamo et al., 2013; Klüg-Baerwald & Brigham, 2017). Thus, bats are also assumed to arouse to drink and hydrate before returning to hibernation. To compensate for water and energy loss, or to minimise arousals, bats hibernate in cold places with low temperatures and relatively high humidity (ca. 99%) or migrate to areas with mild winters where they can find water and insects to feed upon (Klüg-Baerwald & Brigham, 2017; Turbill & Geiser, 2008; Zahn & Kriner, 2014).

In temperate areas, wetlands host essential biomass of insects and freshwater for bats during winter nights (Duffy & LaBar, 1994) and are crucial as “productive environments” even at low temperatures (Lindsay et al., 2015). Thus, their strategic location and connection to roosting sites (Lookingbill et al., 2010) are vital aspects favouring or impeding their use as hunting grounds in winter. Recent reviews of bat research in aquatic habitats have reported that most studies are commonly carried out in summer, thereby highlighting a critical gap in ecological studies of bat hibernation (Mas et al., 2021; Salvarina, 2016). Wetlands are decreasing at alarming rates worldwide (Hu et al., 2017), and the predicted increase in temperatures due to climate change is likely to affect bat resilience in winter and their conservation (Robinson et al., 2005). Despite this, little research has addressed the effects of increasing winter temperatures on bats, especially in Mediterranean wetlands (Mas et al., 2021).

New remote-sensing technologies such as passive acoustic detectors now enable us to survey much more efficiently insectivorous bats in open habitats such as deserts or wetlands over long periods of time (Conenna et al., 2019; Domer et al., 2021; Silva & Bernard, 2017). Bioacoustics can improve the understanding of bat behaviour during hibernation at a fine-scale that was never previously possible. In this study, we assessed the use of wetlands in winter by bats, evaluated the weather conditions that favour bat arousals, and used historical climate data to discuss potential changes in a future bat winter activity. Specifically, the aims of our project were to i) determine whether wetlands are winter bat foraging and drinking hotspots compared to surrounding habitats (i.e. urban areas, dry rice paddies and salt marshes); ii) describe differences in bat activity patterns and seasonality in each habitat; iii) model the effect of environmental and climatic variables (temperature, precipitation, wind speed and habitat type) on bat activity; iv) establish the minimum night-time temperature for bat detections and the temperature that triggers a rapid increase in bat winter activity

(massive arousal); v) predict and discuss how climate change will potentially affect bat activity due to temperature trends. We hypothesised that wetlands would represent an essential habitat during winter as foraging grounds and that there would be a greater amount of bat activity throughout the winter, but that bats would only be active during the first hours of the night in these habitats. We also predicted a negative effect for precipitation and wind on bat activity and expected the temperature to be the most accurate predictor. Finally, we expected to find the temperature threshold that triggers bat winter activity at ca. 10°C, as previously assumed for other habitats (Barros et al., 2021); value that is likely to rise in future winters due to climate change.

## 3.2. MATERIAL AND METHODS

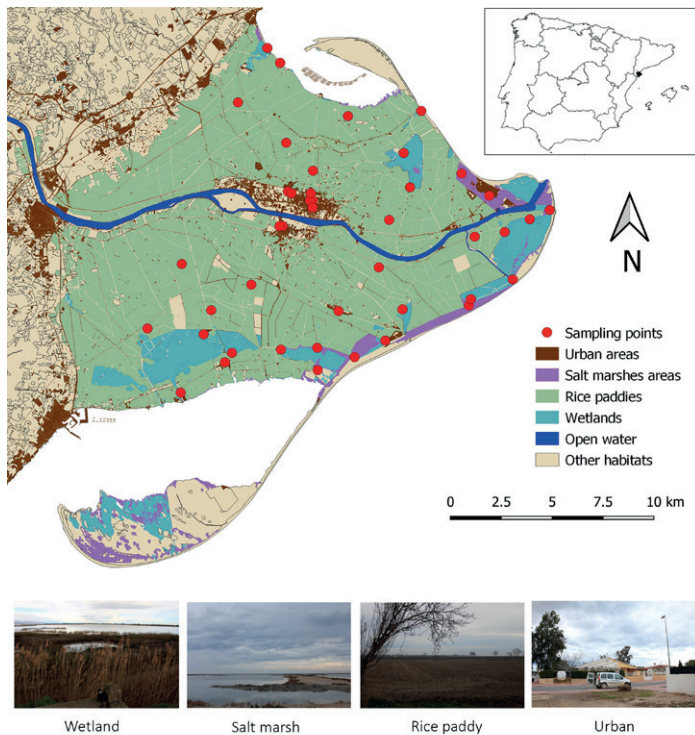
### Study area

The study was carried out in the Ebro Delta, one of the largest river deltas in Western Europe (NE Iberian Peninsula; 40.704776 N, 0.740710 E; Fig. 3.1). This delta is an excellent study site and model area for investigating bat responses to climate change. It is known to host a large population of Mediterranean pipistrelle bats, including opportunistic and migratory species that roost in and around natural wetlands and extensive rice paddies, and there is a long history of bat research in the area (e.g. Flaquer & Jarillo, 2003; Flaquer et al., 2005, 2006, 2009; Montauban et al., 2021; Puig-Montserrat et al., 2015). This delta covers about 320 km<sup>2</sup>, penetrates around 25 km into the sea and is formed principally of sands, clay and mud washed down by the river Ebro. It harbours a mosaic of wetlands (ca. 65 km<sup>2</sup>), rice paddies (ca. 203 km<sup>2</sup>), salt marshes (ca. 20 km<sup>2</sup>) and built-up areas (ca. 16 km<sup>2</sup>) (Fig. 3.1; Curcó, 2006; Puig-Montserrat et al., 2015). Small built-up areas, as well as isolated buildings in and around the rice paddies, are scattered throughout the delta. Differences in the composition of plant species depend on the habitat and its distance from the sea (see Table S3.1). During winter, wetlands are the only habitats that offer freshwater availability for wild fauna, as water channels and rice paddies are completely dry, and the presence of other sources of water such as ponds and pools in urban areas are scarce, and most of them are empty (Ancillotto et al., 2019; Nystrom & Bennett, 2019). Average annual temperatures oscillate between 16–18°C, with a minimum in January (ca. 9°C) and a maximum in August (ca. 27°C). The annual total rainfall lies in the range 445–627 mm (Curcó, 2006).

### Acoustic surveys

The study was performed in January–March in two successive winters (2016 and 2017). We surveyed aerial insectivorous bats at 40 sampling sites, with ten sites

randomly distributed in each of four different habitats: wetlands, urban areas, salt marshes and dry rice paddies. Sampling sites were selected so they would have easy accessibility, low human frequentation and were located far from habitat edges (usually more than 50 m). Five or six acoustic detectors (SM2Bat+, SM3Bat and SM4Bat; Wildlife Acoustics, Maynard, USA) with multidirectional microphones (SMX\_US, SM3\_U1 and SMM\_U1, respectively) were used to record bat activity. They were placed simultaneously and programmed to record for seven whole nights per survey period from dusk till dawn (frequency range: 256kHz and high-pass filter set at 12 kHz, with the minimum trigger level at 12dB), as recommended in bat monitoring guidelines ([www.batmonitoring.org](http://www.batmonitoring.org)). After each survey period, all detectors were randomly moved to other sampling sites. Microphones were placed 1–2 meters above ground level to avoid echoes in the recordings and focused to the sampled habitat. Due to the reduced availability of sampling areas for some habitats (e.g. salt marshes), to guarantee the independence of the recorded data, all detectors were located at least 250 m from the nearest sampling site, so bats could never be recorded by two detectors simultaneously (Adams et al., 2012; Monadjem et al., 2017; Voigt et al., 2021).



**Figure 3.1:** Study area in the Ebro Delta with the distribution of all the acoustic sampling sites with photographs of each surveyed habitat. Font: map downloaded and adapted from land cover maps of Catalan Habitat Cartography (Departament Territori i Sostenibilitat 2018, <http://territori.gencat.cat/>) using QGIS v.3.4 Madeira (Boston, USA).

## Bioacoustics analysis

To standardise the acoustic data, all recordings were pre-processed and separated into smaller files with a maximum duration of five seconds using Kaleidoscope software v.4.3.2. (Wildlife Acoustics, Maynard, USA). As acoustic data cannot be processed at the individual level, the most widely used surrogate for abundance is 'bat activity', measured as the number of bat passes per time unit (Azam et al., 2015). A bat pass is taken as a sound file of five seconds containing a minimum of two distinguishable bat echolocation calls from a particular species (Adams et al., 2005; Law et al., 1998; Millon et al., 2015). All acoustic data was pre-analysed and automatically classified using the Tadarida classifier for European bat species (Bas et al., 2017). Afterwards, all classifications were manually post-validated to avoid species misidentifications (false positives or false negatives) using Avisoft-SASLab Pro's program v.5.2.15 (Avisoft Bioacoustics, Glienicke/Nordbahn, Germany). Bat recordings were classified to species level (Middleton et al., 2014; Russ, 2012; Russo & Jones, 2002) or as mixed groups (phonic groups) if bat calls could not be assigned to a specific species (e.g., *Eptesicus/Nyctalus* or *Myotis* sp.) (Tuneu-Corral et al., 2020). As suggested by Montauban et al., (2021), the phonic group *Pipistrellus pygmaeus/Miniopterus schreibersii* and the species *P. pipistrellus* were assigned to *P. pygmaeus*. Likewise, the phonic group *P. kuhlii/nathusii* was assigned to *P. nathusii* given the absence of captures of *P. kuhlii* in over 20 years of bat research, hundreds of reports for *P. nathusii*, and the fact that the Ebro Delta represents an optimal habitat for *P. nathusii*. All social calls and feeding/drinking buzzes were noted during the classification process.

## Environmental variables

Habitats were separated into four types – urban areas, rice paddies, salt marshes and wetlands using vectorial land cover maps (scales 1:50 000 with a minimum polygon size in 1 ha) from the Catalan Habitat Cartography 2018 (<http://territori.gencat.cat>). All the geographical analyses were conducted with QGIS v.3.4, Madeira (Boston, USA).

Temperature, wind speed and precipitation were obtained from a meteorological station on the Illa de Buda (Ebro Delta) belonging to the Catalan Meteorological Service ([www.meteo.cat](http://www.meteo.cat)). Due to the great homogeneity of the landscape and its proximity to the sea, climatic variables were assumed to be constant throughout the delta. The maximum, mean and minimum of all climatic variables were calculated per night (temperatures were averaged from sunset to sunrise) and were averaged per hour specifically for the activity patterns. The maximum daily temperature was also calculated (from sunrise to sunset). All the climatic variables collected by the Catalan Meteorological Service at this meteorological station were recorded every half hour.

Historical temperature trends were calculated using a dataset with information for the coldest months (January and February) from 1940–2020, obtained from Observatori de l'Ebre ([www.obsebre.es](http://www.obsebre.es)). In this case, temperatures were recorded hourly.

## Data analyses

To assess the effect of habitat type and climatic conditions on winter bat activity (number of bat passes/night), the influence of environmental and climatic variables (categorical and numerical predictors, respectively) on total bat activity was modelled using Generalised Linear Models (GLMs) built with the `glm` function from the *stats* R package. A negative binomial family (NB) was run using the 'log' link function to account for overdispersion. All numerical predictors were scaled from zero to one using the *rescale* function from the *scales* R package (Wickham, 2018). Autocorrelation between predictors was checked using Spearman's rho correlations (Crawley, 2012); maximum and minimum wind speed and minimum temperature variables were excluded. In order to evaluate the multicollinearity between predictors, the variance inflation factor (VIF) was calculated using the function *vif* from the *regclass* R package (Petrie, 2020). All predictors had VIF values <2, and therefore, all were kept for the model. The precipitation variable was excluded since there were very few days of rain. Finally, the model included the mean night-time temperature, the maximum daily temperature, the mean wind speed and the habitat type as predictors. Significant differences between habitats were tested with a Post-Hoc Tukey pairwise comparison test (Zuur et al., 2010) using the *multcomp* R package (Hothorn et al., 2008). The effect of the categorical variable habitat was plotted using the *allEffects* function from the *effects* package.

To estimate the effect of climatic variables on bat occurrence (rather than relative abundance), the previous response variable (bat activity) was transformed into a binary format (presence/absence per hour) and modelled using a GLM with a binomial distribution. To estimate the temperature that triggers winter bat occurrence, the inflexion point of the estimated model was calculated using the function *changept* from the *ShapeChange* package (Liao & Meyer, 2016). Finally, to establish the minimum temperature at which bats were active in the Ebro delta, we provide the minimum temperature at which bats were recorded throughout the sampling period.

To quantify the temperature change along the period 1940–2020, a linear regression was used with the number of nights with mean night-time temperatures above the temperature threshold registered per year. Additionally, the number of night-hours per year with temperatures exceeding the temperature threshold was summarised and plotted. Finally, the maximum daily temperature for each winter was



extracted and compared for the period 1940–2020 using a linear model.

In order to estimate how long it will take for bats to stop hibernating, we used monthly average minimum temperatures from four IPCC scenarios: 2021–2040, 2041–2060, 2061–2080 and 2081–2100 ([www.worldclim.org](http://www.worldclim.org)). Global Climate Model (GCM) MIROC-ES2L (Hajima et al., 2019) with the Shared Socio-economic Pathways 585 (ssp585) were used for climate projections based on the methodology used in Bilgin et al., (2012). We calculated the average minimum temperature for the Ebro Delta region for each period using the software QGIS v.3.4, Madeira (Boston, USA). The climatic data was downloaded with the spatial resolution of 2.5 minutes (ca. 4.5km) to get more predicted temperatures matching our study area.

All statistical analyses were carried out with R v.4.1.1 (R Core-Team, 2021).

### 3.3. RESULTS

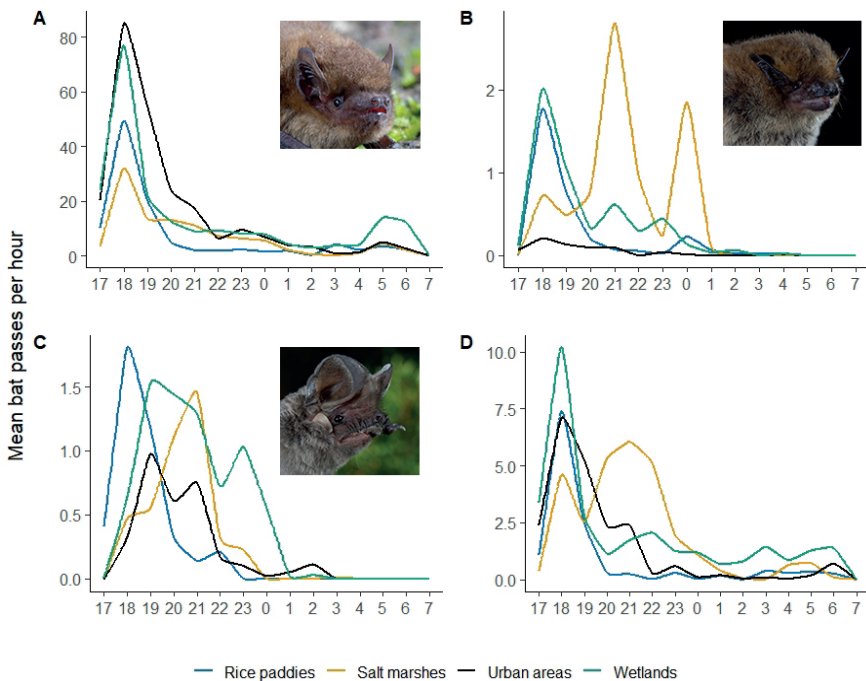
During the two sampled winters, we recorded a remarkably high – and unexpected – level of bat activity (164±18 passes/night-detector on average). The minimum temperature value with bat activity was 5.4°C, and the suggested nocturnal temperature value that triggers bat activity was 11.02°C. According to our models, the night-time temperature is the key factor causing bat winter arousals. If increasing temperature trends persist, bats could stop hibernating in ca. 60–80 years across the coastal Mediterranean regions.

We recorded on a total of 469 nights-detector (6,122 recording hours) and gathered 76,920 echolocation bat passes, 21,063 recordings of social calls and 10,423 feeding/drinking buzzes. We found significant differences in total bat activity between years: 28,606 bat passes were recorded with an effort of 271 nights-detector (3,534 hours) in 2016, while in 2017, 48,594 bat passes were recorded during only 198 nights-detector (2,589 hours). In terms of mean bat passes per habitat, we obtained 209±36 passes/night in wetlands and 237±38 in urban areas, but only 107±19 bat passes/night in rice paddies and 107±42 salt marshes.

In total, we recorded bat activity on 388 nights (83% of the total). We identified five bat species (*P. pygmaeus*, *P. nathusii*, *Barbastella barbastellus*, *Rhinolophus ferrumequinum* and *T. teniotis*), along with three phonic groups (*Eptesicus/Nyctalus* sp., *Myotis* sp. and *Plecotus* sp.). The most recorded bat species/phonic group was *P. pygmaeus* (72,766 bat passes), followed by *T. teniotis* (2,087), *P. nathusii* (1,928), *Myotis* sp. (55) and *Eptesicus serotinus/Nyctalus* sp. (47) (Table 3.1).

To assess bat activity patterns in each habitat, we selected the three most detected species representing 99.82% of all bat recordings (Table 3.1, Fig. 3.2). Our results

showed that winter bat activity was concentrated during the first six hours after sunset, with an activity peak within the first three hours (Fig. 3.2). These activity patterns did not differ during the winter. Despite detecting an activity peak for *P. pygmaeus* one hour after sunset in all habitats (Fig. 3.2A), patterns for the remaining species were unclear. *Pipistrellus nathusii* had activity peaks in wetlands and saltmarshes during the first six hours after sunset but then clearly reduced its activity after midnight, (Fig. 3.2B). For *T. teniotis*, activity patterns were erratic, albeit more or less evenly distributed during the first six hours after sunset, with a drastic decrease in activity after midnight (Fig. 3.2C). Feeding and drinking buzzes – mostly from *P. pygmaeus* – showed the same pattern for all habitats, with a peak one hour after sunset and then low but constant levels throughout the rest of the night (Fig. 3.2D).



**Figure 3.2:** Bat activity patterns during winter nights. Mean bat passes/hour in each habitat. **A)** *Pipistrellus pygmaeus*; **B)** *Pipistrellus nathusii*; **C)** *Tadarida teniotis*; **D)** Drinking and feeding buzzes. The x-axis shows the night sampling hour in Coordinated Universal Time (UTC).

Wetlands and urban areas were the most used habitats, with 26,108 and 25,387 bat passes, respectively (Tables 3.2-3.3; Fig. 3.3A). We recorded a few contacts for the phonic groups *Myotis* sp. and *Plecotus* sp. in salt marshes and rice paddies (Tables 3.1-3.2; Figs. 3.3A-3.3B), while *Eptesicus serotinus*/*Nyctalus* sp. was equally recorded in all habitats. 34% of feeding and drinking buzzes were recorded in wetlands, followed by salt marshes (31%) and urban areas (21%). Finally, almost 60% of recordings of social calls were registered in urban areas (Table 3.1).

**Table 3.1.** Number of bat passes, social calls and drinking/feeding buzzes recorded in each habitat for all identified bat species and phonic groups. RBP indicates the total percentage (%) of bat passes per species. (n) represents the number of nights recorded per year.

Bat species and phonic groups	2016 (n=271)			2017 (n=198)			Total	RBP
	Wetland	Rice paddies	Salt marshes	Wetland	Rice paddies	Salt marshes		
<i>Pipistrellus pygmaeus</i>	9805	3536	3225	10180	14840	8795	72766	94.60
<i>Pipistrellus nathusii</i>	223	259	58	44	389	846	1928	2.51
<i>Tadarida teniotis</i>	775	106	6	203	76	471	2087	2.71
<i>Eptesicus serotinus/Nyctalus sp.</i>	2	14	0	0	18	6	47	0.06
<i>Rhinolophus ferrumequinum</i>	0	0	0	0	6	3	9	0.01
<i>Barbastella barbastellus</i>	0	1	0	0	0	0	1	0.00
<i>Myotis sp.</i>	0	5	44	1	0	0	55	0.07
<i>Plecotus sp.</i>	0	6	1	0	0	0	27	0.04
<b>Total</b>	<b>10805</b>	<b>3927</b>	<b>3334</b>	<b>10428</b>	<b>15329</b>	<b>10121</b>	<b>76920</b>	<b>100</b>
Drinking/feeding buzzes	1017	224	149	599	2474	3171	10423	
Social calls	1890	720	962	2537	2144	1294	21063	

Bat activity was significantly influenced by the mean night-time temperature, maximum daily temperature and mean wind speed (Table 3.2; Fig. 3.3B). While the mean night-time temperature was positively related to bat activity, the mean wind speed had a strong negative effect (Table 3.2). High daytime temperatures resulted in increased bat activity the following night (Fig. 3.3B).

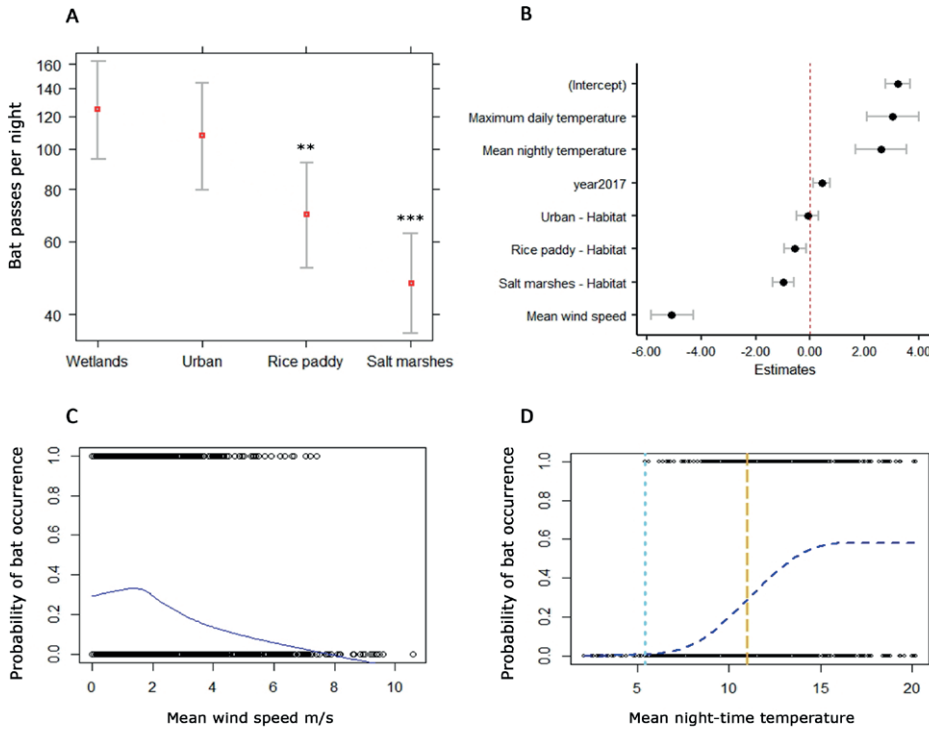
During the two winters, temperatures ranged from a minimum of 2.1°C to a maximum of 20.2°C. Bats were active above 5.4°C (dotted blue line in Fig. 3.3D). However, at ca. 11°C (dashed orange line in Fig. 3.3D), we found an abrupt increase in the probability of bat occurrence (Fig. 3.3D), which started to increase from 8°C and reached a maximum at 15°C. Overall, the probability of recording winter bat activity at temperatures above 15°C remained relatively steady at ca. 54%.

**Table 3.2:** Results of the Generalised Linear Model with negative binomial family (GLM-NB). The response variable is total bat activity/night. The categoric variable ‘Wetland habitat’ was used as a baseline for model comparisons between habitats. Significance codes: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ .

Predictors variables	Estimate	Std. Error	Z value	P-value	
(Intercept)	3.221	0.234	13.780	<2e-16	***
Rice paddies	-0.560	0.203	-2.758	0.006	**
Salt marshes	-0.975	0.196	-4.967	6.79e-07	***
Urban areas	-0.085	0.206	-0.413	0.680	
Mean night-time temperature	2.622	0.493	5.319	1.04e-07	***
Mean wind speed	-5.101	0.338	-15.092	<2e-16	***
Maximum daily temperature	3.239	0.479	6.763	1.54e-10	***
Year 2017	0.436	0.149	2.923	0.003	**

**Table 3.3:** Results from the multiple comparisons of habitat means using Post Hoc-Tukey tests. Significance codes: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ .

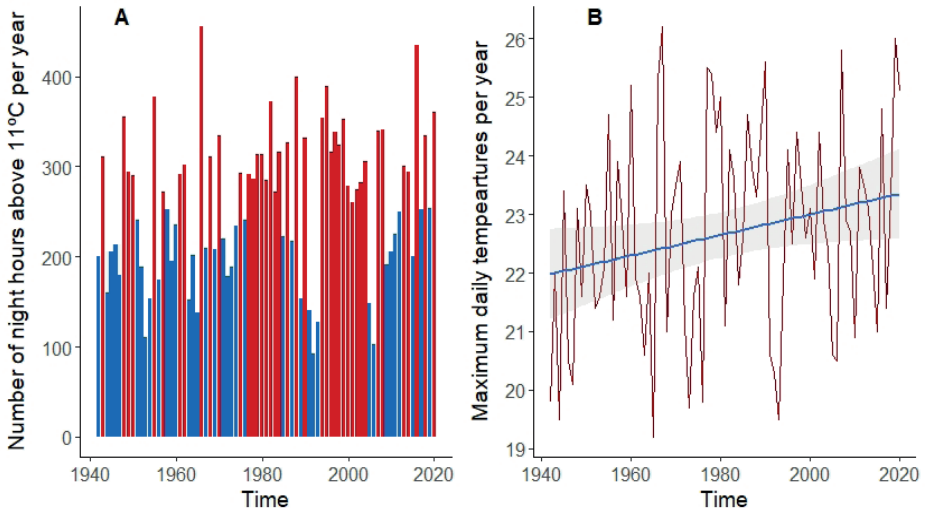
Habitat comparisons	Estimate	Std. Error	Z value	P-value	
Urban-Wetlands	-0.085	0.205	-0.413	0.976	
Rice paddies-Wetlands	-0.560	0.203	-2.759	0.029	*
Salt marshes-Wetlands	-0.976	0.196	-4.973	<0.001	***
Salt marshes-Urban	-0.892	0.205	-4.343	<0.001	***
Salt marshes-Rice paddy	-0.416	0.203	-2.048	0.1705	
Rice paddy-Urban	-0.475	0.211	-2.255	0.109	



**Figure 3.3:** Effects of climatic and environmental variables on bat activity modelled using a GLM with a Negative-Binomial distribution: **A)** Predicted bat activity in the four sampled habitats; \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* indicates significant differences in predicted bat activity compared to wetlands; **B)** Climatic and environmental variables influence on bat activity. Black dots represent the predicted estimates for each variable; bars represent the Interval of Confidence (2.5% and 97.5%); Effects of the specific environmental variables (mean wind speed and mean night-time temperature) on bat occurrence modelled using a GLM with a Binomial distribution: **C)** Predicted effect of mean night-time wind speed on bat occurrence. The blue line shows the probability of bat occurrence according to wind speed (meter/second); **D)** The sigmoidal line represents the estimated value of the probability of bat occurrence according to the mean night-time temperature. The light-blue dotted line indicates the minimum temperature at which bats were recorded, while the orange dashed line indicates the inflexion point of the bimodal logistic curve.

If we considered 11°C as the threshold baseline value that triggers winter bat activity, over the last 80 years, the number of night-time temperature records above 11°C in the Ebro Delta has increased by 180% from approximately 200 in 1940 to 360 in 2020 (Fig. 3.4A). To illustrate this pattern, in 1940, there were 30 winter nights with temperature records above 11°C, while in 2020, there were 50 (see Appendix S3.2). Following the trend of increasing temperatures as predicted in *ssps585*, we found an increase of ca. 2-3°C for the minimum temperatures across the Ebro Delta within 60

years (Table 3.4). According to these predictions, we suggest that in less than ca. 80 years most winter nights will probably have temperatures above 11°C (maybe except during the month of January), impeding bat hibernation (Table 3.4). Furthermore, the highest daily temperature registered each winter since 1940 has increased over the past 80 years by ca. 1.5°C (Fig. 3.4B).



**Figure 3.4:** Trends in winter temperatures (January-February) during the period 1940–2020 in the Ebro Delta. **A)** Each bar shows the total number of night hours above 11°C per year. Red colour represents the years with more hourly records than the average (259), while blue represents those with fewer records; **B)** Maximum daily temperatures registered per year. Data taken from the Observatori de l'Ebre ([www.obsebre.es](http://www.obsebre.es)).

**Table 3.4:** Summary of average minimum temperatures (°C) predicted using the four IPCC Scenarios for the Ebro Delta. The Global Climate Models used were MIROC-ES2L with Shared Socio-economic Pathways 585 (ssp585) in 2.5 minutes spatial resolution (ca. 4,5 km). December, January and February were used as the coldest months for our study area. All data were processed using QGIS v.3.4, Madeira (Boston, USA).

Periods of IPCC scenarios	December's T°C	January's T°C	February's T°C
MIROC-ES2 ssp585 2021-2040	8.1°C	6.7°C	7.5°C
MIROC-ES2 ssp585 2041-2060	8.7°C	7.3°C	8.7°C
MIROC-ES2 ssp585 2061-2080	10.1°C	8.3°C	9.6°C
MIROC-ES2 ssp585 2081-2100	10.9°C	8.9°C	10.9°C

### 3.4. DISCUSSION

This study provides evidence of extremely high winter bat activity in non-forest habitats in the Mediterranean region and highlights the importance of wetlands for bat species during the winter, especially as drinking and foraging reservoirs. Our results show a non-bimodal bat activity pattern during winter, suggesting that arousals only occur during the first six hours of the night. Most importantly, we reveal a minimum temperature of 5.4°C for winter bat records and, for the first time, suggest a winter temperature threshold value of 11.02°C triggering bat arousals. This study could be understood as a cautionary note for future bat studies since we detected non-sporadic bat behaviour during the winter season. Our study suggests that plasticity might be crucial for bat survival in the face of the current and rapid environmental changes, and more alterations in winter bat behaviour in coming decades are to be expected since maximum winter daily temperatures have increased by ca. 1.5°C over the past 80 years. We highlight the fact that the ecological needs of bat populations in winter – above all, in light of the environmental changes predicted by climate change scenarios – are yet not thoroughly understood.

#### Reports of winter bat activity

Winter bat activity is often reported (e.g. North America) on a monthly basis (i.e. Lausen & Barclay, 2006; Treanor et al., 2016; Whitaker et al., 1997). However, in Europe, bats' winter behaviour has never been fully investigated, and studies report, variously, high bat activity (on 50% of January nights) in midwinter (Avery, 1985), occasional and irregular activity on warm evenings (Avery, 1986; Park et al., 1999, 2000), activity on 15–40% of January and February nights for *Pipistrellus* species (Zahn & Kriner, 2014), or reported in all winter months for *Myotis nattereri* (Hope et al., 2014). Most of these European studies have been carried out inside or close to hibernating roosts, and only a few have ever focused on foraging areas. For example, Barros et al., (2017) monitored winter activity at foraging sites and found the greatest bat activity (89.9% of the total) in early winter. Our study reveals that bat activity in Mediterranean coastal regions in winter is more common than previously reported for other habitats (e.g. Barros et al., 2017), especially in open foraging areas such as wetlands (Mas et al., 2021). The winter bat activity reported in this study is equivalent to ca. 10% of the summer activity reported at the same location (see [www.batmonitoring.org](http://www.batmonitoring.org)).

Winter bat activity and the causes of arousal bouts have been attributed to a variety of factors that are still under debate: human disturbances, changes in temperatures and humidity (Davis, 1970) or poor body condition (Hope & Jones, 2012) and dehydration, as occurs in other hibernating mammals (Ben-Hamo et al., 2013; Thomas & Geiser, 1997). Despite this, all authors suggest that these arousal bouts

are associated with foraging or drinking activity, which underscores the importance of habitats where bats can find prey and fresh water in abundance.

### Effects of climatic variables on bat activity

Feeding/drinking buzzes were recorded during the first hours of the night, mainly linked to the foraging or drinking behaviour of *P. pygmaeus*. This bat is common in temperate areas and forages in humid and riparian habitats (Davidson-Watts et al., 2006). Its winter activity pattern differs from the bimodal pattern described for other seasons (e.g. Bartonička & Řehák, 2004) and from its conspecific *P. pipistrellus* (e.g. Swift, 1980).

We found that night- and daytime temperatures and wind speed strongly affected bat foraging in winter. In terms of wind speed, high bat activity was reported below 2m/s and continued up to 8 m/s, which agrees with existing values in the literature (Amorim et al., 2012; Caprio et al., 2020). Some studies in Europe have reported that bat foraging activity mainly occurs on warm, calm winter nights (Avery, 1986; Barros et al., 2017), suggesting that temperature might be one of the best predictors of bat winter activity. Here, we provide a temperature threshold (ca. 11°C) that triggers bat activity in winter. Similar results have been reported by Park et al., (2000) for hibernating bats (i.e. *Rhinolophus ferrumequinum*), which sustain extended arousal episodes when hibernaculum temperatures exceed 10°C. Unlike in other studies (i.e. Barros et al., 2021), we found that, while the probability of bat occurrence increases from 11°C onwards, there is a relatively steady trend when temperatures are above 15°C. However, because mean winter temperatures in the Ebro Delta are ca. 9°C, temperatures above 11°C are relatively uncommon. We thus suggest that bat arousals could be related to either abrupt rises in insect availability given that warm temperatures (>10°C) provide favourable conditions for the emergence of aquatic species (Chippendale, 1991; Nebeker, 1971), or to rapid environmental changes causing dehydration in bats hibernating in non-deep roosts including caves, building cavities and tree-crevices (Turbill, 2008). Cold temperatures seem to affect insect numbers and drastically reduce their activity (Chippendale, 1991), thereby hindering bat foraging activity.

The number of social and echolocation calls recorded in urban areas underlines the use bats make of this habitat as roosting/hibernating sites. The lack of woodland in the Ebro Delta and the absence of nearby rocky areas (more than 5 km from the nearest sample point; Fig. 3.1) could force bats to roost in concrete buildings (urban areas) or non-hibernating wooden bat boxes. Moreover, bats also probably concentrate part of their foraging activity in these areas with artificial light since, as is well-known, night-time lights attract flying insects (flight-to-light behaviour) (Owens & Lewis, 2018).



Artificial roosts (e.g. buildings or bat boxes) are not well insulated from environmental temperatures and absorb the sun's heat, and therefore, they could experience higher temperatures than natural roosts (Martin-Bideguren et al., 2019). According to Turbill, (2008), when bats are exposed to high daily temperatures in winter, they suffer passive warming, increasing their metabolic rates, fat-reserve consumption, and water loss.

### The importance of wetlands for hibernating bats

To cope with the energy they consume and water loss during hibernation, bats use wetlands as foraging areas due to the high concentrations of insects and the availability of freshwater (Mas et al., 2021). Wetlands represent one of the few habitats in the Mediterranean region that remain productive when low temperatures hamper insect activity in other habitats (Duffy & LaBar, 1994; Lindsay et al., 2015). Rice paddies in the Ebro Delta were not widely used in winter, probably due to the absence of water – they were completely dry – and a lack of roost sites, food and water for insects. Therefore, although rice paddies host many volant species in summer (especially birds) and are considered substitutes of natural wetlands, they cannot replace the ecological function of the latter. Salt marshes represent vast areas of vegetation with high concentrations of mineral salts (salinity). MacKenzie, (2005) reported that variations in salinity concentration affect insect production and emergence. Therefore, the high number of echolocation calls and feeding buzzes recorded in salt marshes in 2017 (concentrated in two nights) could be related to massive insect emergences.

Mediterranean wetlands are characterised by stable water dynamics and warm winter temperatures that prevent water from freezing in a region in which the availability of freshwater is limited. These permanent wetlands and their connection to other habitats could increase ecosystem carrying capacity for many bats, especially less mobile species (Lookingbill et al., 2010; Salsamendi et al., 2012). However, the lack of riparian forests or other vertical structures (e.g. cliffs) to act as roost sites in wetlands could hamper their use during critical seasons such as hibernation. Studies carried out by Flaquer et al., (2009) and Puig-Montserrat et al., (2015) have reported that providing bat roosts in wetlands increases bat presence and the use of these habitats.

Wetlands have been reported to be essential for guaranteeing feeding and drinking sites for bat populations (Mas et al., 2021; Salvarina, 2016). However, the loss globally of over 30% of wetlands (Hu et al., 2017) and their inexorable transformation into agricultural land threatens all their ecosystem services and, specifically, winter bat survival. Although novel technologies (e.g. acoustic methods, LIDAR or GPS) facilitate the study of bats over large distances and time, more research is still needed to understand precisely how bat populations will respond to new climatic scenarios.

## Potential effects of climate change on bat hibernation

Maximum temperatures in the Mediterranean region have increased since 1940 by approximately 1.5°C, while records of night-time temperatures above 11°C have increased by 180% during the same period. According to our results and in the context of the climate change scenario (Trenberth, 2018), we expect that the frequency of warmer nights during future winters will increase, thereby altering current ecosystem dynamics, especially those related to bat activity. While minimum night-time temperatures have barely increased in the past 80 years, the increase in maximum daily temperatures could lead to more cases of bat dehydration and more arousal bouts during hibernation. Although we do not fully understand how climate change will impact species, we predict that in ca. 60-80 years, minimum winter temperatures would increase in ca. 2-3°C, reaching temperatures of 11°C during winter months (except January), which could interrupt or put an end to bat hibernation in coastal Mediterranean habitats. These changes could threaten bat survival due to an asynchrony between bat arousals and insect production. Similar changes have already been reported by Stefanescu et al., (2003), who reported that some first generations of butterflies fly 1–5 weeks earlier due to climate change. Marshall et al., (2020) reported that changes in winter temperatures modify the biological life cycle of certain insects by provoking an extra generation or delaying phenology. These asynchronies between bats and prey could affect other phenological phases such as pregnancy/breeding season. Ransome et al., (1994) reported that a 2°C increase in spring temperatures results in an early birth date for *Rhinolophus ferrumequinum*, which may, therefore, not coincide with an outbreak of insect availability. Aligned with our findings, some studies of hibernating mammals have shown that rising winter temperatures can cause the early emergence from hibernacula in suboptimal environmental conditions as a means of recovering energy and increasing roost competition (e.g. Goldberg & Conway, 2021; Koppmann-Rumpf et al., 2003).

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### 3.7. APPENDIX

**Appendix S3.1:** Description of plant species composition in the Ebro Delta for each present habitat.

Salt marshes, located in the coastal areas, are the most diverse environment formed by halo-nitrophilous and halophilous vegetation (e.g. *Saudeo-Salsoletum sodae* or *Salicornia emerici*), including threatened species such as *Limoniastrum monopetalum*, *Zygophyllum album* and *Limonium* sp.. Wetlands are wrapped by common reed (*Phragmites communis* and *Phragmites communis isiacus*), swamp sawgrass (*Cladium mariscus*) and narrowleaf cattail (*Thypha* sp). A generalised lack of forested areas characterises the Ebro Delta. However, in some isolated areas such as the Illa de Buda, some tree lines can still be found in the riparian zones with alders (*Alnus glutinosa*), narrow-leaved ash (*Fraxinus angustifolia*) and some eucalypts (*Eucalyptus globulus*). Vegetation in urban areas is characterised by small patches of the *Eucalyptus globulus*, palm trees (*Washingtonia filifera*) and poplars (*Populus alba*).

**Appendix S3.2:** Evolution of the night-time temperatures through the period 1942-2020 in the Ebro Delta. The linear regression was calculated using the number of nights with mean night-time temperatures above 11°C and the year.

Call:

Lm(formula = nights ~ year, data = trigger2)

Residuals:

Min	1Q	Median	3Q	Max
-19.2045	-4.9878	0.8228	5.534	16.0326

Coefficients:

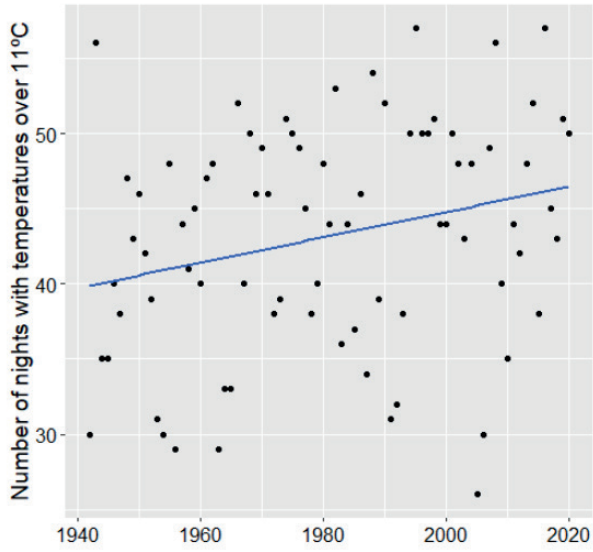
	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-124.157	71.81446	-1.729	0.0878 .
year	0.08447	0.03625	2.33	0.0224 *

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 7.347 on 77 degrees of freedom

Multiple R-squared: 0.06587, Adjusted R-squared: 0.05374

F-statistic: 5.43 on 1 and 77 DF, p-value: 0.02241







## Chapter 4

*Are Natura 2000 protected wetlands enough to sustain bat species of conservation priority in a highly degraded Mediterranean Delta?*



This chapter is under review in the Animal Conservation Journal

## Chapter 4

### Are Natura 2000 protected wetlands enough to sustain bat species of conservation priority in a highly degraded Mediterranean Delta?

#### ABSTRACT

Mediterranean wetlands, often protected under the Natura 2000 network, constitute less than 2% of the global wetlands, yet they represent essential hotspots for biodiversity. However, their current conversion to agriculture threatens the ecosystem services they provide and their role in many vertebrate species conservation. The effectiveness of Natura 2000 protected lagoons and salt marshes to sustain bat assemblages in a highly degraded delta was evaluated by comparing their nocturnal activity with that in artificial humid habitats. Additionally, we also assessed the seasonal patterns of bat activity in different habitats and the effects of lagoons' salinity on bat foraging activity. Bat activity was recorded using passive acoustic monitoring in lagoons, rice paddies, urban areas and salt marshes throughout the year, with half of the sampling points inside Natura 2000 areas, and salinity was simultaneously measured for each lagoon and sampled season. Surprisingly, only four bat species of conservation concern from three distinct guilds were detected. The proximity of protected areas positively influenced their occurrence, increasing general bat richness. However, while the two gleaner bat species selected lagoons and salt marshes during summer, the migratory *Nathusius pipistrelle* showed the highest activity around the largest lagoons with relatively high tree cover areas in autumn. Evidence of an adverse effect of the freshwater salinity was only marginally detected for a few species. The presence of Natura 2000 sites may not be enough to ensure a high bat diversity in a large delta surrounded by highly degraded habitats, but they might produce a pull effect for threatened bat species providing well-preserved habitats for drinking and foraging. In contrast, artificial humid habitats are characterised by a drastic seasonal water cycle, where pesticides and herbicides are regularly used, and therefore, they should never be understood as substitutes for natural wetlands.

**Keywords:** chiroptera, gleaner bats, lagoons, migratory bats, PAM, rice paddies, salt marshes, freshwater salinity



## 4.1. INTRODUCTION

Wetlands such as lagoons and salt marshes represent only 1-6% of the global land cover (Bartholomé & Belward, 2005; Junk et al., 2013), yet they provide numerous ecosystem services to our society (e.g. food resources, flood regulation and human well-beings such as the called “sense of peace”; Millennium Ecosystem Assessment, 2005; Maltby & Acreman, 2011). However, all these benefits are currently at risk worldwide due to the continuous exploitation of wetlands and their conversion to agricultural lands (Finlayson et al., 2018). According to Hu et al., (2017), humid global areas have been reduced by 30% since the last decade, jeopardising their associated fauna, also due to water pollution or the dramatic rate of habitat loss (Tucker et al., 2018; Williams et al., 2020).

Fortunately, during the last decades, new international and national legislation has favoured protecting and conserving these natural areas, considerably reducing their degradation (e.g. RAMSAR-Secretariat, 2014; Ramsar Convention on Wetlands, 2018). Their restoration and protection it is an imperative need at the global scale since these areas are essential for wetland-dependent species, such as amphibians or fishes, and also for migratory species, such as birds and bats (Davidson, 2018; Alcalde et al., 2021). Improving the protection of wetlands and their associated fauna does not always need to be too complex or unfeasible to implement, and usually, these initiatives have been reported as highly successful and efficient. For instance, a study in Wisconsin (USA) reported that an efficient wetland management plan could rapidly and easily provide breeding sites for some birds of conservation concern (Fournier et al., 2021). In some other cases, applying specific guidelines for a threatened species conservation could benefit other species of interest (a process called a two-for-one deal) (e.g. Beranek et al., 2021).

In 2000, Europe applied new legislation to guarantee a stable relationship between the exploitation of wetlands and their fauna and flora conservation and established the largest global network of protected areas on the continent. That legislation is known as Natura 2000 Network, implemented under the Birds Directive (2009/147/EC) and Habitats Directive (EEC/92/43) ([www.eionet.europa.eu](http://www.eionet.europa.eu)), and has been generally considered the most effective conservation initiative at the continental scale, at least for bird populations (McKenna et al., 2014).

Mediterranean wetlands represent 1.1-2% of the global wetlands (Geijzendorffer et al., 2018). Their conservation status is frequently poor, and the extent to which these few remaining natural habitats buffer and minimise the generalised biodiversity loss remains unassessed. Most of them are lagoons located near the coast or in deltas, which support more than 30% of Mediterranean vertebrates. They are located

all over the Mediterranean basin, numerous in Spain, Greece, Turkey and Morocco (Geijzendorffer et al., 2018). Ebro Delta (Spain) is one of the most extensive deltas in West Europe, with vast important areas of wetlands (lagoons) for migratory birds as stopover areas (CEDEX, 2021) and hosts the southernmost mating colonies of some migratory bat species (Flaquer et al., 2005).

The inclusion of wetlands in Natura 2000 has to meet some criteria described in the Directiva 2013/17/UE, but these criteria have relevant limitations in designing priority conservation areas for terrestrial mammals. For instance, none of the 13 bat species considered in Annex II of Directive Habitats is officially categorised as a conservation priority species. A comprehensive review by Jantke et al., (2011) used freshwater wetland-dependent species as surrogates to measure how much biodiversity is currently protected under the Natura 2000 network. Their results highlighted that most mammal species had less than 50% of their home range protected by this network. Unfortunately, the review only included two bats as target species (i.e. *Myotis dasycneme* and *Myotis capaccinii*), both classified as threatened by the IUCN RedList.

Artificial humid habitats, such as rice paddies, have been considered alternatives to wetlands providing similar environmental functions such as flood control or stopover areas for migrating bats (Elphick, 2000; Natuhara, 2013; Toffoli & Rughetti, 2017). However, although not fully known, these humid habitats might not be enough to guarantee bat conservation due to their fluctuant water regime (Toffoli & Rughetti, 2020).

Bats are the 2nd most diverse order of mammals, with more than 140 species described worldwide (Burgin et al., 2018; Wilson & Mittermeier, 2019). Thirty-four bat species are present in Spain, all insectivorous, and only four strongly related to humid habitats: two trawling bats *Myotis capaccinii* and *Myotis daubentonii*, and two hawking bats *Pipistrellus pygmaeus* and *Pipistrellus nathusii*. After more than 20 years of bat research in the Ebro Delta, trawling bats have never been spotted, probably due to the lack of riparian forests and the high concentration of water pollutants (Flaquer et al., 2009; López-Baucells et al., 2017; Montauban et al., 2021; Peris et al., 2022). While the population of *Pipistrellus pygmaeus* is one of the largest recorded in the region, only a few other bat species have been identified in Ebro Delta, such as the migratory *Pipistrellus nathusii* ([www.batmonitoring.org](http://www.batmonitoring.org)). Because some bat species populations are highly mobile, difficult to recover and sensitive to habitat degradation, some species are considered good bioindicators of habitat maturity. Their absence in specific habitats might be understood as a red flag for ecologists and conservationists.



Studies of bats in wetlands have been generally focused on non-threatened bat species (Salvarina, 2016; Mas et al., 2021), and more than 70% of these studies have been carried out during summer, leaving a critical knowledge gap regarding the role of well-conserved areas during winter or migration periods (but see Mas et al. 2022). Therefore, the role played for these habitats for the migratory species and other guilds (e.g. gleaner bats) has not been investigated in depth. This study's main aim was to evaluate how Natura 2000 protected wetlands and salt marshes favour the presence of gleaners, forest specialists and migratory bats in the Ebro Delta, a highly degraded Delta that represents the second most significant humid region of the occidental Mediterranean coast (Cabrera et al., 2010). More specifically, we modelled and evaluated: i) the pull effect of Natura 2000 areas (i.e. lagoons) on bat richness within the delta, ii) the effects of the freshwater conductivity (salinity) on bat activity, and iii) species-specific habitat selection and foraging activity seasonal patterns.

## 4.2. MATERIALS AND METHODS

### Study area

This study was conducted in the Ebro Delta, in the NE Iberian Peninsula (40.704776 N, 0.740710 E; see Mas et al., 2022 for the full study design description). This delta is formed by a mosaic of extensive rice paddies, lagoons, salt marshes (with brackish waters or not) and urban areas. While the largest urban areas are located at the centre of the Ebro Delta, the lagoons and salt marshes are generally situated at the coastal edge, and rice paddies areas cover more than 60% of the area, more or less evenly distributed. Riparian native forests are sparse due to their drastic reduction to convert them into agricultural fields (i.e. rice paddies), except for small islands (Mariano et al., 2023). The rice paddies follow a specific three-phasic water management cycle leaving them a) completely dry during winter, b) covered by rice plants and water in summer, and c) covered by water and rice stubbles resulting from the harvest season in autumn. Temperatures in Ebro Delta reach their maximum in summer (ca. 27°C), with mild temperatures during winter (ca. 9°C). The regime rainfall is around 330 mm/year, having a maximum of rainy days during the autumn and spring ([www.meteo.cat](http://www.meteo.cat)).

### Acoustic surveys and bioacoustics analysis

Aerial insectivorous bats were acoustically sampled during three seasons: winter (January – March), summer (July – August) and autumn (September – November) in 2016 using ultrasonic bat detectors (see Mas et al., 2022 for the acoustic settings and scheduled specifications). A total of 40 sampling sites were sampled during each season, randomly distributed in lagoons, urban areas, salt marshes and rice paddies.

After each sampling week, all detectors were moved and placed in other locations. To avoid recording the same bat simultaneously with two bat detectors, these were separated at least 250 m from the nearest sampled location (Adams et al., 2012; Monadjem et al., 2017). Ultrasonic microphones were placed 1-2 m from the ground to avoid microphones damages caused by wild fauna (such as rodents) and to avoid echoes in the recordings.

Bioacoustics analyses were carried out following the methodology used by Mas et al., (2022). Bat recordings were pre-analysed using the Tadarida program (Bas et al., 2017), followed by a manual identification using the Avisoft-SASLab Pro v.5.12.15 software (Glienicke/Nordbahn, Germany) to avoid misidentifications (López-Baucells et al., 2021). For this study, we only considered the following bat species and phonic groups from three different ecological guilds: gleaner bats (*Rhinolophus ferrumequinum* and *Myotis myotis/Myotis blythii*), forest-dwelling bats (*Barbastella barbastellus*) and migratory bats (*Pipistrellus nathusii*). *Myotis myotis/Myotis blythii* were grouped within the phonic group due to the impossibility of distinguishing them at the species level (Russ, 2021). Since bioacoustics methods are unsuitable for absolute abundance or counts, we used the mean bat activity (total number of bat passes divided by the total nights recorded) in each location as the response variable (bat passes/night-detector-locality). We considered a bat pass of a certain species, each sound file with a maximum of five seconds, with a minimum of two distinguished bat calls of this species (Law et al., 2015).

## Environmental variables

To assess the pull effect of Natura 2000 sites and the habitat use for each bat guild and species, we categorised the environment where the detectors were placed in four habitat categories: rice paddies, lagoons, salt marshes or urban areas. Then, we calculated the extension of the wetland for each lagoon separately (including water and wetland vegetation) and the total forest cover (as potential habitats with natural bat roosts) using a buffer of 2,000 m from the edge of each lagoon. Additionally, we calculated the linear distance from each sampling point to near habitats (scrublands, lagoons, urban areas, rice paddies, unproductive fields, meadows and tree lines) and to the limits of Natura 2000 sites. All the environmental variables were extracted from land cover maps of Catalan Habitat Cartography 2018 (<http://territori.gencat.cat>), using the software QGIS v.3.28.1 (QGIS Development Team, 2009)

Furthermore, to understand how changes in salt concentrations in freshwaters affected bat activity, we used water conductivity (millisiemens/centimetre -mS/cm-) as a surrogate of salinity. We extracted all the measurements for each month and lagoon from the database provided by the Area of Protection and Research from the

Natural Park of Ebro Delta. Water conductivity was available for nine out of the ten studied lagoons.

## Statistical analysis

### Pull effect of the Natura 2000 wetlands on bat richness

To evaluate the pull effect of the Natura 2000 sites on bat richness, we calculated for each sampling location the maximum number of bat species detected (response variable). We used the distances from different habitats (scrublands, lagoons, urban areas, rice paddies, unproductive fields, meadows, tree lines) and the distances to the Natura 2000 as predictors. We ran a Spearman test to avoid correlation between our variables and excluded variables correlated with values  $>0.80$ . A dredge analysis was run following the Akaike criterion ( $AICC's < 2$ ) (Cayuela & de la Cruz, 2022), and model averaging was used to select the final model using the *MuMIn* package (Barton, 2022). We used Generalised Linear Models (GLM) with the *gaussian* family, as data did not show overdispersion. The final model only included the distance to Natura 2000 sites as a predictor and was run using the *MASS* R package. Finally, to visualise the detected pull effect of the Natura 2000 areas, we plotted the distance effect using the Inverse Distance-Weighted (IDW) from QGIS with the distance coefficient  $P=3$ .

### Freshwater conductivity

To assess the effect of freshwater salinity on bat activity, we calculated the mean of water conductivity for each month and lagoon. A Generalised Linear Mixed Model, with *negative binomial* family to cope with overdispersion, was run for migratory bats including averaged bat activity per locality as a response variable (only considering sampling locations in lagoons), the conductivity as a predictor and the locality as a random factor. We used the *lme4* R package to run all the models (Bates et al., 2015).

### Habitat use and seasonality

Finally, to model how bat activity (independent variable) changes spatially and temporally, depending on the surrounding environment and along the year, we considered the following predictors: habitat type of the sampling location, lagoons and riparian forest coverage area in 2,000 m buffers, and sampled season (winter, summer, and autumn). We also conducted correlation tests and a dredge analysis to select the final model. All predictors were scaled from 0 to 1 using the function *rescale* from the *scales* R package. As bat species were analysed separately, we finally selected a 1) Generalised Linear Model for both gleaner bats with bat activity as the response variable and the habitat type and the sampled season as two categoric

predictors; and a 2) Generalised Linear Model with negative binomial family (GLM-NB) for the migratory bats, including the lagoon area, the riparian forest cover and the sampled season as predictors. The negative binomial family was used to cope with overdispersion data. For the gleaner bats, the response variable was log-transformed to ensure the normality assumption.

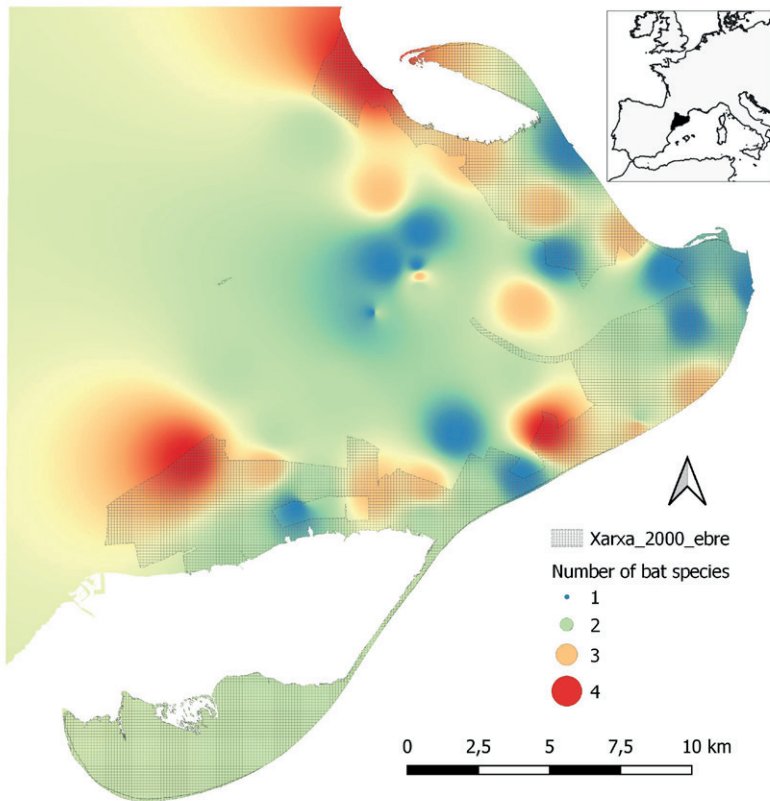
Maps from Ebro Delta were plotted using *raster* and *rgdal* R package. All analyses and plots were run using R V.4.1.0. (R Core-Team, 2021).

### 4.3. RESULTS

We conducted a total sampling effort of 713 nights-detectors, with 8,466 hours recorded. The sampling effort between seasons was slightly different: 271 nights-detector in winter, 241 nights-detector in summer and 201 nights-detector in autumn (Table 1). We only found four bat species/phonic groups of conservation priority: *Rhinolophus ferrumequinum* and *Myotis myotis/blythii* (two gleaner bat species), *Barbastella barbastellus* (a forest-specialist bat) and *Pipistrellus nathusii* (a migratory bat species), covering a relatively small range of different species of conservation concern, potentially occurring on these habitats. Common species, such as *Pipistrellus pygmaeus* or *Eptesicus serotinus*, were therefore excluded from the analyses. Overall, we recorded a total of 19,975 bat passes, classified as *P. nathusii* (19,279), *M. myotis/blythii* (366), *R. ferrumequinum* (234), and *B. barbastellus* (96) (Table 4.1).

#### Pull effect of the Natura 2000 protected wetlands on bat richness

An uneven bat richness distribution was found across the Ebro Delta, generally with hotspots on the coastal line (Fig. 4.1). The four targeted bat species were recorded simultaneously only inside the limits of Natura 2000 areas. In only 12 sampling localities (33% of the total), we found three or four bat species of conservation concern, mainly located nearby the lagoons (5 localities) and salt marshes (5 localities). Bat richness significantly decreased when distances to Natura 2000 areas increased (Appendix S4.2). Therefore, low bat richness was more related to urban areas and rice paddies, mainly outside or far from the natural protected areas (Fig. 4.1).



**Figure 4.1:** Interpolated bat richness in the Ebro Delta, considering only species of conservation concern: a gleaner species (*Rhinolophus ferrumequinum* and *Myotis myotis/blythii*), a migratory species (*Pipistrellus nathusii*) and forest-dwelling species (*Barbastella barbastellus*). The circles represent the location of sampling points, and the colour indicates the number of bat species detected. Shadow areas correspond to Natura 2000 Network sites.

### Freshwater conductivity effect on different bat guilds

Lagoons are dynamic aquatic systems, having changes in water discharge and mineral salt concentration. We recorded different conductivities ranging from 1.44 ms/cm (less salty) to 53.60 ms/cm (very salty). Up to seven of the nine sampling lagoons underwent some differences during the year, with ca. 10-20ms/cm between the minimum and the maximum measured values. Only two lagoons remained steady throughout the year.

In general terms, freshwater conductivity had a negative marginal effect on the migratory bat *P. nathusii* activity only during summer (Appendix S4.3).

**Table 4.1:** Number of complete nights recorded in the Ebro Delta (Spain) in 2016, and the total amount of bat passes registered for each species depending on the habitat and season. All the dataset is stored and can be found in the online repository [www.batmonitoring.org](http://www.batmonitoring.org).

	<i>Pipistrellus nathusii</i>	<i>Myotis myotis/blythii</i>	<i>Rhinolophus ferrumequinum</i>	<i>Barbastella barbastellus</i>	Total bat asses	Number of nights	Mean bat passes/night
<b>Winter</b>							
Lagoons	223	0	0	0	223	67	3.32
Rice paddies	259	0	0	1	260	67	3.88
Salt marshes	58	0	0	0	58	70	0.82
Urban areas	44	0	0	0	44	67	0.66
<b>Summer</b>							
Lagoons	2,080	58	83	1	2,222	59	37.66
Rice paddies	2,516	24	67	2	2,609	54	48.31
Salt marshes	447	162	27	1	637	65	9.8
Urban areas	429	4	0	1	434	63	6.9
<b>Autumn</b>							
Lagoons	8,149	6	51	6	8,212	54	152.07
Rice paddies	2,765	54	1	84	2,904	56	51.85
Salt marshes	1,154	55	5	0	1,214	42	28.90
Urban areas	1,155	3	0	0	1,158	49	26.63
<b>Total</b>	<b>19279</b>	<b>366</b>	<b>234</b>	<b>96</b>	<b>19975</b>		

### Habitats use and seasonality

Our models suggest guild- and species-specific significant differences regarding habitat use and seasonality.

#### Gleaner bats

We detected two bat species, *R. ferrumequinum* and *M. myotis/blythii*, with non-sporadic contacts throughout the year. Both species presented a similar seasonal pattern, absent during the winter (Fig. 4.2A and 4.2B), evading urban areas and having their maximum of contacts during the summer (Table 4.1), but with a segregated spatial distribution and habitat use (Appendix S4.1).

*Rhinolophus ferrumequinum* was recorded in three different habitats in summer in 40% (16/40) of the sampled localities. Although we did not find significant differences in habitat type, except for urban areas, we recorded a total of 83 bat passes in lagoons ( $1.41 \pm 0.42$  bat passes/night-detector on average), 57 bat passes in rice paddies ( $1.24 \pm 1$  bat passes/night-detector) and 27 bat passes in salt marshes ( $0.415 \pm 0.16$  bat passes/night-detector). In autumn, its activity slightly decreased to 51 bat passes, recorded principally in lagoons ( $1.06 \pm 0.59$  bat passes/night-detector) (Fig. 4.2A, Table 4.2, and Appendix S4.1).

*Myotis myotis/blythii*, however, was recorded in 65% (26/40) of the sampled localities. It had its maximum activity in summer, with slightly higher activity on salt marshes, where we recorded a total of 162 bat passes ( $2.50 \pm 0.70$  bat passes/night-detector), followed by lagoons with 58 bat passes ( $0.98 \pm 0.25$  bat passes/night-detector) and rice paddies with 24 bat passes ( $0.44 \pm 0.133$  bat passes/night-detector). In autumn, salt marshes and rice paddies had similar bat activity, with 55 and 54 bat passes, respectively (Fig. 4.2B, Table 4.2 and Appendix S4.1).

### Forest specialists

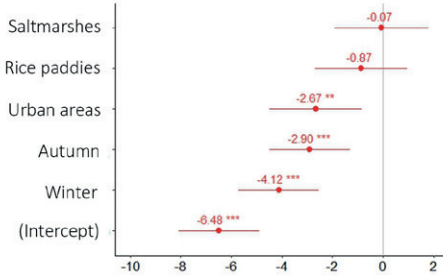
We recorded only one forest-dwelling bat species (*B. barbastellus*) during twelve different nights (not evenly distributed, as we got a maximum of 38 bat passes in one night during autumn) in only 6 of the 43 sampled localities. We gathered 96 contacts during the whole year, primarily concentrated in rice paddies and autumn (Table 4.1). Although *B. barbastellus* is a forest-dwelling bat species, all the recordings were concentrated in areas with scarce or absent trees or tree lines, usually near wetlands (Appendix S4.1).

### Migratory bats

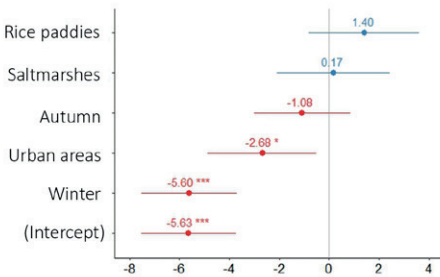
The *P. nathusii* was the most recorded species during the year, in 100% of the sampled localities, with an activity peak in autumn. We recorded *P. nathusii* on 126 different nights, 31 in winter, 49 in summer (100% of the total recorded nights) and 46 in autumn. During winter, *P. nathusii* was frequently recorded in rice paddies ( $3.92 \pm 2.62$  bat passes/night-detector) and wetlands ( $3.37 \pm 1.04$  bat passes/night-detector) (Table 4.1). Although *P. nathusii* is highly related to humid habitats, during summer, we reported foraging activity over rice paddies ( $46.59 \pm 10.54$  bat passes/night-detector) being slightly more active than in lagoons ( $35.25 \pm 7.22$  bat passes/night-detector), or salt marshes and urban areas ( $6.81 \pm 1.5$  bat passes/night-detector). However, lagoons became the most frequently visited habitat during autumn, increasing its activity until its maximum of  $170 \pm 72.50$  bat passes/night-detector (Fig. 4.2C and Table 4.1). This migratory bat was strongly related to the lagoons' size and the forest cover area,

being significantly more active in large wetlands surrounded by trees (Fig. 4.2C and Appendix S4.1 Figure S4.1).

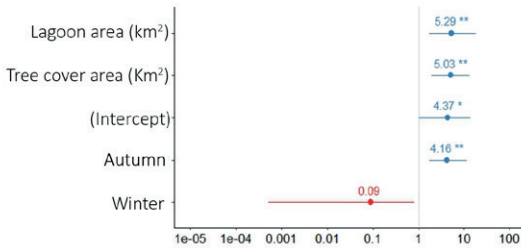
A)



B)



C)



**Figure 4.2:** Effects of the environmental variables (habitat type, lagoon’s area and tree cover) and seasonality on bat activity in the Ebro Delta during 2016 for (A) *Rhinolophus ferrumequinum*, (B) *Myotis myotis/blythii* and (C) *Pipistrellus nathusii* based on the GLM analysis. \*Indicates variables with significant effects ( $p < 0.05$ ). The model uses the “lagoons” as a baseline habitat and “summer” as the baseline season, for comparison in categorical variables.



**Table 4.2:** Results of the generalised linear models (GLM) assessing the effects of environmental variables and seasonality in the Ebro Delta in 2016 on *Rhinolophus ferrumequinum*, *Myotis myotis/blythii* and *Pipistrellus nathusii* activity. The models used the “lagoons” habitat and the “summer” season as a baseline for all the categorical comparisons. \* Represents the significance codes being \*\*\* 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1.

### *Rhinolophus ferrumequinum*

	Estimate	Std. Error	t value	P-value	
(Intercept)	-648.4	0.810	-8.01	1.16e-12	***
Habitat Rice paddy	-0.874	0.934	-0.94	0.352	
Habitat Salt marshes	-0.071	0.952	-0.07	0.941	
Habitat Urban	-267.1	0.927	-2.89	0.005	**
Season Winter	-412.5	0.810	-5.10	1.40e-06	***
Season Autumn	-289.6	0.815	-3.55	0.001	***

### *Myotis Myotis/blythii*

	Estimate	Std. Error	t value	P-value	
(Intercept)	0.773	0.395	1.94	0.054	.
Habitat Rice paddy	0.121	0.456	0.27	0.792	
Habitat Salt marshes	0.824	0.464	1.77	0.079	.
Habitat Urban	-0.311	0.452	-0.69	0.493	
Season Winter	-0.927	0.395	-2.35	0.021	*
Season Autumn	-0.340	0.398	-0.86	0.394	

### *Pipistrellus nathusii*

	Estimate	Std. Error	z value	P-value	
(Intercept)	14.75	0.657	2.24	0.028	*
Lagoon area (Km <sup>2</sup> )	16.67	0.589	2.83	0.006	**
Tree cover area (km <sup>2</sup> )	16.15	0.493	3.28	0.001	**
Season Winter	-24.22	15.18	-1.60	0.114	
Season Autumn	14.25	0.468	3.04	0.003	**

## 4.4. DISCUSSION

In recent years some authors have challenged the effectiveness of the Natura 2000 network since populations of both targeted and non-targeted species included in Directive Habitats seemed to continue declining regardless of the protection of these habitats (Portaccio et al., 2021). This study provides insight into the efficacy of several Natura 2000 protected wetlands for bat species of conservation priority in a highly degraded delta. Compared with other similar European deltas or Mediterranean areas, such as the Danube Delta or the Empordà wetlands, a disproportionately low number of bat species were detected despite a significant effort and comprehensive field sampling (Flaquer et al., 2004; Pocora & Pocora, 2011). Moreover, our results suggest that rice paddies cannot replace the role of natural wetlands in maintaining bat populations. These agricultural lands are either flooded or dry throughout the year, negatively selected by some bat species during critical periods. And finally, our data also suggest that water discharges from Ebro River during summer and from flooded rice paddies during autumn produce a variation in lagoons' mineral salt concentration that could affect bat foraging activity in natural wetlands.

### Natura 2000 wetlands vs. rice paddies

The role of rice paddies as substitutes for natural wetlands has been widely discussed in the literature (e.g. Fasola & Ruiz, 1996; Natuhara, 2013). Studies comparing species richness and bat activity reported that some species actively avoided rice paddies (Toffoli & Rughetti, 2017). However, the role of these artificial habitats in bat conservation remained unclear, especially regarding seasonality. Our results show that rice paddies do not play the same role as wetlands for foraging and drinking grounds during all seasons, especially during summer or autumn. During these seasons, the fields are covered by rice plants or stubbles, hampering bats from drinking water. However, just for migratory bats, rice paddies seem to offer a high concentration of food resources in summer, resulting in high bat foraging, probably also due to the rice pests' outbreaks (Table 4.1) (e.g. Puig-Montserrat et al., 2015)

Rice paddies could replace some general ecosystem services that wetlands provide but may not replace some key roles that wetlands represent for many bat species (e.g. water and prey availability all year round). In the Mediterranean region, we are experiencing more and more severe droughts and heat waves every year due to Climate Change, potentially increasing dehydration in bats and causing significant mortality events (Turbill & Geiser, 2008; Martin-Bideguren et al., 2019; Àrea de Climatologia, 2021; Ali et al., 2022; Festa et al., 2022). With increasing droughts, wetlands will be an essential reservoir of freshwater that could help bats cope with dehydration. Moreover, rice paddies follow a specific water management cycle to guarantee rice

production, and many pesticides and herbicides are applied, polluting the freshwater, although the direct relation between them and bat health needs yet to be unraveled.

The low number of species detected in our study suggests that Natura 2000 sites, *per se*, are not enough to ensure high bat diversity. We suggest that in highly degraded areas, such as Ebro Delta, Natura 2000 sites alone do not suffice as diversity reservoirs but might produce a pull effect for threatened bat species buffering and sustaining some of the remaining populations. Combining conserving these protected areas with promoting well-preserved riparian forests or non-homogeneous landscapes could represent an excellent strategy to increase bat diversity. In the Danube Delta, high bat activity of threatened species, such as *Myotis daubentonii* or *Myotis mystacinus*, was recorded in wetlands (Pocora & Pocora, 2011). Similarly, in the case of the Empordà wetlands, up to 13 bat species (including threatened or trawling bats species such as *Myotis daubentonii* and *Miniopterus schreibersii*) were detected in humid habitats surrounded by dense riparian forests (Flaquer et al., 2004).

### How freshwater conductivity affects bat activity

*Pipistrellus nathusii* was slightly affected by high salinity levels during summer. An increase in water conductivity is associated with a rise in mineral salt concentration, increasing or decreasing the emergence of several insect species in freshwaters (MacKenzie, 2005) and, therefore, the potential of these areas for foraging.

During summer, Ebro Delta lagoons are under intense pressure due to the low precipitation rate and the rice paddies' use of river water. All these effects result in a lower river flow from the Ebro River, resulting in a saline intrusion from the sea (Rodríguez-Santalla & Navarro, 2021). On the contrary, lagoons used to have relatively lower salinity during autumn due to the adjustments in fresh/marine water supplies, the water coming from rice paddies irrigation and precipitation events.

Human-induced practices in agricultural lands could directly impact bat diversity by modifying the salinity of the natural wetlands during specific seasons. According to the current Climate Change predictions, the decrease in precipitations in the near future could result in higher salinity levels during autumn with unforeseen consequences for bat conservation. More specific research should be directed to understand the seasonal changes in water salinity and their immediate effects on flying invertebrates and vertebrates.



## Bats distribution and habitat use

All different bat guilds were mainly reported near the edges of the Ebro Delta, nearby wetlands and salt marshes (Fig. 4.1). This habitat preference is probably related to their higher food resources and freshwater availability. Our results coincide with previous studies that suggested gleaner species often selected lagoons and salt marshes as feeding areas. For example, Toffoli & Rughetti, (2017) reported that *R. ferrumequinum* foraging activity was only recorded in wetlands. Differences in habitat selection between *R. ferrumequinum* and *M. myotis/blythii* could lie with their flight manoeuvrability or hunting strategy. *Rhinolophus ferrumequinum* presents more manoeuvrability in clutter habitats than *M. myotis/blythii* (Siemers & Ivanova, 2004; Altringham, 2011), increasing its capacity to hunt close to aquatic vegetation. Also, its hunting strategy consists in waiting immobilised or perched in a tree for available prey and “jumping” over them. This species might be more frequent in lagoons because they are the only productive habitats where some trees can still be found. *M. myotis/blythii* was probably more frequent in salt marshes due to the presence of their principal terrestrial prey and the absence of water surfaces. This bat species is a strict gleaner bat, and its hunting strategy relies on capturing its prey directly from the ground (Altringham, 2011), hindering its hunting activity in lagoons.

Regarding the forest-dwelling bat, *B. barbastellus* – a species highly related to mature forest habitats – was sporadically recorded during mating season (autumn) at least 10 km from the nearest forest habitat and 25 km from the nearest mature forest. These distances are relatively large if we consider that the maximum distance flown by *B. barbastellus* to reach the foraging zone is ca. 20 km (Zeale et al., 2012). The same authors reported that this bat species usually preferred foraging habitats in a radius of 7 km from the roost. The detection of *B. barbastellus* close to wetlands areas and the scarcity of natural roosts around the detection zone suggest that humid could be critical feeding hotspots for them.

Finally, the migratory *P. nathusii* presented its maximum bat activity at Buda Island, on the eastern side of the delta, close to the river’s outflow (Appendix S4.1). Flaquer et al., (2009) and Paunović & Juste, (2016) reported that *P. nathusii* is strongly related to natural wetlands and forested areas where they can find roost and forage. Our data support this hypothesis, as Buda Island has the second-largest lagoon in the Ebro Delta and is the only area with relatively wide tree lines with alders (*Alnus glutinosa*), narrow-leafed ash (*Fraxinus angustifolia*) and some centenarians eucalypts (*Eucalyptus globulus*) (Curcó, 2007) that offer natural roosts. Buda Island represents a unique habitat in the southernmost part of the species distribution, the only location in the country where the species have been detected abundantly, and therefore, it deserves species conservation care and protection.

## Seasonality patterns

Generally, the three detected guilds had marked seasonality patterns, absent or reducing their activity in winter and increasing during summer (gleaners) or autumn (migratory species).

In winter, the absence of gleaners' bats might result from their type of roost and hibernation behaviour. *Rhinolophus ferrumequinum* and *M. myotis/blythii* are strictly cave-dwelling bats overwintering in caves or underground roosts (Altringham, 2011). Underground systems offer perfect conditions for bats to keep extensive torpor periods with high humidity and stable temperatures throughout all winter (Park et al., 2000; Ben-Hamo et al., 2013). However, forest-dwelling such as *B. barbastellus* and *P. nathusii* are more exposed in winter to environmental changes since their roosts are not well-isolated. Turbill, (2008) reported that when environmental temperatures increase, bats suffer a passive rewarming, increasing their thermoregulation and dehydration and favouring their arousals in relatively cold weather (Mas et al., 2022). After 20 years of studying *P. nathusii* in the Ebro Delta, we know that some male individuals remain in bat boxes during the winter season, and some are still active during warm winter nights (Turbill & Geiser, 2008; Mas et al., 2022). In this case, the availability of water and insects in wetlands might become critical for their survival.

Summer was the season when almost all guilds were more active. The overall increase in *R. ferrumequinum* bat activity could be related to the presence of a few breeding colonies in the Ebro Delta and its proximities (unpublished data – [www.batmonitoring.org](http://www.batmonitoring.org)). For *M. myotis/blythii* the increase in bat activity could be associated with the presence of several males in bat boxes (Flaquer et al., 2020) and the proximity of certain sea caves. Although this bat is a cave-dwelling species, it has also been detected in wooden and rice chaff bat boxes (Martin-Bideguren et al., 2019), probably conquering new foraging grounds. Our findings suggest that salt marshes and lagoons might have become critical for gleaners' bats that breed in sea cavities near Ebro Delta. Following the same patterns as the other guilds, *P. nathusii* increased their bat activity during summer, probably due to the increase of rice pest populations (Puig-Montserrat et al., 2015), since *P. nathusii* breeding colonies have never been spotted in the region.

In autumn, migratory bats substantially increased their activity. *Pipistrellus nathusii* has the longest known migration route in Europe, flying more than 2,400 km to reach breeding and winter roosts (Vasenkov et al., 2022). Considering migration distances and the results by Flaquer et al., (2009) and Šuba, Petersons & Rydell, (2012), it becomes obvious that *P. nathusii* selects this kind of lagoons during the migration season as stopover areas to recover their fats on the route. In our case, it

also represents the ending point of their journey and, potentially, their perfect spot to hibernate. Well-conserved wetlands such as those in the Ebro Delta allow the survival and continuation of these migratory colonies within the limit of their distribution. Their correct management and improvement should be prioritised in conservation plans.

## 4.5. ACKNOWLEDGMENTS

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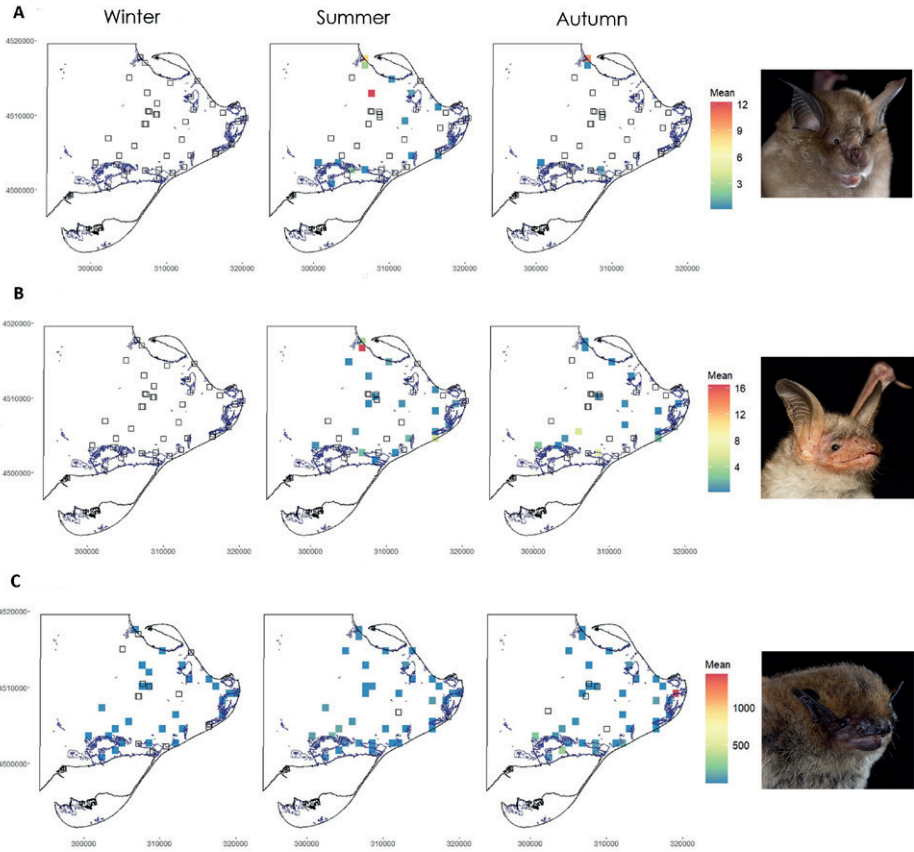


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## 4.7. APPENDIX



**Appendix S4.1:** Distribution of different bat species of conservation concern in the Ebro Delta: **A)** *Rhinolophus ferrumequinum*; **B)** *Myotis myotis/Myotis blythii*; **C)** *Pipistrellus nathusii*. The map shows the mean bat activity per night and locality. White squares are localities with no acoustic detections, and the blue polygons represent the wetlands.

**Appendix S4.2:** Effect of changes in bat richness depending on the distances to Natura 2000 Network. \* Represents the significance codes being \*\*\* 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1.

	Estimate	Std. Error	t value	P-value	
(Intercept)	2.370	0.175	13.504	<2e-16	***
Distance to Natura 2000 Network	-0.0002	0.0001	-2.258	0.029	*

**Appendix S4.3:** Effect of freshwater conductivity on the activity of *Pipistrellus nathusii*.

	Estimate	Std. Error	t value	P-value	
(Intercept)	12.407	12.252	1.013	0.3112	
Salinity	-11.627	20.995	-0.554	0.5797	
Summer	0.9823	10.815	0.908	0.3638	
Autumn	27.006	12.683	2.129	0.0332	*
Salinity in Summer	33.643	19.328	1.741	0.0817	.
Salinity in Autumn	0.1541	24.174	0.064	0.9492	







*Chapter 5*  
*General discussion and conclusions*

## General discussion and conclusions

Despite wetlands being one of the most threatened habitats in Europe, they are disappearing from the Earth's surface at a dramatic rate, and their role in guaranteeing the resilience and preservation of bat populations under the context of global change remains largely unknown. This study has focused on the importance of these humid habitats for bats in highly degraded Mediterranean areas, where climate change will probably hit bat populations strongly in the near future. Throughout this thesis my main objective has been to enhance the scientific knowledge about bats and wetlands conservation. In order to understand how they are interlinked, I described which conservation and research gaps exist to improve societal awareness including amongst the general public and stakeholders. I also provided, for the first time, an easy tool to identify which countries need to reinforce studies on bats and wetlands, what I named the "knowledge Bat Index" (kBI) (Chapter 1).

Then, because European bats have different behaviours that fluctuate between periods to cope with uneven food and water availability (e.g., cessation of nocturnal activity during hibernation vs high foraging activity during energy-demanding periods such as the breeding season or migration), in chapter 2 I studied the role of these humid habitats for one of the most sensitive periods in bat life: hibernation. I also predicted the effects of climate change and rising temperatures in the future hibernation dynamics in coastal wetlands. Finally, I assessed the buffer effect of protected wetlands, such as those included in Natura 2000 areas in highly modified and degraded regions, in maintaining populations of species of conservation priority. As a conclusion I highlighted the ecosystem services provided by these wetlands, that could never be replaced by artificial humid habitats such as rice paddies (Chapter 3).

The whole study has been designed and carried out in the Ebro Delta Natural Park in the western region of the Mediterranean Sea, where one of the most significant and long-term bat research projects on wetlands, ecosystem services and bat bioacoustics has been taking place over the last two decades in Europe. The bat community in the Ebro Delta is characterized by a clear dominance of the generalist species *Pipistrellus pygmaeus*. However, the recurrent presence of other relevant species such as *Barbastella barbastellus*, *Rhinolophus ferrumequinum* or *Myotis myotis* have allowed assess the responses of different bat guilds to environmental stressors. The project represents the culmination of several years of continuous research efforts led by the BiBio Research Group from the Natural Science Museum of Granollers, with particular emphasis on applied conservation, and the beginning of a new era for bat research through bioacoustics in the Iberian Peninsula.

## 5.1. THE NEW ERA OF BAT STUDIES

Wetlands are gaining prominence in newspapers, amongst policymakers, and the scientific community due to the poor conditions and the rapid global loss they face (Ballut-Dajud et al., 2022; Jones, 2022; Weston, 2023). However, the relationship between wetlands and bats is far from well-known (Mas, Flaquer, Rebelo, & López-Baucells, 2021). Humid habitats have been widely underrepresented in bat studies principally due to their vast open areas and also due to their lack of roost availability and delimited pathways, which challenges traditional research survey methods. In the first chapter I reviewed all studies on bats and wetlands from the literature, and reported that these habitats had been inadequately surveyed since the last century (ca. 120 years) (Mas et al., 2021). However, this trend does not seem to be reversing in the early 21<sup>st</sup> century, despite the technological advances that are currently aiding bat researchers in deciphering and deepening the ecology and behaviour of these mammals.

Recent studies have reported the relatively high efficiency of studying insectivorous bats using new and improved bioacoustics methods in wide open areas (Duffy et al., 2000; MacSwiney, Clarke & Racey, 2008; Thomas & West, 1989). It has, therefore, been possible, for the first time in the Iberian Peninsula, to monitor and record all year long natural bat behaviour and activity in one of the areas with the highest bat densities (Mas et al., 2022 and Chapter 3). One of the main challenges related to bioacoustics studies in humid habitats is the colossal amount of data automatically gathered and the difficulty of identifying some bat species in the recordings (Altringham 2011; Mas et al., 2022). Fortunately, recent advances in machine learning and AI (artificial intelligence) have helped reduce time when it comes to identifying bat species by providing first tentative species identification or bat call clustering tools (López-Baucells et al., 2019).

The recent development of new acoustic recorders and price reductions are also increasing the amount of acoustic data now being generated (Hill et al., 2019). Because this was one of the first studies accumulating such vast amounts of acoustic data in Spain, this project also represented the beginning of a recently established collaboration between the BiBio Research Group and the CSUC centre (Catalan Consortium of University Services) to store biological acoustic data in their servers, solving one of the most critical and complex issues related to bioacoustics studies: data storage, automatic processing and backup creation. This collaboration has been possible thanks to the Spanish Supercomputing Network and the Catalan Government.

The association of ecological and bioacoustics data and supercomputers will improve our knowledge of animal ecology, not only in Europe but also in other regions (i.e. Yoh et al., 2022), where the relationship between wetlands and bats has yet to



be studied fully, and humid habitats are decreasing at the most alarming rates. By working together, new data centres and researchers could achieve mutual benefits. On the one hand, supercomputing centres offer a massive capacity for data storage that could be used to train specific AI algorithms and improve their own databases fostering interdisciplinary projects (Zhu et al., 2023). This collaboration would provide the opportunity to analyse biological data in ways humans cannot, resulting in improved ecological studies. On the other hand, researchers could also employ it as a tool to store, modify, analyse, and reanalyse their data without data storage capacity and Random Access Memory (RAM) limitations. Thus, data centres and their servers are key elements for future bat research and conservation, and through this project, I have set the first steps to enhance this.

## 5.2. PAST AND FUTURE RESEARCH IN THE EBRO DELTA

The BiBio Research Group from the Natural Sciences Museum of Granollers has been studying the bat populations in the Ebro Delta for more than 20 years now, covering a wide variety of topics, always with the aim to improve bat conservation and to preserve their habitats. The first steps of bat conservation in these Mediterranean wetlands date back to the early 2000s with the realisation of its first inventory of bat species (Flaquer & Ruíz-Jarillo, 2002). Afterwards, several other studies were developed, such as the report of the first resident population of Nathusius' pipistrelle (*Pipistrellus nathusii*) in the Iberian Peninsula (Flaquer et al., 2005), the first study suggesting that these wetlands were used as stopover areas by the migratory Nathusius' pipistrelle (Flaquer et al., 2009) and another study where we quantified the pest control service provided in rice fields by one of the largest colony of Soprano pipistrelle (*Pipistrellus pygmaeus*) in the Mediterranean region (Puig-Montserrat et al., 2015). All these projects gained a very positive reputation amongst the scientific community and projected the research group to the international audience.

Different scientific investigations have also been published in recent years to broaden the knowledge of bats from the Ebro Delta. For example, Montauban et al., (2021) studied the plasticity of echolocation calls of soprano pipistrelle in wetlands and reported an exceptional acoustic adaptation of these bats in open areas with no interspecific competition. Montauban et al., (2020), also described how to use bat guano as a non-invasive technique to monitor insect diversity in agricultural lands. This study (Mas et al., 2022 and Chapter 3) is the latest piece of scientific information that our team has published in the Ebro Delta and represents a new perspective in ecological bat studies carried out in the region using bioacoustics. We have deepened the knowledge of winter bat activity in temperate areas and put the spotlight on the real conservation power of protected threatened wetlands for conservation priority species.

A long road is still ahead to understand the relationship between wetlands and bats accurately. For instance, as I reported in Mas et al., (2021), many studies carried out on wetlands have been focused on the trawling bat *Myotis daubentonii*. However, after all these years of intense work in the Ebro Delta, the presence of any trawling long-finger bat (*Myotis capaccinii* or *Myotis daubentonii*) has never been reported ([www.batmonitoring.org](http://www.batmonitoring.org)), while in other small wetlands from the same region or in similar European deltas they are currently recorded, usually abundantly (Pocora & Pocora, 2011). The lack of both species and the absence of other species of conservation concern could be related to the direct effects of roost loss or the indirect effects of agricultural pollution (Mañosa et al., 2001). Understanding why the Ebro Delta cannot sustain diverse bat communities like other wetlands should be a critical topic and priority for future research.

Rice farming in the Ebro Delta is exerting intense pressure upon wetlands and their associated fauna and flora. The application of pesticides to control the rice borer moth (*Chilo suppressalis*), mosquitoes and other insects, and herbicides to prevent weed growth have been polluting the waters of wetlands and bioaccumulating in their fauna, flora, and soil for decades (Mañosa et al., 2001; Matamoros et al., 2020). Unfortunately, there is a lack of knowledge about the potential detrimental effects of insecticides on wildlife (Mañosa et al. 2001) and how reducing chironomids and mosquitoes could affect the resident fauna, including bats. On the other hand, a study by Matamoros et al. (2020) demonstrated that wetlands could reduce pollutant concentration from rice irrigation water by 60% to 80%. However, the pollutants' concentration that might affect wildlife such as bats is still unknown. Studies focused on wetlands' carrying capacity to reduce pollutants and the affect upon wild fauna are essential in order to develop adequate management plans under the new global change scenarios (Browning et al. 2021).

Bats are predators at the top of the food web, potentially resulting in high bioaccumulation in their fats or organs. The systematic review carried out by Zupal et al., (2015) reported that these mammals are presumed to be highly tolerant to pollutants – heavy metals like lead or cadmium – but there are few studies reporting some detrimental effects of these metals on European bats, such as trawling bats (i.e. *Myotis dasycneme* or *Myotis daubentonii*) or *Pipistrellus* sp. Thus, the Ebro Delta represent an excellent study system to open new research lines in order to evaluate the effect of these contaminants on bats through systematic monitoring, as has already been done for birds (Mateo et al., 2014), and to assess the efficiency of the implementation of the current management plans to decrease pollutants concentrations coming from the agricultural lands. The BiBio research group will collaborate on a recently granted Horizon2020 project specifically addressing these questions in the Ebro Delta.

### 5.3. MEDITERRANEAN WETLANDS CORRIDOR

Understanding the connection between habitats and how animals use them to move across the landscape is essential to develop adequate conservation guidelines or to provide solid evidence for policymakers. Landscape connectivity is strongly affected by habitat fragmentation due to the conversion of natural habitats into agricultural lands or human settlements. Fragmentation effects are largely described in the literature, from changes in ecosystem services (e.g., pollination) to changes in species abundance (e.g., decrease/increase in species richness) or the restriction of species movements (e.g., dam construction) (Buijse et al., 2002; Mitchell et al., 2013). Wetland fragmentation has only been assessed in four studies (Esberard et al., 2013; Montiel et al., 2006; Silveira et al., 2018; Walsh & Harris, 2009) of all retrieved papers (Mas et al. 2021) and all in tropical regions. This leaves some research opportunities to study how wetland fragmentation and their connection loss might affect bat conservation and bat movements, as has been observed with other flying animals.

The relationship between birds and wetlands is a topic that has been exhaustively studied since 1990, with a maximum of ca. 600 indexed scientific publications in a year, mostly due to the presence of many water-dependent bird species (Mas et al. 2021). Europe's largest global network of protected areas (Habitats Directive) was created to protect and preserve Important Bird Areas (IBA), mostly wetlands. However, specific legislation protecting a particular habitat alone does not guarantee its functionality. It has been demonstrated that the conservation success for species with large distances movements increases when their distribution areas are part of a well-connected network of natural areas (Mazaris et al., 2013). For example, Xu et al., (2019), reported that a significant decrease in migratory bird populations was related to the loss of connectivity between migration areas.

Bats are not exempt from the effects of habitat connectivity changes. As birds do, bats use wetlands as stopover areas to continue their migration route (Flaquer et al., 2009; McGuire et al., 2012), and according to Lookingbill et al., (2010), bat activity increases in interconnected wetlands compared to isolated ones. In this study, I described how the migratory *Pipistrellus nathusii* use wetlands during the migration periods to recover their fats and to mate (Chapter 3), but the route this bat species follows remains unclear, as no other bat colonies have been found in this Mediterranean region. Assuming that *P. nathusii* commutes along the coastline during its migration route (Kruszynski et al., 2021; Petersons, 2004) and the fact that it is strongly associated to humid habitats, well-preserved wetlands along their migration route could help the conservation of this bat species. At present, the migration routes of *P. nathusii* and other bats are still a mystery in the Mediterranean region, and therefore, more research is needed to understand which wetlands are connected and

which ones they use during their migration route. However, the strong pressure that Mediterranean coastal areas suffer from human activity and settlements is reducing existing wetlands areas and hampering the provision of the ecosystem services they provide. The presence of these humid habitats in the Ebro Delta could represent the last remaining natural hideouts for *P. nathusii* and other different bat species during their short and long movements.

It is important to note that the success of this network is strongly related to the health status of well-connected Mediterranean wetlands. According to Geijzendorffer et al., (2018) and Taylor et al., (2021), the conservation status of Mediterranean wetlands is currently poor or unfavourable. However, there is a large number of wetlands that remain in unknown conditions due to the lack of indicators to evaluate their conservation status ([www.eea.europa.eu](http://www.eea.europa.eu)). The knowledge of the wetlands' state could be easily assessed by employing citizen science (i.e. McInnes et al., 2020). Using organisations such as NGOs or naturalists' associations, we could gather enough information about wetlands to implement enhancements in local, national, and international conservation plans, and to create a well-defined Mediterranean wetland corridor.

## 5.4. NATURAL WETLAND PROTECTION AND RESTORATION

Wetland protection and restoration might be challenging for many researchers, conservationists and public organisations due to the potential disagreements between indicators to evaluate the restoration process (Zhao et al., 2016). Accurate assessments of how wetlands preservation and restoration could benefit bat populations have yet to be carried out. In fact, no work has ever been carried out to assess the consequences of wetlands restoration in terms of bat conservation. There is still much work to do to get a comprehensive view of their functionality for bat populations, especially if we consider that bats can change or adapt their behaviour to cope with new environmental situations due to the global change.

According to the bat research community, wetlands are essential habitats for bat conservation (Mas et al. 2021), but their conservation status seems to decrease through the years, jeopardising the services they provide. The principal drivers of European wetlands loss are related to their conversion into agriculture fields and the extraction of minerals and soil (Verhoeven, 2014). Some authors suggested that ecosystem services provided by wetlands could be replaced by artificial ones, such as rice paddies (Fasola & Ruiz, 1996; Natuhara, 2013). However, as I report in this study, these artificial humid areas might not be enough to ensure the survival of some bat populations (Chapter 3).

Fortunately, new environmental projects are currently restoring wetlands and creating new humid habitats, as well as protecting the remaining ones. This is the case of the Danube or Elbe deltas (Verhoven 2014). The restoration of the Danube Delta is one of the most ambitious programmes to recover one of the largest deltas in Europe and represents an excellent example of a successful recovery project. This delta was deeply modified for 129 years (1860-1989) by the construction of channels and dams and the conversion of 41% of its lands into agricultural fields. Consequently, the wetland cover ended up declining by 62% (Gómez-Baggethun et al., 2019). Although achieving a full recovery of wetlands and their associated functions requires a long period of time (Gómez-Baggethun et al., 2019), thanks to restoration policies in 1990, some ecosystem services have already started to recover in the Danube Delta, such as social, ecological, and economic services, and also the diminution of nutrient concentrations (nitrogen and phosphorus) in freshwater.

According to Buijse et al., (2002), planning a restoration project in rivers, floodplains and wetlands is difficult to implement due to the presence of different environments and species. It has to be designed as a long-term project and needs cooperation between organisations, scientists, and governments. Thankfully, some new European agreements seem to be aligned with the need of wetland recovery and protection. “Biodiversity Strategy 2030” is an ambitious programme led by the European Commission to completely restore at least 25,000 km of rivers and their associated habitats by 2030 (European Commission, 2022). “Wetland protection” is addressed internationally in the Birds and Habitats Directives and the Ramsar-Convention, and includes many bird species, amongst others. However, bats are not described as species of conservation priority when it comes to protecting new wetlands areas, and, therefore, with this study I would like to emphasise the need to develop and apply new holistic management plans to guarantee wetlands protection together with the survival and resilience of bat populations.



## 5.5. CONCLUSIONS

1. The Mediterranean region is one of the 25 Global Biodiversity Hotspots, and its wetlands represent 1.1-1.5% of global wetlands. These humid habitats are suffering from a reduction in size and water quality due to anthropogenic pressures and climate change, leading to a poor wetland conservation status, but the effects of their loss and inadequate conservation and preservation on bat conservation is not completely understood.
2. In continents with high rates of wetlands loss, such as Africa or Asia, there is an important lack of knowledge on the detrimental effects for bat populations. On the other hand, in temperate areas studies on wetlands are clearly biased to high bat activity periods, something that might change in the near future thanks to the technological advances (e.g. automatic ultrasound detectors) which will improve studies in wide open areas such as wetlands.
3. For the first time, bat activity during winter was comprehensively assessed in a Mediterranean coastal region. Bats were active during the whole period, although at lower bat activity levels, and wetlands were the most used habitats by bats to recover fats and hydrate themselves. Winter bat activity was influenced by night temperatures significantly increasing bat activity when temperatures exceeded 11°C. Using this temperature threshold and future climate change scenarios, I suggest that hibernation might potentially end for Mediterranean temperate bats in coastal wetlands by 2080-2100.
4. It has been suggested that artificial wetlands, such as rice paddies, provide equivalent ecosystem services to natural wetlands to protect wildlife. However, I found that natural wetlands are necessary and irreplaceable for sustaining bat populations, especially for those species of conservation priority. Rice fields are characterised by a specific water management regime that produces changes in water levels and pollution, therefore, affecting both food and water availability for bats.
5. Reducing the loss of wetlands and restoring them is essential in Europe if we want to prevent biodiversity and ecosystem services loss. Until now, legislation on wetland protection has been focused on protecting these habitats using birds as umbrella species. Bats are still not considered when designating the protection of new wetlands, although the effectiveness of wetlands for bat conservation, will depend on a well-defined wetlands network. Filling the knowledge gaps reported in this thesis will improve our knowledge of wetlands services and provide a theoretical basis for policymakers and government to create holistic management plans including wetlands and bat conservation.

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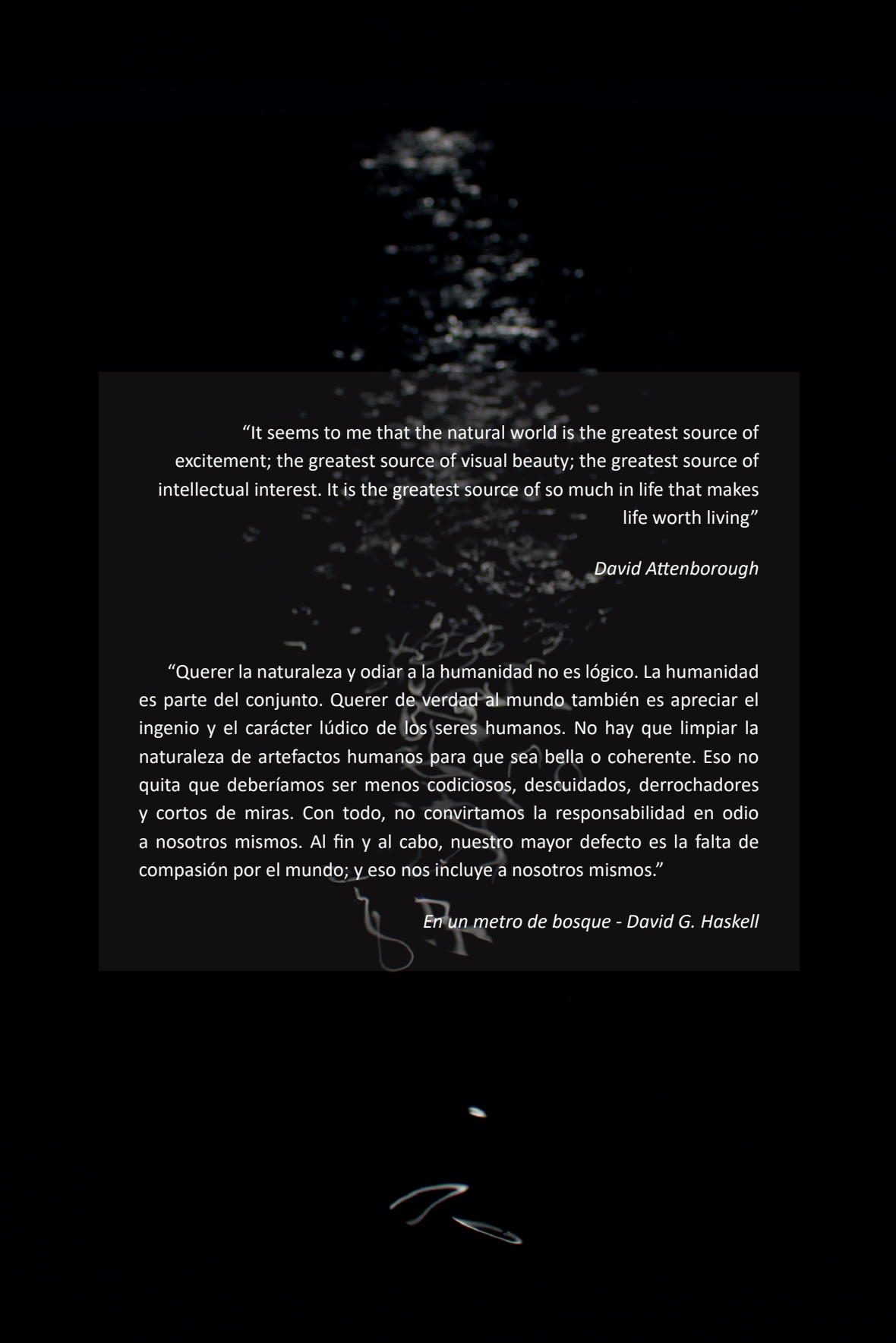
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“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living”

*David Attenborough*

“Querer la naturaleza y odiar a la humanidad no es lógico. La humanidad es parte del conjunto. Querer de verdad al mundo también es apreciar el ingenio y el carácter lúdico de los seres humanos. No hay que limpiar la naturaleza de artefactos humanos para que sea bella o coherente. Eso no quita que deberíamos ser menos codiciosos, descuidados, derrochadores y cortos de miras. Con todo, no convirtamos la responsabilidad en odio a nosotros mismos. Al fin y al cabo, nuestro mayor defecto es la falta de compasión por el mundo; y eso nos incluye a nosotros mismos.”

*En un metro de bosque - David G. Haskell*

