Bats in urban Sweden

A multiple regression analysis of bats' relationship to urbanization

By: Nils Andersson Skog

Supervisor: Kari Lehtilä
Södertörns Högskola | School of Natural Sciences, Technology and Environmental Studies
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Abstract

Human development continues to use up more physical space in the natural world, threatening the natural habitats of many organisms. To combat the loss of biodiversity science needs to explore what landscape features are important for different organisms so that we can incorporate these into the modern environment. As bats play an important role in many ecosystems and can reflect changes through trophic levels, analyzing their preferred habitats can help planners improve biological diversity of the urban habitat. Using acoustically identified bat sightings from Artportalen.se for the years 2017-2018, this paper studied the habitats of bats in Sweden. Through multiple regression analysis we examine the response in abundance and/or diversity of bats to physical and socio-cultural attributes of the urban habitat. We examined a total of 10160 bats from 18 species in 418 land cover locales and 306 demographical statistical areas with varying degrees of urbanization. Our results indicate that bat abundance and diversity decrease significantly with higher urbanization while deciduous forests are the most important land cover type for all bats. The results also indicate that wealthier areas have less abundance and diversity even when factoring in population density. Species specific analysis suggested that bat species who are better adapted at foraging in open vegetated landscapes and over water were less susceptible to the negative impacts of the urban habitat. We conclude that diverse habitats with a mixture of open vegetated areas, watercourses and broadleaf forests are the most important land features for a diverse bat fauna along with high connectivity via tree cover and linear landscape elements. If urban planning could incorporate these features into the urban habitat, some of the negative impacts of urbanization could be prevented.

Key words: Urban ecology, Insectivorous bats, *Chiroptera*, Species composition, Bioindicator, Sustainable development

Contents

1. Introduction

The human population is larger than it has ever been, and more and more people live in cities or urban environments. From having been 2 billion people in the year 1950 there are expected to be approximately 10 billion by the year 2050 (United Nations 2017). Out of the almost 8 billion people alive today, 55% live in urban environments, with the most urbanized regions having up to 82% urban residents currently. The number of urban citizens is expected to rise with the increase in human populations and the UN expects up to 42 countries to have more than 90% urban residents by the year 2050 (United Nations 2019). Increasing urbanization is one of the leading causes of land degradation (IPBES 2018) as well as the loss of biodiversity (Sala et al 2000) and changes globally to ecosystem structures (Vitousek et al 1997), which leads to the loss of ecosystem services, human well-being, and natural habitats (IPBES 2018). As cities and urban environments need to house more people, they must either sprawl outwards claiming more space, or grow upwards to accommodate more people. This leads to further impacts on the environment through increased land-use as well as increased energy consumption (Heinonen & Junnila 2014) which could lead to further releases of CO^2 from fossil fuels into the atmosphere. The urban sprawl has been shown to have multiple effects on wildlife and ecosystem structures, especially insectivorous birds have been shown to have difficulty adapting to urban environments without much green spaces (Máthé et al 2015). The change from natural habitats to human-made environments lead to fragmentation of natural habitats or even their complete disappearance. The reduction of habitats consequently leads to many species disappearing among both animals and plants. Even though some species can adapt or even thrive in urban and/or fragmented environments (McKinney 2008; Riley et al 2003; Fahrig et al 2019), other species may be unable to adapt to the man-made landscape (Riley et al 2003) and their services to the environment will be lost, some of which (i.e., pollination or air filtration) human societies are dependent on.

With any change in the environment there will be winners and losers, if prolonged changed conditions favor one species over another, the favored species will eventually replace the species which is worse at adapting to the new conditions (McKinney & Lockwood 1999). It is thus important out of a conservation perspective to analyze and understand the factors that drive the urban assemblage of species (Sol et al 2014) and to study the impact urbanization has on different organisms. This has prompted science to research the ecological effects of urbanization along a theoretical gradient of increasing urban exploitation (Berland 2013; Vizzari et al 2018). Diversity has also been observed within urban environments themselves and linked to socio-cultural variables like income and population density affecting organisms both positively and negatively (Tonietto et al 2011; Lowenstein et al 2014; Li et al 2019). Lowenstein et al (2014) found greater bee abundance and diversity in neighborhoods with higher human population density (Lowenstein et al 2014), while Li et al (2019) found a positive correlation between bat activity and income for one species and a negative correlation for another species (Li et al 2019). By observing and investigating these relationships between anthropogenic factors and ecological response, science can better understand the effects that the increased urban sprawl has on biodiversity so that measures can be taken to reduce its negative effects on the future environment.

Bats can be commonly found in both urban and rural areas, across all continents except Antarctica (Russo & Ancillotto 2015; Threlfall et al 2016), providing ecosystem services like pollination, seed dispersal and the consumption of pest insects (Voigt et al 2016). Their wide distribution along with their functional and taxonomic diversity make bats a good indicator of human-induced changes to both climate and habitat quality as they may show responses to many different changes of the urban environment (Jones et al 2009). Changes in temperature can affect their hibernation and reproductive cycle (Racey & Entwistle 2000), drought can affect their availability of food, artificial light can change the hunting environment so that it is harder for some species and easier for others (Rydell 1992; Stone et al 2015), traffic noise can disrupt their communication and echolocation and pesticides can accumulate to reach dangerous levels in insectivorous bats (Jefferies 1972; Clark 1981). Urban constructions can also affect bats negatively as roads can divide and fragment habitats through physical, acoustic, and visual means (Russo & Ancillotto 2015) and wind farms can pose immediate dangers to migrating (Arnett et al 2016) as well as insect feeding bats (Rydell 2016). While many of the aspects of the anthropogenic environment have been proven harmful, some species, especially fast-moving ones, are better at adapting to the changed, now urban, environments than others and may even establish larger populations in the areas (Avila-Flores et al 2005; Russo & Ancillotto 2015; Threlfall et al 2016).

Bats wide arrange of vital ecosystem services globally and their tendency to reflect features of habitat deterioration on a wide range of taxa make them good indicators of ecosystem health (Jones et al 2009). In this study I will use the presence and diversity of bats to study the effects of urbanization on the wildlife in Sweden. Through statistical testing the study intends to investigate whether urbanization has any effect on bat numbers and/or diversity of species, and if there are any species that are found more often in certain environments.

1.1 Research Problem

Humans have been influencing ecosystems and the environment for thousands of years. With increasing amount of anthropogenic environments and human population it has become increasingly important to further study and understand how these changes affect the ecology both locally and globally. Thus, to understand the earth's ecosystems we must account for the strong, often dominant influence of humanity (Vitousek et al 1997). While the effects of the human influence on different species and individuals can vary locally, urbanization in general tends to lead to reduced biodiversity and species richness (McKinney & Lockwood 1999). This necessitates the need to not only understand the ecology in cities; physical environment, but also the ecology of cities; citywide species richness and social dimension of the urban ecology (Pickett et al 2001). By studying the interactions and feedbacks between human and ecological systems we can better understand ecosystem dynamics both locally and globally, facilitating better decision grounds for public policies and land management (Grimm et al 2000).

Due to their wide geographical spread (Russo & Ancillotto 2015), their phylogenetic diversity (Teeling et al 2005) and the fact that they can be commonly found in many urban areas around the world (Russo & Ancillotto 2015; Threlfall et al 2016), bats are a suitable unit for analyzing the impact on the ecology that urban environments pose as well as the socio-cultural relationship of the urban ecology. Different species of bats may show different response to urban landscape traits and response can even vary between different sites (Jones et al 2015; Russo & Ancillotto 2015). Insectivorous bats occupy high trophic levels which makes them good indicators of the ecosystem health down through the trophic levels and monitoring their populations both short- and long-term can reflect changes throughout the ecosystem such as changes in climate, water quality, agricultural intensification, forest fragmentation and diseases (Jones et al 2009). By monitoring the Swedish bat populations along the urbanization gradient, we can better understand the effects that the urban environments may have on the ecosystem. While there has been an increasing number of inventories of bats in Sweden in recent years (Ahlén 2011; de Jong et al 2020), few studies have been made that analyze the effects that the urban environment may have on the bat fauna on a larger scale. Most studies and inventory of bats in Sweden are made as part of an environmental impact assessment in conjunction with the development of new structures such as wind farms, factories, or roads. This study intends to fill some of that gap by studying the diversity of bats in Sweden in relation to some variables of both the physical environment and some of the social dimension of the urban ecology on a larger national scale.

1.2 Objective & Research questions

The aim of this paper is to study the bat population in Sweden and analyze if there is any relationship between the abundance and diversity of bat species and some variables that explain the urbanization level of the environment. The study intends to study both variables that explain the physical environment as well as some variables that explain the social dimension of the urban environment. As such the study can be formulated in a couple of questions which it intends to answer:

i. How are the bat populations and/or diversity affected by increased physical urbanization?
ii. How are the bat populations and/or diversity affected by increased socio-cultural urbanization?
iii. How does the bat community structure change along the urbanization gradient or with changing environmental or anthropogenic conditions?

1.3 Bats in Sweden

As of 2020, 19 bat species have been recorded in Sweden (de Jong et al 2020) out of which seven are red listed in the Swedish Red List 2020 in accordance with the IUCN Red List Criteria (SLU Artdatabanken 2020). All bats in Sweden are insectivores and either hibernate or migrate during the winter and are protected by the Swedish Species Protection Ordinance which means it is forbidden to catch, kill, disturb, or move any bats (SEPA 2020). The protection of bats is part of the measures undertaken by Sweden as part of the EUROBATS agreement which includes the protection and conservation of bats and their hunting grounds (SEPA 2006). The protection of bats can also be viewed as part of some of Sweden's environmental objectives, as reaching goals like Thriving Wetlands, A varied Agricultural Landscape, Sustainable Forests and A Rich Diversity of Plant and Animal Life would benefit most bat species (SEPA 2018). Unfortunately, most of the environmental objectives were not met by the set time of 2020 and more efforts are needed to reach the goals in the future.

How the bat populations have changed long term in Sweden is unclear since proper inventory of bats has only started to be common practice since the late 1990s due to technical advancements making auditory inventory methods more accessible (Ahlén 2011; de Jong et al 2020). Bats can be found in all parts of Sweden with varying abundance and diversity, all 19 species have been sighted in southern Sweden while only some can be found in the north (de

Jong et al 2020). Some of the most common species in Sweden; *Eptesicus nilssonii*, *Myotis daubentonii*, and *Pipistrellus pygmaeus* likely grew in numbers during the 2000s and benefit from some urban habitat traits like street lighting, built environments and added nutrition to water bodies (Ahlén 2011). The sheer abundance in these species likely cause them to outcompete some of the less common species like *Plecotus auratus* and *Barbastella barbastellus*, at least locally (Ahlén 2011). Among the most common species it appears that *Eptesicus nilssonii* has declined slightly in numbers in the last 10 years while *Myotis daubentonii* numbers have remained unchanged and *Pipistrellus pygmaeus* has likely increased slightly (de Jong et al 2020). The most common species in Sweden appear to be ones that can benefit from the more urban environments and the moving trend towards a few dominant species corresponds with the homogenizing effect of urbanization observed in other cases (Threlfall et al 2012; Threlfall et al 2016; Russo & Ancillotto 2015).

2. Theory

When we study an environmental change, we often look to the harmful aspects of the changed environment, which species are reduced in numbers or disappear due to changed conditions. However, with any disturbance in any environment and the reduction of one species, another may thrive (Morris et al 1997; McKinney & Lockwood 1999). Changed conditions can favor an opportunistic species which capitalizes on a new niche in the ecosystem and grows in number. With deteriorating conditions this often leads to biotic homogenization as some few species favor the new conditions while multiple, often more specialized species, are reduced in numbers (McKinney & Lockwood 1999). This has been observed to be the case with previous mass extinctions in the earth's history which have led to low-diversity biotas dominated by widespread adaptive species (Erwin 1998). The earth is now heading towards its sixth mass extinction, mainly caused by the expansion of the human race and its increasing urban disturbance to nature, as the rate of extinction have increased rapidly over the past 200 years, corresponding to the rise of the industrial society (Ceballos et al 2015).

In the same vein of winners and losers of disturbance, Russo & Ancillotto (2015) suggests that a gradient of increasing urbanization can be used to describe and analyze winners and losers within the bat fauna of urban environments. Some more adaptive species can utilize the environments introduced with the urban environment while less adaptive species are less fit for the urban conditions (Russo & Ancillotto 2015). This point of view allows for the distinction between synurbic bats that exploit the new ecological conditions and those that are affected by the loss of the natural habitat (Russo & Ancillotto 2015). By this Russo & Ancillotto (2015) suggest that species fitness follows different theoretical paths along the urbanization gradient; Urban-sensitive species which decrease with increasing urbanization, Synurbic species which are better adapted to increased urbanization and some semi-urban that specialize in the areas halfway along the gradient.

Following the hypothesis of intermediate disturbance (Connell 1978), we would assume to find the highest species diversity and/or bat abundance in suburban areas as it produces “optimal” levels of disturbance which maximizes biodiversity. This has been the case in some bat studies (Coleman and Barclay 2011; Luck et al 2013) which found peaks in richness and/or abundance in suburban areas, halfway along the urbanization gradient. However, Threlfall et al (2011) found that the net productivity of the habitat and individual species functional traits played a bigger role in structuring the community than the disturbance hypothesis. This further gives weight to the concept of winners and losers of the increasing urbanization as some species may have a phylogenetic susceptibility to urban environments. Indeed, Jones et al (2003) showed that lower wing aspect ratio (wingspan squared divided by wing area) was a significant predictor of extinction risk in microbats. Smaller wing aspect ratio is associated with species that have lower flight efficiency and higher flight costs, utilize smaller foraging ranges and are poorer dispersers and migrators (Norberg and Rayner 1987). These species often forage in more cluttered habitats (spatially complex) and over a smaller area than those with larger wing aspect ratios (Jones et al 2003). For example, fast hunting species like *Eptesicus nilssonii, Vespertilio murinus*, *Nyctalus noctula* have been found to often hunt under streetlight, and *Eptesicus nilssonii* individuals hunting moths under streetlight have a higher energy intake than those who do not (Rydell 1989; 1992). Some other, slower, species like the *Myotis* family and *Plecotus auritus* are however found less often hunting near streetlights (Rydell 1992). Similarly, species with low frequency echolocation use more open spaces for moving and hunting while species with lower intensity calls depend on acoustic cues in the landscape and use structures, hedgerows and tree lines when navigating their environment (Kyheröinen et al 2019).

Since the bats’ response to anthropogenic environments varies between species, we need to understand these species specific needs to identify how the bats are affected by the urban environments. These traits have been identified by previous scientific inquiries and can be found summarized for all European bats in the EUROBATS project (Kyheröinen et al 2019). More traits specific to bats in Sweden such as dwellings used during summer and winters in Sweden have also been summarized by SEPA (2020), Ahlén (2011) and de Jong et al (2020).

2.1 Swedish bat species traits

As mentioned earlier, 19 species of bats have been recorded in Sweden (de Jong et al 2020). The bats can be divided familywise into 7 taxonomic groups, although some species within the same family possess different traits. This section will be devoted to compiling some of the knowledge on the Swedish bat species and their needs from the EUROBAT project (Kyheröinen et al 2019) as well as their dispersion and preferred habitats from additional sources such as SEPA (2020), The Swedish Red List (SLU Artportalen 2020) and de Jong et al (2020). Species specific preferences can be found summarized in table 1 and are followed by a general summary of habitats and landscape features that are important to bats in Sweden as well as a few mitigating measures that can diminish some of the negative impacts of urban environments.

2.1.1 *Barbastella barbastellus*

The Western Barbastelle *Barbastella barbastellus* is a rather rare species in Sweden classified as Near Threatened (NT) by the Swedish Red List 2020 (SLU Artdatabanken 2020) but has seen an increase in number in recent years (de Jong et al 2020). In Sweden it has been found in environments such as farmland, forests, cities, and wetlands as far north as Uppsala county (SLU Artdatabanken 2020). It mostly feeds on small moths in richly structured mature forests 2-4 meters above the canopy (Sierro & Arlettaz 1997) but can also be found hunting below the canopy, along forest trails and roads (Kyheröinen et al 2019). It roosts mainly in caves and tree hollows, but is also found commonly in houses, attics, window shutter and old forts (SEPA 2020). The Barbastella bat can travel long distances, up to 25 km, between roost and hunting areas, mainly using forest corridors and edges as commuting routes, although it can cross open areas (Kyheröinen et al 2019).

To conserve the Barbastelle, EUROBAT recommends the preservation of highly structured forest, dead trees, and tall riparian vegetation. As well as favoring forest continuity by promoting corridors and high underpasses and preserving small ponds and waterbodies along forest edges (Kyheröinen et al 2019).

2.1.2 *Eptesicus* Family

Two bats of the *Eptesicus* family in Sweden are *E. nilssonii* and *E. serotinus*. They can both be found in farmland, forests, cities, limnic environments and wetlands, and they are both classified as Near Threatened (NT) (SLU Artdatabanken 2020). Both *Eptesicus spp.* are commonly found roosting in buildings, under roof panels or in attics as well as tree hollows (SEPA 2020).

Eptesicus nilssonii is known as an opportunistic species found foraging anywhere from forest glades and edges to urban parks and over water, but it prefers deciduous forests near water and areas with high insect abundance within 5 km of its roost (Kyheröinen et al 2019). It can often be found hunting near artificial light sources (Rydell 1992). When commuting between roost and hunting area it usually takes the shortest route and gives little weight to linear landscape elements (de Jong 1995), unlike many other species. Conservation efforts for *Eptesicus nilssonii* (Northern bat) should, according to EUROBATS (Kyheröinen et al 2019) focus on natural forests and grasslands as well as areas with high insect production (Kyheröinen et al 2019).

Eptesicus serotinus (Common Serotine) on the other hand is more of a forest edge and open-area specialist where it hawks for many different flying insects among the canopy or up to 20 m above open pastures (Kyheröinen et al 2019). The Serotine bat is generally larger than *nilssonii* (de Jong et al 2020) and does most of its foraging within 2 km of the roost but can travel up to 5-7 km to hunt (Kyheröinen et al 2019). Conservation efforts for *Eptesicus serotinus* should focus on permanent pastures, preservation of park-like tree groups and the creating of unbuilt urban areas like gardens, parks, and fallow land. When commuting the Serotine bat usually takes the direct path but can opportunistically utilize linear elements in the environment. The preservation of broadleaf woodlands and woodland borders adjacent to grassland are also important habitats in need of protection, especially near roosts (Kyheröinen et al 2019).

2.1.3 *Myotis* Family

The M*yotis* family is the most diverse family with 8 different species having been recorded in Sweden. They are generally more specialized than the *Eptesicus spp.* and can be found foraging in forest, over lakes or over meadows depending on species. Common for the species is that almost all of them use linear and acoustic landmarks when commuting, some can cross open areas but prefer to follow linear elements like waterways, hedgerows, and other corridors.

Myotis daubentonii is the most common *Myotis* and is currently one of the few Least concern bat species in Sweden. It is mainly found trawling for insects in aquatic habitats and thus prefers open flowing or static water bodies with little clutter (Kyheröinen et al 2019). It can be found roosting in houses, tree hollows and sometimes caves (de Jong et al 2020; SEPA 2020) and commutes following waterways and tree lines ((Downs & Racey 2006).

Myotis dasycneme is in many ways similar to M. *daubentonii* but larger and has a more straight and direct flight path. It is found in the same habitats and environments as *M.*

daubentonii but can travel farther between roost and foraging area and can easily cross open areas like arable land, meadows, or large blocks of coniferous plantations (Ciechanowski & Zapart 2012). It is found regularly up to Uppsala county but has occasionally been sighted further north, it is considered as Near Threatened (NT) (SLU Artdatabanken 2020).

To conserve the water specialist bats like *M. daubentonii* and *M. dasycneme,* EUROBATS recommends the preservation of waterbodies and linear waterways and otherwise riparian vegetation. Avoiding eutrophication of lakes and reducing pesticide use are also important measures (Kyheröinen et al 2019).

Myotis alcathoe, brandtii and *mystacinus,* are all species found mainly in forests where they forage in the canopy but also near the ground around tree stems. They are the smallest bats in Sweden. *M. mystacinus* and *brandtii* roost in buildings and tree hollows while *alcathoe* builds its colonies in tree hollows (de Jong et al 2020). *M. alcathoe* is classed as Endangered (EN) and have in Sweden been found in farmland, forests, urban areas, and wetlands (SLU Artdatabanken 2020), *brandtii* and *mystacinus* are both classed as Least Concern (SLU Artdatabanken 2020) but *brandtii* is rarely found in urban environments (Kyheröinen et al 2019). When commuting they follow linear fixed routes along wood lanes, hedges, streams, and forest edges. Conservation of these species should, according to EUROBATS (Kyheröinen et al 2019), focus on the restoration of mature broadleaf forests, woodlands, and riparian zones around roosts as well as avoiding the trespass of artificial light (Kyheröinen et al 2019).

Myotis bechsteinii and *M. myotis* are much larger than the other *Myotis* species and are some of the rarest in Sweden. They are both classed as Endangered (EN) and are exclusive to the southern parts of the country (SLU Artdatabanken 2020). They both prefer to hunt in open deciduous forests with little understory as they sometimes catch insets on the ground. *M. myotis* can build colonies in houses while *M. bechsteinii* keeps to tree hollows (de Jong et al 2020). While *bechsteinii* generally only commutes within the forest area (Kerth & Melber 2009), *M. myotis* commutes directly from roost to foraging area (Kyheröinen et al 2019). Conservation of these species should focus on maintaining and increasing the proportion of deciduous forests and promote continuity of forests. Further the controlling of shrub and maintenance of forest alleys clear of vegetation is important, while pesticides and light trespass should be avoided (Kyheröinen et al 2019).

Myotis nattereri is classed as Near Threatened (NT) and has been found as far north as Västernorrlands county (SLU Artdatabanken 2020). This bat is mainly a forest foraging bat found mostly in swamp forests and along streams (de Jong et al 2020) but can also commonly be found in meadows, pastures, and orchards (Kyheröinen et al 2019) as well as in cattle sheds

(Simon et al 2004). It roosts in both houses and tree hollows and commutes following linear landscape elements like hedgerows and waterways with riparian vegetation (Kyheröinen et al 2019). Conservation of this species is much like the other M*yotis* species with the addition of keeping cattle sheds and stables unlit and accessible to bats (Kyheröinen et al 2019).

2.1.4 *Nyctalus* Family

There are two Swedish bats of the *Nyctalus* family. *Nyctalus noctula* (LC) is one of the more common bats in Sweden found throughout most of the country while *Nyctalus leisleri* is one of the rarest. *N. leisleri* is significantly smaller than *N. noctula* and classed as vulnerable (VU) and found mostly in southern Sweden (SLU Artdatabanken 2020) where it forages in most open and half-open biomes (de Jong et al 2020). These bats often hunt before dark over open and half-open habitats like lakes, riparian meadows and pastures and can regularly travel far from the roost to forage. They mostly roost in tree hollows but can sometimes be found roosting in buildings during the winter (de Jong et al 2020), often in ventilation of multistory buildings (SEPA 2020). However, most of the population migrates out of the country in the autumn, which makes windfarms a dangerous obstacle along its migratory path (Rydell 2017). When commuting to foraging areas, these bats usually take the most direct path (Kyheröinen et al 2019). Conservation of the *Nyctalus* bats should focus on the protection of riparian vegetation, broadleaf forests, and natural pastures as well as unmanaged woodlands. Additionally, windfarm projects need to take migratory paths into consideration (Kyheröinen et al 2019).

2.1.5 *Pipistrellus* Family

Three bats in Sweden are of the *Pipistrellus* family. *P. pipistrellus* (VU) and *P. pygmaeus* (LC) are very similar but *P. pygmaeus* is substantially more common as one of the most numerous bat species. *P. nathusii* (LC) is similar in behavior to the other two but larger and has slightly wider wings (de Jong et al 2020). These bats prefer to forage along forest edges and in sparse woodlands, especially broadleaf forests (de Jong et al 2020) but can also be found in parks and garden with deciduous trees and wetlands (Kyheröinen et al 2019). They roost in tree hollows and commonly in buildings, sometimes in large colonies of 300-500 individuals (de Jong et al 2020). *P. nathusii* is a pronounced migrator and can migrate as far as to south France (de Jong et al 2020), making it extra susceptible to the negative impacts of windfarms (Rydell 2017). These bats generally forage relatively close to the roosts and use linear landscape elements to navigate, although *P. nathusii* may sometimes commute across open fields (Kyheröinen et al 2019). To conserve the Pipistrelle bats, conservation efforts should focus on the preservation of riparian habitats, wetlands, and especially mature deciduous forests. Linear landscape elements like hedgerows, tree lines and waterways are also important landscape factors to maintain. Finally, windfarms need to consider the movement of these bats when deliberating on location and take mitigating measures (Kyheröinen et al 2019).

2.1.6 *Plecotus* Family

Two Swedish bats are of the *Plecotus family*, *Plecotus auratus* (NT) is one of the more common bats found regularly as far north as Västernorrland county, while *Plecotus austriacus* (CR) is one of the rarest and have only been sighted in Skåne county (SLU Artdatabanken 2020; de Jong et al 2020). These bats mainly forage in larger woodlands, along forest edges, bushes, and hedgerows where they glean insects of off trees and meadows, *Plecotus austriacus* is also found often in more open habitats like open meadows and pastures (Kyheröinen et al 2019; de Jong et al 2020). *Plecotus auratus* have traditionally been found roosting in churches in Sweden, but when these have been increasingly lit up in recent years, they are no longer suitable roosts. This may explain some of the species recent decline in number (de Jong et al 2020). Linear landscape elements can be important for the *Plecotus* bats to follow when commuting and are important to preserve to keep environments habitable for these bats (Kyheröinen et al 2019), Conserving traditional woodlands, gardens and orchards near roosts is also important and avoiding the trespass of light, especially near roosts, is particularly essential for this species (Kyheröinen et al 2019).

2.1.7 *Vespertilio murinus*

Vespertilio murinus is in some ways much like *Eptesicus nilssonii*, it hunts in a variety of habitats, over water bodies, agricultural areas, meadows and forests to human settlements and it seems to prefer a mosaic of habitats in open to half-open areas (Kyheröinen et al 2019). *Vespertilio murinus* can be found as far north as Västernorrlands county and is classed as Least Concern (LC). It mostly hunts 20-40 meters above the ground and can commonly be found foraging around streetlights (Rydell 1992a; Rydell & Baagøe 1994). They mainly roost in buildings and some colonies spend the winters in buildings, while some migrate south during (de Jong et al 2020). Traveling from roost to foraging area this species commutes directly, about 2-3 km from the roost. Due to some of the population migrating during the winter, these bats are extra susceptible to the negative impacts of windfarms and extra avoidance and mitigation measures should therefore be implemented in these projects to help conserve the bat population (Kyheröinen et al 2019). Further conservation should focus on facilitating heterogenous areas with high insect abundance, such as wetlands and deciduous forests (Kyheröinen et al 2019).

Table 1. Summary of species preferred habitats based on theoretical framework.

Species	Feeding areas	Commuting routes	Roosts
Barbastella barbastellus	Mature forests above canopy or below along trails and roads	Forest edges are important but can cross open areas and travels far	Buildings, Caves
Eptesicus nilssonii	Opportunistic, forests, parks, deciduous forests	Often takes the shortest route	Buildings, Tree Hollows
Eptesicus serotinus	Forest edges and open area specialist	Can fly straight to feeding area, opportunistically using linear landscape elements	Buildings, Tree Hollows
Myotis alcathoe	Forest specialist, canopy and near ground	Linear landscapes, hedges, streams, forest edges	Tree Hollows
Myotis bechstenii	Open deciduous forest	Only forested areas, prefers underpasses for crossing motorways	Tree Hollows
Myotis brandtii	Forest specialist, canopy and near ground	Fixed routes along wood lanes, hedges, and forest edges, does not cross open areas.	Building, Tree hollows
Myotis dasycneme	Water specialist, trawling	Crosses open areas, can utilize linear elements like tree lines and hedgerows	Buildings, Tree Hollows and Caves
Myotis daubentonii	Water specialist, trawling	Waterways and tree lines	Buildings, Tree Hollows and Caves
Myotis mystacinus	Forest specialist, canopy and near ground	Hedgerows, acoustic landmarks	Buildings, Tree hollows
Myotis myotis	Open deciduous forest	Direct flight, utilizes corridors	Buildings, Tree hollows
Myotis nattereri	Swap forest and along streams, meadows, and cattle sheds	Hedgerows and waterways with riparian vegetation	Buildings, Tree hollows
Nyctalus leisleri	Open and half open biomes like pastures and meadows, before dark	Commutes directly	Tree Hollows, buildings (Winter)
Nyctalus noctula	Open and half open biomes like pastures and meadows, before dark	Commutes directly	Tree Hollows, buildings (Winter)
Pipistrellus nathusii	Forest edges, parks, and gardens with deciduous trees	linear landscape elements, streams, forest edges, hedges tree lines	Tree Hollows, migrates during winter
Pipistrellus pipistrellus	Forest edges, parks, and gardens with deciduous trees	Follows streets, hedgerows, tree lines or woodland edges, can cross open areas for a few hundred meters.	Tree hollows, buildings
Pipistrellus pygmaeus	Forest edges, parks, and gardens with deciduous trees	Linear landscape elements	Tree hollows, buildings
Plecotus auritus	Large woodlands, forest edges	Can use linear landscapes	Churches, tree hollows
Plecotus austriacus	Large woodlands, forest edges	Linear landscape elements, can cross open meadows	Buildings
Vespertilio murinus	Mosaic of open to half-open habitats	Commutes directly	Buildings, some migrate during winter

2.1.8 General important landscape elements and measures.

In summary, although different bats utilize different environments, there are some landscape features and measures that can benefit the bat fauna as a whole. First and foremost is to secure appropriate feeding areas around and nearby roosts. This requires knowledge of the bat populations and any project that is likely to affect any bats, should include a bat survey and analysis of potential affects (Kyheröinen et al 2019). By knowing which bats are present and their needs, projects can easier implement mitigating measures. Knowledge on migration paths is also important in this context, but academic understanding in this field is still lacking.

In general, areas with high insect production, such as woodlands near waterbodies, broadleaf forests, parks, and orchards are beneficial for all bat species, especially reproducing females (Kyheröinen et al 2019). Further, connectivity within the landscape is essential as many bats favor linear structures and edges which they can follow when commuting to and from feeding habitats. As such, bats greatly benefit from planning strategies that take the whole landscape into consideration (Kyheröinen et al 2019). Bats normally favor older forests as these provide more tree cavities for roosts and natural patches in the woodworks, such as streams, fallen tree patches and small open landscape structures that provide good feeding areas (Kyheröinen et al 2019). Large size clearings from forest management are usually too wide for many bats to cross and bats crossing open areas run higher risk of being preyed upon by predatory birds (Lesiński et al 2009). These large openings in the environment therefore risk fragmenting the habitat.

While most urban landscape elements like roads, residential areas, wind energy, artificial lighting, large scale agriculture and forest management would mostly affect bats negatively, there are some measures that can be implemented to mitigate the negative impact of these urban features. Solid linear landscape elements like fences, stone walls and natural rock formations can to some extent substitute for hedgerows and tree lines, although lacking the foraging opportunities (Kyheröinen et al 2019). Green roofs have been found to have significantly higher diversity and activity among urban bats than non-green roofs (Pearce & Walters 2012; Parkins & Clark 2015). Forest operations that negatively impact bats, like clearcutting and small patch cutting can be mitigated by retaining tree lines and old trees (Kyheröinen et al 2019). By creating and maintaining ponds, dikes and riparian areas, more suitable habitats can be made available for bats in both urban and rural environments. Preserving old buildings like watermills, barns and bridges can also facilitate better habitats for bats in otherwise less than ideal environments (Kyheröinen et al 2019). And finally assessing the impact of current, and implementation of new artificial light, is crucial in ensuring the suitability for many bats as artificial light sources can both harm habitats and fragment areas from each other (Voigt et al 2018).

3. Method

The goal of this paper is to examine the relationship between the bats in Sweden and anthropogenic environments in the form of land cover types as well as socio and economic data showing the socio-cultural development of the studied areas. Thus, there are three sets of data that lay the foundation for the study; (i) Bat sightings through sound recordings reported to artportalen.se, (ii) National Land Cover data provided by the Swedish environmental protection agency (SEPA) through the CadasterENV Sweden project (NMD, Naturvårdsverket 2020) and (iii) Demographical statistics (DeSO) provided by the Swedish Central bureau of statistics (SCB). These data allow the study to examine individual species as well as the bat population as a whole along two urbanization gradients: increasing urban land cover and socio-cultural development. The land cover data is used to analyze the level of anthropogenic exploitation in a radius around the areas where bats have been sighted, while the spatial combining of demographic data and bat sightings allows for a study on their geographical relationship. As such, the study aims to study how the bats in Sweden are affected by some aspects of urbanization. The analysis is thus formulated as follows: (i) How are the bat populations and/or diversity affected by increased physical urbanization? (ii) How are the bat populations and/or diversity affected by increased socio-cultural urbanization.

For further and deeper studies of the anthropogenic effects on bats and wildlife in Sweden, science should move in closer and study more specifically what in the urban environment is the driving factor to the change. This could be done by studying individuals living in such environments and collecting more specific data through tests and observations over a long time to determine what is the leading cause of a species rise or decline in the area. Some studies have done this by examining the heterogeneity (Monck-Whip et al 2018) and connectedness (Heim et al 2015) of bat habitats and found valuable results, however, more investigation is needed to better our understanding of the environment. Due to the time frame of this study this was not possible since most of the work has been done during the winter and early spring when bats are hibernating and studying them up close would risk disturbing their wellbeing. Instead, this study has focused on general patterns on a national level with the aim of providing better knowledge of the anthropogenic relationship to the bats.

3.1 Collection of data

As mentioned, the data for this study consists of three parts (table 4), these three datasets are combined geographically using the GIS-software ArcMap 10.8.1.

The data of bat sightings provides the basis for the study. This dataset consists of recordings of bats from the years 2017 and 2018 that have been reported to the artportalen.se database maintained by the Swedish Species Information Centre (SLU) at the Swedish University of Agricultural sciences on behalf of the Swedish Environmental protection agency (SEPA) (artportalen.se 2021). Sightings are reported by both private individuals and enthusiasts as well as professionals such as researchers. Methods of observation vary from visual observations to audio recordings however, for the purpose of species identification this study has only included audio recordings. Some reports do not specify any species and have thus been discarded from the dataset, this results in a total of 13038 bat sighting spread across most of the country. The datapoints include such information as XY coordinates, species, and threat level according to the Swedish red list.

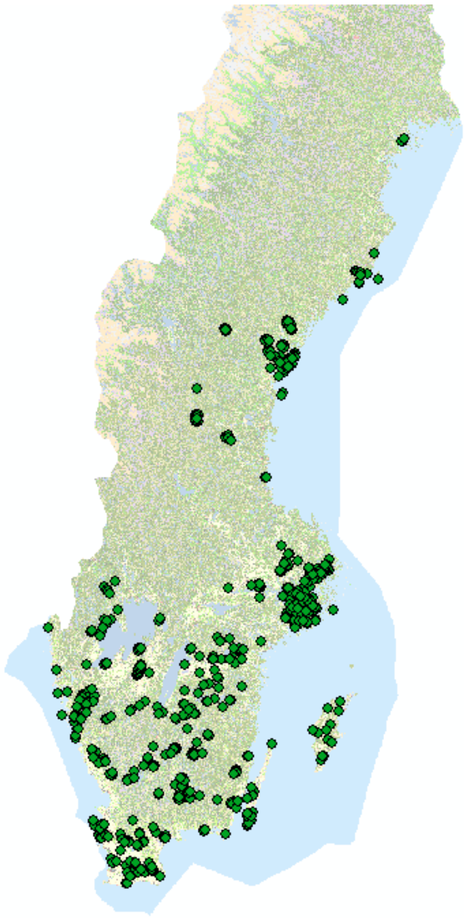

Figure 1. Map of all bat sightings, NMD Naturvårdsverket

The bat-data is combined with the other two datasets to examine the physical and socio-cultural relationships between bats and urban environments. The land cover data from SEPA is used to analyze the physical environment. This data consists of satellite data from 2015-2018 combined with laser scanning from 2009-2019 and has been developed to cover the whole country in a resolution of 10-meter/pixel. The map-layer generally gives a high accuracy of representation of the land cover, only having trouble with accuracy where there is dramatic topography (NMD, Naturvårdsverket 2020). This set of data supplies the study with information on what kind of landcover bats have been sighted in. Originally the landcover is divided into multiple variables of exploited land, forest types and wetland types. For this study these have been combined into single variables of total exploited land, overall forest, broadleaved forests, and total wetlands to reduce the number of variables in the statistical testing. The combined variables are listed in table 2.

Table 2. Combined land cover variables and their original names from the NMD land cover data. Original land cover attributes are combined into the Land cover variables used in the testing of this study. Original landcover attributes have been translated to English from the original Swedish names.

Land cover variable	*Original landcover attributes*
Exploited land	Buildings
	Railroads
	Exploited land - not buildings or railroads
Water	Lakes and watercourses
Farmland	Farmland
Open ground without vegetation	Open ground without vegetation
Open ground with vegetation	Open ground with vegetation
Forest	Spruce outside wetland
	Coniferous forest outside wetland
	Deciduous/coniferous forest outside wetland
	Trivial deciduous forest outside wetlands
	Broadleaf outside wetland
	Deciduous/broadleaf outside wetland
Broadleaf forest	Broadleaf outside wetland
	Deciduous/broadleaf outside wetland
	Broadleaf on wetland
	Deciduous/broadleaf on wetland
Wetlands	Open wetlands
	Pine on wetland
	Spruce on wetland
	Coniferous on wetland
	Deciduous/broadleaf on wetland
	Trivial deciduous on wetland
	Broadleaf on wetland
	Deciduous/broadleaf on wetland
	Temporary no forest on wetland

For the purpose of the land cover analysis bat points that are within 500 meters of each other have been integrated and grouped by locales (see Figure 1). Around each locale a 500-meter buffer is used to summarize the land cover of the surrounding area using the Tabulate area function in ArcMap 10.8.1 which calculates the pixel area of the National land cover data within each buffer. To avoid misrepresentation, original points that are located outside of these buffers are excluded from the study, as are buffers that were made in between two points and thus did not contain any original bat points. These are not given their own buffers as overlapping buffer areas do not work with the tabulate area function. This reduces the dataset to 10160 points of bat recordings distributed across 418 different locales and a total of 18 species which can be used for the analysis.

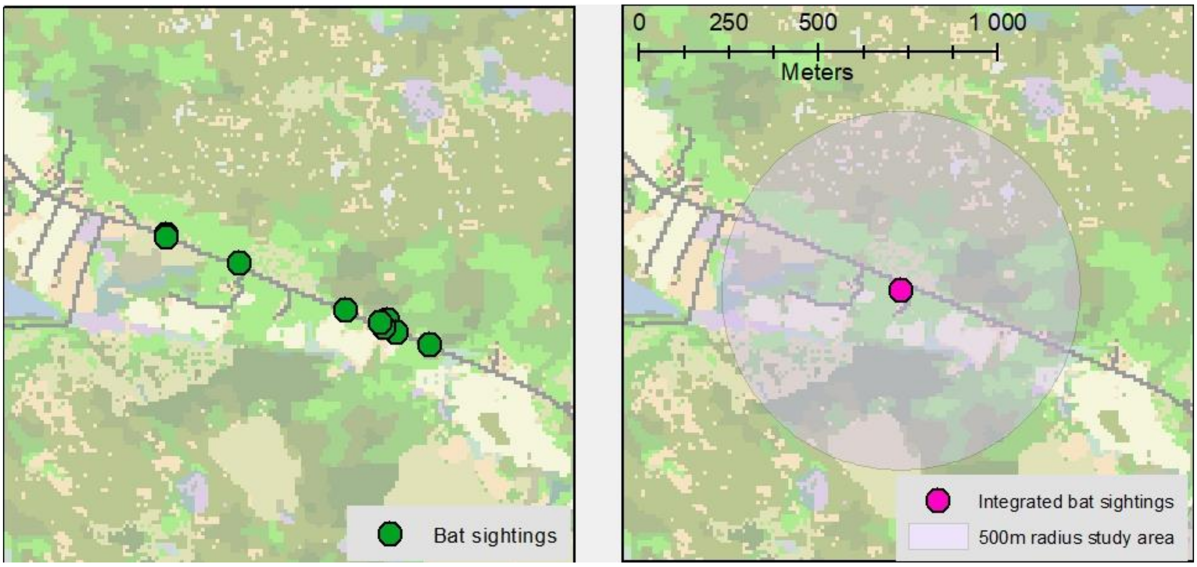

Figure 2 Example of how bat-points have been integrated into a single point representing a locale. Left picture shows bat-points (green) before integration. Right picture shows all bat points integrated into one point (pink) representing the locale around which land use is analyzed in a 500-meter radius (large pink circle).

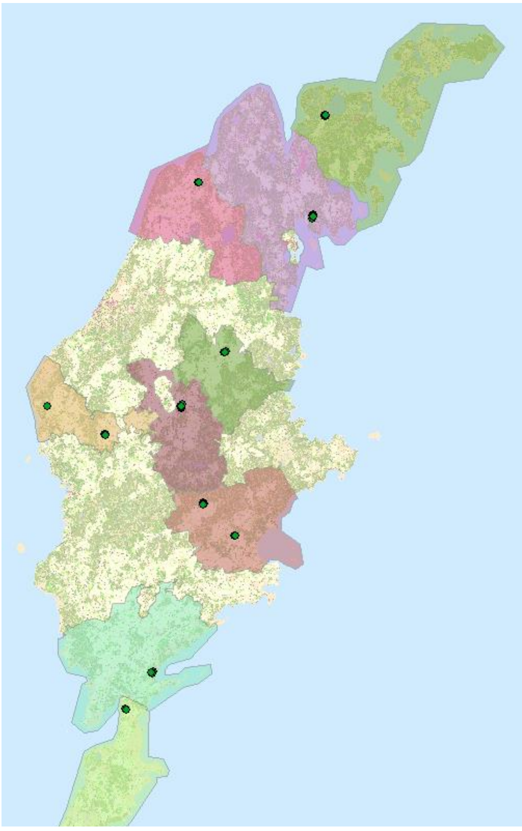

Figure 3. Map exemplifying DeSO-zones with bats found in them on Gotland. NMD Naturvårdsverket, SCB

Demographical statistical areas (DeSO) provided by SCB are used to analyze the socio-cultural environments. This is a nationwide division of areas based on population numbers and natural landmarks which divides the nation in 5984 areas (SCB 2021). Each of these areas hold statistics of how many reside in the area, the general income level, and the most common type of living etc. By spatially combining the bat-points with the DeSO-zones which they reside in the study is left with 306 DeSO-zones in which bats have been found. These have then been analyzed to determine whether there are any significant relationships between the bats' occurrence and these socio-cultural variables such as average income, housing types, population density and the proportion of citizens with low financial standard (economic standard less than 60% of the national median). The DeSO-zones are divided based on population numbers ranging from approximately 700 – 2700 people as well as natural landmarks (SCB 2021). This means the size of the DeSO-areas differ in size as there are smaller ones within more densely populated areas and larger zones outside the city centers. Thus, the population density (DeSO-population/DeSO-area) in this study is different from the national population density and varies considerably between DeSO-zones. Population density is used in the analysis since population number in itself correlates too much with the other variables in the data. The DeSO variables used in this study, their original description and how they have been combined is listen in table 3.

Table 3. DeSO variables used in the analysis of this study.

DeSO variable	*Original DeSO variables*
p/km^2	$Population \div DeSOzone\ area\ (km^2)$
Average income	average income of households in thousand crowns (tkr)
Apartments	Number of apartment buildings
Low financial standard	Proportion of low financial standard (average income <60% national standard)
Detached houses	Number of detached houses

Since this study is more on a general, national level as opposed to an in-depth local analysis it warrants a digital inventory of the land cover and the bats' relationship to anthropogenic environments. While a digital study risks missing some small-scale details that a physical in-situ study would likely find, it allows for broader more general patterns to be identified and studied in a more time efficient manner.

Table 4 Input data used in ArcMap to gather data on environments where bats have been found.

Data, format	Attributes	Source, Year
Bat sightings, Points	Species, Coordinates, Locales	Artportalen.se, 2017-2018
Land Cover data, Pixels	Land cover type/10m	NMD Naturvårdsverket 2020
DeSO-zones, Polygons	Demographic statistics	SCB, 2018

3.2 Analysis of data

Through the analysis the study seeks to answer the questions of whether the bats are affected by urbanization, both physical and socio-cultural. This analysis is done by statistically studying the relationship between the different variables in the statistics program R 4.0.4 (R core team 2021) and the additional packages; Political Science Computational Laboratory (pscl 1.5.5) for zero-inflation models (Jackman 2020; Zeileis 2008); Analyses of Phylogenetics and Evolution (ape 5.4-1) (Paradis 2019), Spatial Covariance Functions (ncf 1.2-9) (Bjornstad 2020) and Spatial Dependence: Weighting Schemes, Statistics (spdep 1.1-7) (Bivand & Wong 2018) for auto covariation analysis; and the package MASS 7.3-53.1 (Venables & Ripley 2002) for negative binomial models and stepwise model selection.

This statistical analysis focuses on determining significant correlations between the number of bats, species and individual species in a locale and land cover types/DeSo variables. For most of the tests the study is using zero-inflation models (package pscl) with negative binomial distribution (package MASS) which mainly helps adjust for the residual dispersion since the response variables often have an inflation of 0:s, or in the case of species 1:s. Zero-inflation models let the study find not only if the explanatory variable (i.e. land cover) correlates to the response variable (bats, species etc.), but also if the explanatory variable correlates to the total absence or presence of the response variable. This is done by the model yielding a count coefficient and a zero-inflation coefficient. The count coefficient explains the correlation between the numeric value of the response and the explanatory variable while the zero-inflation coefficient explains weather the explanatory variable affects the occurrence of the response (i.e., bats). For example, if bats were to have a significant negative zero-inflation correlation to exploited land, it would imply that exploited land makes it less likely for any bats to be found in a locale.

In the models the study also factors in the spatial autocorrelation of the bats, that is, if the number of bats or species in neighboring sites (up to 100km away) influences the number of bats or species. The auto covariate is mainly included to improve the statistical models, it is part of the study and included in every statistical analysis, but the results of the auto covariate is not reported in the results. The MASS package is used for stepwise model selection which selects the explanatory variables that gives the best model to explain the correlation using stepwise AIC comparisons. The correlations of general bat numbers (all bats) and landcover/DeSO data used a normal linear regression since there is no inflation of 0 due to every locale having at least 1 bat sighting. Similarly, the zero-inflation model on number of species tests on the presence of only 1 species due to each locale having at least 1 species of bats.

The models yield a coefficient estimate which indicates whether the correlation is positive or negative and a p-value which (if <0.05) indicates if we can accept the correlation as statistically significant. A species which shows a positive correlation to a type of land cover could thus be considered as favored by that type of environment and possible assumptions can be made about how the bats would be affected if the landscape changed. Plotting the residual of each test to verify their residuals allowed for diagnosing for over/under dispersion in the model.

Since the models are using multiple regression analysis, we are analyzing several variables at the same time, meaning that we factor in other relationships between the variables when we find a significant relationship. For example, poorer areas may also have more natural environments. By factoring in both economic variables and population density at the same time, we can adjust to the risk of observing the bats relations to natural environments when studying the economic association. If we observe a significant relationship between bat abundance and economic standard while factoring in population density, we minimize the risk of actually observing the bats relation to population density through the economic variable.

4. Results & Analysis

In this section the results of the statistical analysis will be presented, introduced by a general summary of the gathered bat data. The study has been conducted on data containing a total of 10160 bat sightings and 18 out of the 19 species occurred in Sweden, only lacking the rarely seen and endangered (EN) *Myotis bechsteinii*. Two *Myotis* species *Myotis brandtii* and *Myotis mystacinus* are combined in the data and analysis since it is difficult to differentiate the two only through sound (Ahlén 2011). The data from artportalen.se also contained several undetermined *Myotis* individuals which have been tested separately in the analysis.

Locales had a mean diversity of 5 bat species, with the most diverse locale having a total of 16 species present while some only had a single bat species. The most common bat species *Eptesicus nilssonii* was recorded 2102 times, followed by *Pipistrellus pygmaeus* (1662), *Nyctalus noctula* (1096) and *Myotis daubentonii* (1080). The least common species were *Plecotus austriacus*, with only a single recorded sighting, followed by *Myotis alcathoe* (4) and *Myotis myotis (11)* all of which are either Critically endangered or endangered and have only been encountered in southern Sweden (SLU Artdatabanken 2020, de Jong et al 2020). Some species occurred in such low numbers that no significant correlations could be found, these were the three previous mentioned as well as *Nyctalus leisleri* and *Pipistrellus pipistrellus.* The bats were divided over 418 locations for the land cover study, ranging from no exploited land up to 73% exploited land cover. Locales also ranged from 0% up 98% forest cover, with as much as 66% broadleaf forest, and from 0% to 75% wetland.

For the DeSO study the bats were divided over 306 DeSO-zones in which the bats correlation to financial standard and population statistics were examined. The DeSO-zones ranged from low populated areas of 718 people to more highly populated areas of up to 3470 people. Important to note is that the size of the DeSO-areas differs greatly since the boarders follow general population numbers and landmarks, thus, the population density ranges from 0,0006 people/km^2 in the least densely populated areas to 10 people/km^2 in the densest populated DeSO-areas. The average economic standard ranged from 209 thousand Swedish crowns (t.kr) per year, a monthly income of approximately US$2000/month, up to 680 t.kr/y (6700 USD/month). The proportion of low financial standard citizens ranged from 1% in the wealthiest areas to 37% in the poorest.

4.1 Land cover analysis

The statistical analysis on the relationship between bats and land cover found multiple significant associations, unfortunately, some of the less common species occurred in such low numbers that they had no individual results but were a part of the overall bats and species tests. Any significant results have been compiled and are presented in table 5.

Both general bat numbers and the number of species showed a negative correlation to exploited land (Figure 2). Species also correlated negatively to open ground without vegetation and positively to water for the count model. For zero-inflation, species correlated positively to open ground with vegetation, suggesting that locales with some open vegetated areas allow for more than one species to share the same habitat area. Both the abundance of bats and the number of species correlated positively to broadleaf forest (Figure 4), indicating that rich and diverse vegetation is important for the occurrence of bats. Species also correlated negatively through zero-inflation with broadleaf forest, indicating that if there is no broadleaf forest it is unlikely for multiple species to be present. The importance of broadleaf forest is also reflected in the individual species analysis as almost every species had a positive count correlation to that type of land cover. *Eptesicus nilssonii*, the most common species, even showed a positive zero-inflation correlation to broadleaf forest, implying that broadleaf forests are a significantly important habitat for the species.

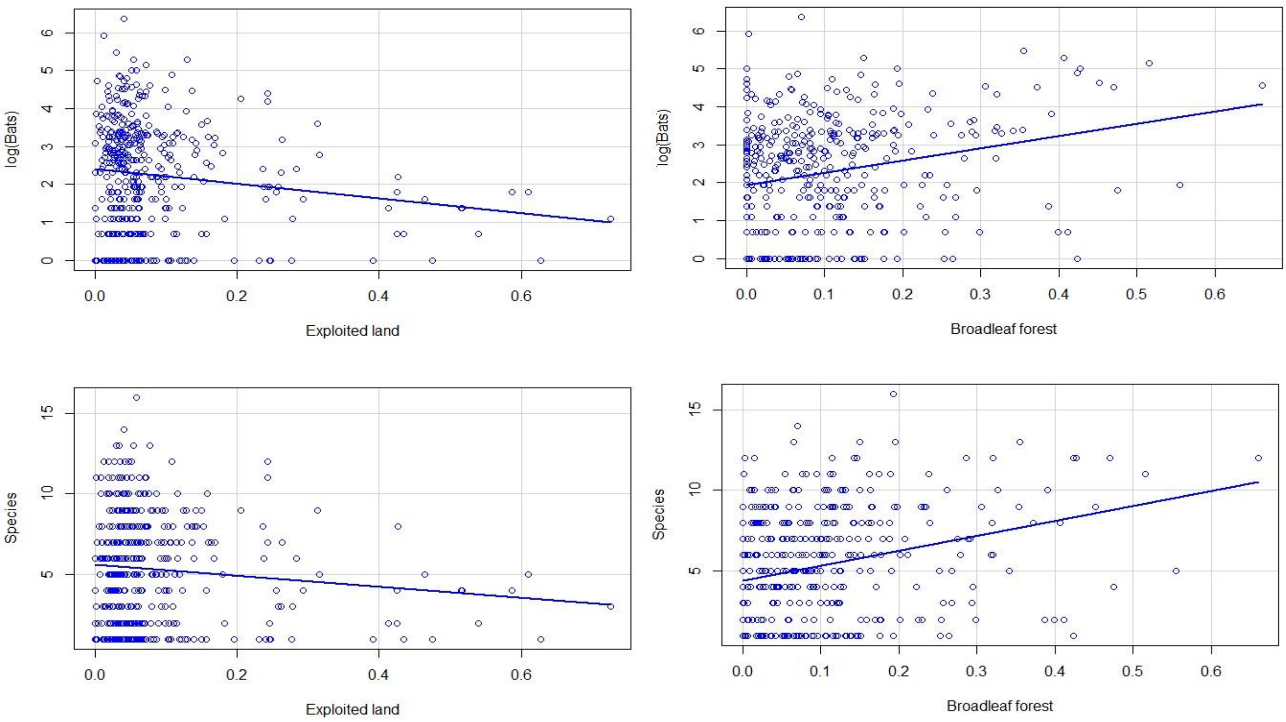

Figure 4. Scatterplots illustrating the count relationships between bats and two land cover types, blue line shows the least-square line which represent the relationship between the two variables. ***Top left****: (log)Bats negative count correlation to exploited land (r=-2,1 p<0,05).* ***Top right****: (log)Bats positive count correlation to broadleaf forest (r=3,29 p<0,05).* ***Bottom left:*** *number of species negative count correlation to exploited land (r=-0,85 p<0,05).* ***Bottom right****: number of species positive count correlation to broadleaf forest (r=1,21 p<0,05).*

Similarly, exploited land cover had a negative correlation to most species, as did farmland. Suggesting that most bats prefer natural environments, especially diverse broadleaf forests, over the human made environments like cities and agricultural farms with a less diverse set of trees and other vegetation. Two tests (*Myotis mystacinus/brandtii* and *Pipistrellus nathusii*) did however show a positive zero-inflation correlation to exploited land while having a negative count correlation to the same variable. This can be interpreted as these bats being found often in urban environments, but in lesser numbers than when observed in less urban locales. A possible explanation for this could be that these bats are more likely to be observed and reported to artportalen.se in environments where there are humans, but when these bats have been observed in other environments they have been found in greater number.

One species however, stood out from the others during the analysis. *Myotis dasycneme* showed no negative correlation to exploited land and a positive correlation to farmland for both the count and Zero-inflation coefficient, indicating that the species is favored by farmland. It also showed a negative correlation to wetlands for both the count and zero-inflation coefficient and a positive zero-inflation correlation to lakes and moving water, as well as a positive zero-inflation correlation to open land with vegetation. This could suggest that *Myotis dasycneme* indeed favors a different kind of habitat compared to most other bats in the study. While most bats seem to favor natural environments and especially broadleaf forests, *Myotis dasycneme* also occurs in more open habitats and is not negatively impacted by the human influence. Indeed, the species even seems to take advantage of the insect rich farm environments that other species appear to dislike. *Barbastella barbastellus* also stood out as one of the few species that did not have a negative correlation to exploited land. This could indicate that the species is not as negatively impacted by urban exploitation as most other bats species, however it does not show that it is favored by anthropogenic environments, as it did correlate negatively (count) to open ground without vegetation.

Open ground appears to be the variable with the most varied responses. Some species like *Eptesicus serotinus* (count), *Myotis dasycneme* (zero-inflation) and *Nyctalus Noctula* (zero-inflation) had a positive correlation to open ground with vegetation while *Eptesicus nilssonii* (zero-inflation), *Myotis mystacinus/brandtii* (count) and *Vespertilio murinus* (count) were found less in locales with this land cover type. This is also reflected in the species diversity positive zero-inflation to open ground with vegetation which saw more than one species in locales with more open ground with vegetation. Similarly, we saw that species diversity decreased with increased open ground without vegetation (count), while *Eptesicus nilssonii* (zero-inflation), *Myotis mystacinus/brandtii* (zero-inflation) and *Pipistrellus pygmaeus* (zero-inflation) were in fact all found more often in locales with open ground without vegetation. *Pipistrellus nathusii* on the other hand had a strong negative correlation to this land cover type for both the count and zero-inflation model. These results suggest that species that utilize a more open landscape seem to thrive since all the most common species had a positive correlation to open ground.

The relationship to water seems to vary between species. Some species like *Barbastella barbastellus* (count) and *Myotis dasycneme* (zero-inflation) showed a positive relationship to water while *Myotis* and *Pipistrellus nathusii* showed a negative (count) correlation to water. Overall species richness also appears to increase with water, indicating that habitats with waterbodies or moving water may allow for more species to find suitable habitat.

Table 5. Significant statistical results on the land cover analysis, Coefficient indicates whether there is a positive or negative relationship between the response and the explanatory variable, p-value indicates the results significance level. Explanatory count results show if the explanatory variable correlates to the number of the bats or species. Zero-inflation results show if the explanatory variable correlates to the presence of bats or multiple species in a locale.

Response Variables	*Explanatory variable Count*	*Coefficient*	*P*	*Explanatory variable Zero-inflation*	*Coefficient*	*p*
(log)Bats	Exploited land	-2.103	<0.001			
	Broadleaf forest	3.298	<0.001			

Species richness	Exploited land	-0.858	0.038	Open ground with vegetation	4.199	0.033
	Open ground without vegetation	-5.956	0.014			
	Water	0.800	0.002			
	Broadleaf forest	1.215	0.001	Broadleaf forest	-6.406	0.015
Barbastella barbastellus	Farmland	3.657	0.016			
	Water	4.931	0.016			
	Forest	6.287	<0.001			
	Broadleaf forest	3.387	<0.001			
Eptesicus nilssonii	Farmland	-1.413	<0.001	Open ground with vegetation	-51.553	0.047
	Exploited land	-3.731	<0.001	Open ground without vegetation	108.317	0.043
	Broadleaf forest	1.389	0.015	Broadleaf Forest	14.867	0.043
Eptesicus serotinus	Open ground with vegetation	4.275	0.043			
	Exploited land	-6.296	0.007			
	Wetlands	8.922	0.004			
	Broadleaf forest	3.390	0.023			
Myotis	Farmland	-5.052	<0.001	Farmland	-5.030	0.004
	Exploited land	-5.200	0.020			
	Water	-2.490	0.020			
	Broadleaf forest	2.618	0.024			
Myotis dasycneme	Farmland	5.126	<0.001	Farmland	19.036	0.002
	Wetland	-13.761	0.001	Wetland	-89.194	0.002
				Open ground with vegetation	24.596	<0.05
	Broadleaf forest	3.483	<0.01	Forest	11.114	0.023
	Water	4.577	0.016	Water	14.295	0.022
Myotis daubentonii	Farmland	-2.292	<0.001			
	Exploited land	-4.448	<0.001			
	Forest	-1.744	0.004			
	Broadleaf forest	2.792	<0.001			
Myotis mystacinus + brandtii	Farmland	-0.999	0.020	Farmland	3.884	0.018
	Open ground with vegetation	-2.116	0.035	Open ground without vegetation	72.544	0.019
	Exploited land	-3.405	0.009	Exploited land	13.177	0.019
	Broadleaf forest	2.397	<0.001			
Myotis nattereri	Exploited land	-4.369	0.044			
	Forest	2.120	0.006			
	Broadleaf forest	3.980	<0.001			
Nyctalus Noctula	Exploited land	-2.957	0.001	Open ground with vegetation	14.737	0.035
	Broadleaf forest	2.030	0.005			
Pipistrellus nathusii	Farmland	-3.054	<0.001			
	Open ground without vegetation	-29.121	0.001	Open ground without vegetation	-1899.463	0.001
	Exploited land	-9.176	0.002	Exploited land	147.245	0.001

	Forest	-3.100	<0.001			
	Wetland	-9.441	0.004			
	Water	-5.475	0.0001	Water	-199.455	0.013
	Broadleaf forest	4.104	<0.001			
Pipistrellus pygmaeus	Farmland	-2.278	<0.001	Open ground without vegetation	66.020	0.035
	Exploited land	-3.766	<0.001			
	Forest	-1.290	0.001			
	Broadleaf forest	2.279	<0.001			
Plecotus auritus	Exploited land	-3.764	0.006			
	Broadleaf forest	4.781	<0.001			
Vespertilio murinus	Farmland	-3.435	<0.001			
	Open ground with vegetation	-4.784	0.008			
	Exploited land	-3.424	0.049			
	Forest	-3.867	<0.001			
	Broadleaf forest	4.893	<0.001			

4.2 Socio-cultural analysis

The analysis on DeSO variables and bats found a less diverse set of correlations, instead most bats had similar results to the socio-cultural variables available through the DeSO statistics. Significant correlations have been compiled in table 6. Both general bat numbers and overall species showed a negative count correlation to population density (p/km^2) (figure 5 &

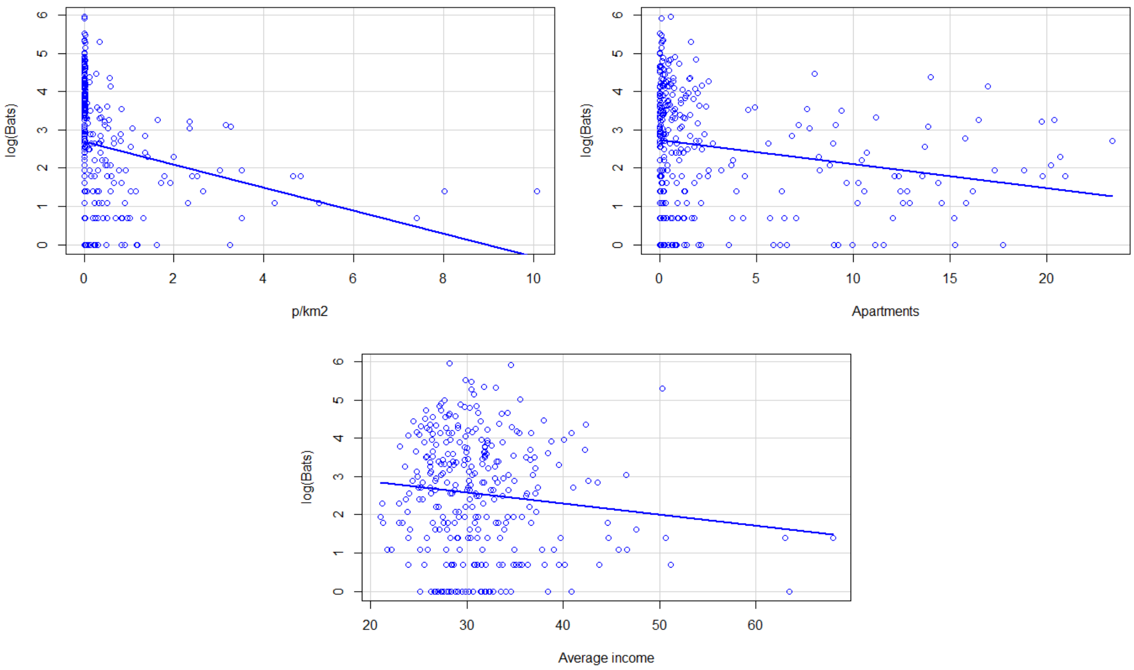

Figure 5 Scatterplots illustrating the count relationships between bats and three DeSO-variables, blue line shows the least-square line which represent the relationship between the two variables. ***Top left:*** *(log)Bats negative count correlation to population density (people/km^2) (r=-0,18 p=0,04).* ***Top right:*** *(log)Bats negative count correlation to the number of apartments in an area (r=-0,05, p<0,05).* ***Bottom:*** *(log)Bats negative count correlation to the average income of the area (r= -0,04, p<0,05).*

6), as did all the individual species that had significant results besides one. While *Pipistrellus pygmaeus* also had a negative count correlation to population density it did also have a positive zero-inflation correlation to population density, indicating that the species is often found in more populated areas but in lesser numbers. Similarly, bats and species both decrease in count with increased apartment buildings, as did several individual species. This further shows that urban land exploitation negatively impacts the bats as was shown in the land cover analysis. *Barbastella barbastellus* however, showed a positive count correlation to apartments, further suggesting that the species may have a positive relationship to semi-urban environments.

Average income also showed a negative count relation to both bat abundance and number of species in a locale (figure 5 & 6), as well as *Myotis mystacinus/brandtii* and *Pipistrellus nathusii*. Species also had a positive zero-inflation correlation to average income, meaning that higher average income DeSO-zones often had more than one species, but the overall diversity still decreases with higher income. In this regard *Vespertilio murinus* stood out as the only species with a positive count correlation to average income. Four species also showed a significant correlation to the proportion of low-income citizens. *Eptisicus nilssonii* and *Pipistrellus nathusii* had positive count relationships to the proportion of low-income citizens while *Myotis daubentonii* and *Myotis mystacinus/brandtii* had negative zero-inflation relationships to low-income proportions.

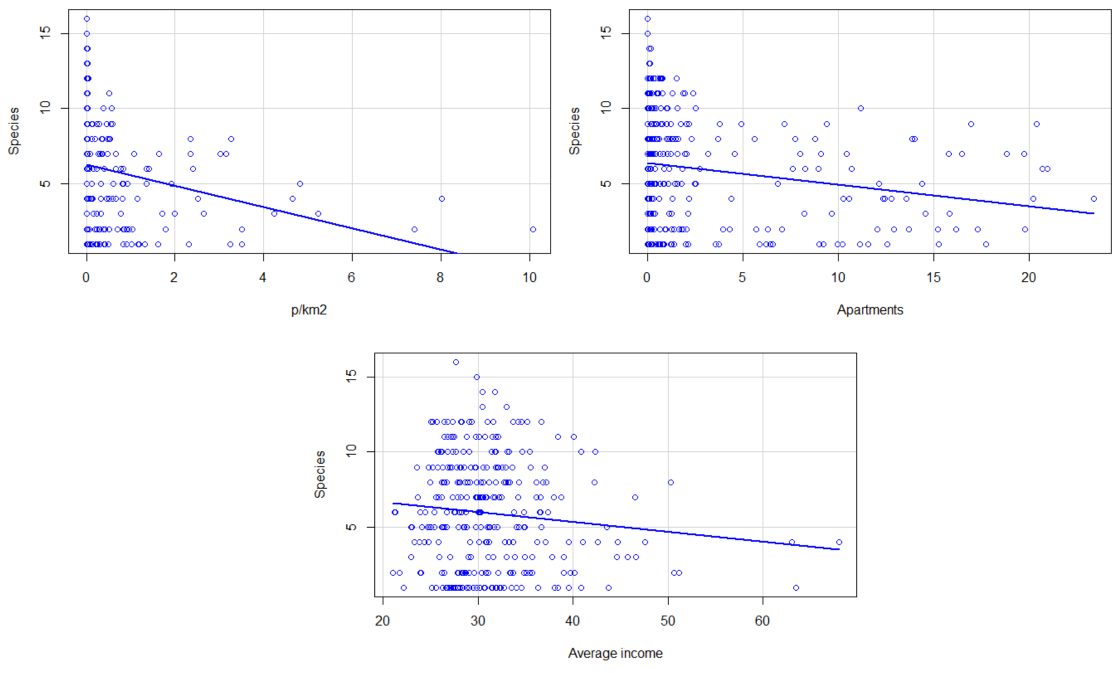

Figure 6. Scatterplots illustrating the count relationships between bat species and three DeSO-variables, blue line shows the least-square line which represent the relationship between the two variables. ***Top left:*** *number of species negative count correlation to population density (people/km^2) (r=-0,16 p<0,05).* ***Top right:*** *number of species negative count correlation to the number of apartments in an area (r=-0,02, p=0,047).* ***Bottom:*** *number of species negative count correlation to the average income of the area (r= -0,019, p<0,05).*

Pipistrellus nathusii was found more often (count correlation) in DeSO-areas with more low-income individuals while *Myotis daubentonii* and *Myotis mystacinus/brandtii* both had negative zero-inflation correlation to low-income proportions. Meaning that these species are less likely to be found in areas with a higher proportion of low-income individuals. On the other hand, these species also showed a positive zero-inflation correlation to apartments, implying they are present more often in areas with more apartments.

Table 6. Significant statistical results on the DeSO-zone analysis, Coefficient indicates whether there is a positive or negative relationship between the response and the explanatory variable, p-value indicates the results significance level. Explanatory count results show if the explanatory variable correlates to the number of the bats or species. Explanatory zero-inflation results show if the explanatory variable correlates to the presence of bats or multiple species in a locale.

Response Variables	Explanatory variable Count	Coefficient	p	Explanatory variable Zero-inflation	Coefficient	p
(log)Bats	p/km^2	-0.188	0.04			
	Avg. income	-0.040	0.003			
	Apartments	-0.059	0.005			
Species	p/km^2	-0.165	0.002			
	Avg. income	-0.019	0.006	Avg. income	0.063	0.042
	Apartments	-0.020	0.047			
Barbastella barbastellus	Apartments	0.724	0.036			
Eptesicus nilssonii	p/km^2	-0.272	<0.001			
	Apartments	-0.037	<0.001			
	Low-income	0.018	<0.001			
Eptesicus serotinus	Apartments	-0.003	0.008			
Myotis	Apartments	-0.144	0.021			
Myotis daubentonii	p/km^2	-0.385	0.006	Apartments	0.580	0.007
				Low-income	-0.311	0.001
Myotis mystacinus + brandtii	p/km^2	-0.397	0.038	Apartments	0.403	0.005
	Avg. income	-0.071	0.001	Low-income	-0.287	0.008
Myotis nattereri	Avg. income	-0.149	<0.001			
	Apartments	-0.143	0.002			
Nyctalus noctula	p/km^2	-0.543	<0.001			
Pipistrellus nathusii	p/km2	-0.744	0.006			
	Apartments	-0.166	<0.001			
	Low-income	0.077	0.036			
	Detached houses	-0.136	0.001			
Pipistrellus pygmaeus	p/km^2	-0.204	0.007	p/km^2	1.279	<0.001
Plecotus auritus	p/km^2	-0.989	<0.001			
Vespertilio murinus	p/km^2	-0.575	0.001			
	Avg. income	0.091	0.001			

5. Discussion

The analysis found numerous associations between the bat fauna and both urban and rural variables. In general, the study found that bat abundance and diversity is lower in areas with more human development and denser population. These results agree with similar studies which have found that urbanization has a homogenizing effect on urban bat populations (Threlfall et al 2012; Threlfall et al 2016; Russo & Ancillotto 2015). A few species, however, did not show any negative correlations to the anthropogenic environments, which could indicate they are not as negatively impacted by the urban environments. *Barbastella barbastellus* and *Myotis dasycneme* had no correlation to exploited land or population density when most other species did (see table 5 & 6). *Barbastella barbastellus* also had a positive correlation to the number of apartment buildings in an area, further indicating that the species displays some synurbic traits. A possible explanation for these species showing such synurbic relationships could be that they are commonly found roosting in buildings, but more importantly they can commute directly to and from roosts and can utilize open areas for hunting (Kyheröinen et al 2019). The fact that these species both have increased in number in recent years (de Jong et al 2020) further attests to the assumption that these species have been able to adapt to urban environments. This reflects what Threlfall et al (2011) found, that open-adapted species were more common in urban environments than clutter-specialists (Threlfall et al 2011). Further evidence of these species utilizing more open environments is that they were both found more in locales with more farmland land cover and *Myotis dasycneme* showed to be more likely to be present in locales with more open ground with vegetation and farmland. Open ground with vegetation showed to be an important land cover for more than one species to be found, which also highlights that bats who can forage and move in open areas, such as *Myotis dasycneme,* are possibly better suited for the current landscape in Sweden.

The complexity of habitats seems to be an important factor for bat abundance and diversity as similar studies have shown that both bat abundance and diversity increases with a more diverse and connected landscape (Heim et al 2015; Monck-Whipp et al 2018). Heim et al (2015) found that bat populations were more numerous and diverse in grasslands that were connected to forest edges and tree groves. Monck-Whipp et al (2018) also confirmed that bat activity increased with farmland heterogeneity. These studies concur with the results found in this study which found more species in locales with more landcovers like broadleaf forest, water bodies and open ground with vegetation such as meadows and pastures.

In Fact, we found that broadleaf forest is the single most important land cover for all bats in Sweden. This variable showed a positive relationship to all species who had any significant correlation and even appeared crucial for multiple species to even be found in the same locale. This association between bats and deciduous forests is hardly surprising since previous knowledge on bats have shown that most bats utilize broadleaf forests to some extent (Kyheröinen et al 2019; section 2.1). Deciduous forests often have high insect production and provide many of the linear landscape elements such as hedgerows and natural alleys that especially smaller bats need for commuting. Broadleaf forests also provide good roosting opportunities for species that rely on tree hollows and provide a more spatially complex habitat than other vegetation. Although this study did not find any significant correlations for species that are Critically Endangered (CR) or Endangered (EN), it showed that deciduous woodlands had a significantly positive impact on all Near Threatened (NT) species. As such, Swedish bat conservation needs to especially focus on preserving and facilitating broadleaf forests to secure vital habitats for bats.

As with any study, there is the risk of human influence on the results. In the case of this study there is the possibility that areas where bats have been recorded is affected by where people decide to look for bats. It is possible that we notice this effect in the results as some species are present more often in more urban areas, shown by a zero-inflation correlation but show a negative correlation to the same variable through the count model. This could suggest that the bat is found more in urban areas simply because there are more people there to notice it. Similarly, it is possible that we find decreasing number of bats in more urbanized areas because bigger inventory of bats is organized mainly in less urban environments with the intent to maximize the number of bats recorded. However, the fact that most but not all bats show similar results to the urban variables and that previous studies draw similar conclusions speaks to the reality of these correlations between bats and the urban environment.

The analysis found little evidence that the income of the population would have any positive effect on bat activity. In fact, we found that bats were less numerous and diverse in areas with higher average income. Assuming that higher income would relate to higher urbanization this would give further weight to the fact that there are less bats in urban environments, however this is factored into the models with other variables. Only one bat, *Vespertilio murinus,* showed a positive correlation to the average income of the population but this species still showed a negative correlation to exploited land so it is difficult to say that it would benefit from the urban habitat. Thus, unlike Li et al (2019) we did not find that the luxury effect has much positive effect on bat activity and diversity in Sweden.

Seeing as most species in this study showed significant negative correlations to urban habitats, it is unlikely that the theory of intermediate disturbance is relevant to the Swedish bat population. Although the study did not perform any groupwise testing on rural-suburban-urban populations, it appears that most species are more numerous in rural areas with more broadleaf forest. Diversity overall also decreased with more urban exploitation and increases with rural variables like broadleaf forest and open ground with vegetation. In fact, we found more evidence in line with that of Threlfall et al (2011) which found that net productivity and species functional traits played a bigger role in determining the community structure. The unanimous positive response to deciduous forests and some species displaying individual relationships to habitats important to them such as water and cluttered meadows or woodlands, indicates that individual functional traits and net productivity plays a bigger role in determining the suitability of the habitat. However, since the bats show such similar results, we cannot draw any conclusion on whether size of the bat or wing load has any effect on the suitability of the bats. To examine this further, studies would have to incorporate such traits in the statistical testing similar to how Jones et al (2003) did.

Our testing method did not include any variables specific to artificial light, but it is possible that the trespass of artificial light sources is one of the reasons for the negative response of exploited land. Much of the previous writing on the urban bats highlights the fact that artificial light sources can affect the bats both negatively and positively (Rydell 1989; 1992; Russo & Ancillotto 2015; Voigt et al 2018; Kyheröinen et al 2019). It is therefore advisable that urban planners evaluate the impact of artificial light especially in areas with broadleaf woodlands and in potential roosts.

6. Conclusion

This study concludes that increasing urban exploitation is a threat to the diversity and abundance of bats in Sweden. Although some species appear to be capable of adapting to the modern habitats, the general effect of the urban spread is negative. Considering the fact that bats often reflect the state of the ecosystem as a whole (Jones et al 2009; Russo & Ancillotto 2015; Voigt 2016) this can be regarded as a sign on the state of the urban habitat. If we continue to expand and develop our environment in the same way we have for the past 100 years, it is likely that we will continue to see losses in abundance and diversity across many different taxa.

If urban planners want to create suitable habitats for bats, this study’s results indicate that urban green areas should use deciduous trees and bodies of water to help form linear elements and preserve connectivity between habitats. Additionally, preserving open vegetated areas such as meadows, pastures, and grasslands in connection to woodlands should help facilitate diversity. These measures would hopefully lead to a more suitable habitat for bats and many other organisms and create a more balanced urban environment for humans in the long run.

7. References

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