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Boar feeding grounds

How wild boar populations affect localised landscapes and ecosystems

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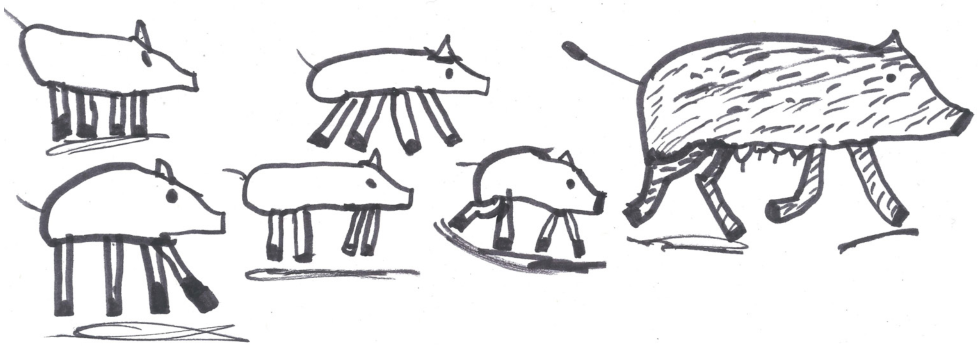

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Boar feeding grounds – how wild boar populations affect localised landscapes and ecosystems

Abstract

The recent recolonisation of wild boar (*Sus scrofa*) across the Swedish landscape has caused substantial impacts on agriculture and has raised concerns about potential consequences for local ecosystems. This thesis aims to enhance our understanding of how wild boar activities affect various ecosystem and landscape elements, as well as to investigate the role of supplementary feeding in mitigating their impact. By combining long-term telemetry data and purpose-directed manipulative experiments, I assessed the impacts of wild boar at various ecological scales. I found that wild boar have extensive and direct effects on agriculture, as well as on both faunal and floral communities. My results suggest that foraging habits of wild boar are expected to continue causing adverse effects on crops and farmland, and that the effectiveness of supplementary feeding in mitigating damage caused by wild boar to agricultural areas remains uncertain. Within the Swedish forest landscape, where modern forestry practices predominate and few natural disturbances occur, wild boar rooting behaviour may provide an ecologically significant form of disturbance that enhances biodiversity. Changes at a broader ecosystem community scale may result from altered resource use by sympatric ungulate species and potential cascading effects following changes in plant communities and habitats. The findings of my thesis indicate that with an inevitable growth in wild boar populations, we may face substantial impacts on habitats and biodiversity, with both positive and negative outcomes. Moreover, human-driven ecological manipulations, such as supplementary feeding, are likely to accentuate these effects and should, therefore, be considered from a broader perspective before implementation.

Keywords: *Sus scrofa*, supplementary feeding, spatial behaviour, habitat use, population density, interspecific interaction, plant community, biodiversity

Vildsvinets födosök – återetablering och växande stammars påverkan på landskap och lokala ekosystem

Sammanfattning

Vildsvinets (*Sus scrofa*) återetablering i det svenska landskapet har medfört omfattande konsekvenser för jordbruksnäringen och väckt frågor kring vad det kan komma att innebära för våra lokala ekosystem. Syftet med denna avhandling är att öka vår förståelse för vilka ekologiska effekter vildsvin har på olika ekosystem och landskap, samt att undersöka hur utfodring av vildsvin påverkar och potentiellt förvärrar eller dämpar dessa effekter. Genom att kombinera GPS-data från märkta vildsvin med vegetationsinventeringar och manipulativa utfodringsexperiment utvärderade jag vildsvinets påverkan på olika delar av dess ekosystem. Jag fann att vildsvin aktivt söker och utnyttjar jordbruksmark i stor omfattning och har betydande effekter på lokala djur- och växtsamhällen. Mina resultat indikerar att vildsvinets födosöksbeteende med största sannolikhet kommer fortsätta att ge upphov till problem i jordbruket, samt att utfodring i de flesta fall är en tveksam metod för att minska vildsvinsorsakade skador på jordbruksmark. I det svenska skogslandskapet som idag domineras av ett intensivt skogsbruk med få naturliga störningar, kan dock vildsvinsbök komma att fungera som ett ekologiskt betydelsefullt störningselement och bidra till en ökad biologisk mångfald. Vildsvinets närvaro kan dessutom ge upphov till indirekta och mer omfattande ekosystemeffekter genom förändrad resursanvändning hos samexisterande klövviltsarter och med potentiella kaskadeffekter till följd av förändrade växtsamhällen och livsmiljöer. En fortsatt tillväxt av vildsvinsstammen kommer således få betydande konsekvenser för habitat och biologisk mångfald, av både positiv och negativ art. Vidare kan utfodring komma att förstärka sådana konsekvenser, varför denna förvaltingsmetod bör beaktas utifrån ett helhetsperspektiv och tillämpas med försiktighet.

Keywords: *Sus scrofa*, utfodring, rumsligt beteende, habitatutnyttjande, populationstäthet, mellanartsinteraktioner, växtsamhällen, biodiversitet

Dedication

To Lin and Juni, for calming my heart and leading the way.

Science cannot solve the ultimate mystery of nature. And that is because, in the last analysis, we ourselves are part of nature and therefore part of the mystery that we are trying to solve.

Max Planck

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Augustsson, E., Kim, H., Andrén, H., Graf, L., Kjellander, P., Widgren, S., Månsson, J., Malmsten, J., & Thurfjell, H. (2024). Density-dependent dinner: Wild boar overuse agricultural land at high densities. European Journal of Wildlife Research, 70(1), 15.

II. Augustsson, E., Bhardwaj, M., Andrén, H., & Kjellander, P. Luring the boar from the field: can artificial feeding sites reduce the use of agricultural fields by wild boar? (Manuscript).

III. Augustsson, E., Ausilio, G., Bhardwaj, M., Andrén, H., Long, N., Hewison, M., & Kjellander, P. Table for one? The behavioural response of roe deer to wild boar at artificial feeding sites (Manuscript).

IV. Augustsson, E., Kjellander, P., Andrén, H., Öckinger, E., & Bhardwaj, M. Benefit of the snout: wild boar rooting disturbance has downstream impacts on species diversity in local vascular plant communities (Manuscript).

Paper I is reproduced with the permission of the publisher (Springer Nature).

The contribution of Evelina Augustsson to the papers included in this thesis was as follows:

I. Main author. Developed the study together with PK, HT, SW and HK. Performed the analysis with support from HT, HK and HA. Wrote the manuscript with contributions from co-authors.

II. Main author. Developed the study together with co-authors (original study design by PK and HA). Performed the analysis with support from HA and MB. Wrote the manuscript with contributions from co-authors.

III. Main author. Developed the study together with PK, GA and NL, with input from HA and MB. Performed the analysis with support from GA, MB, and HA. Wrote the manuscript with contributions from co-authors.

IV. Main author. Developed the study together with co-authors (original study design by PK and HA). Performed the analysis with support from HA, MB and PK. Wrote the manuscript with contributions from co-authors.

1. Introduction

Large-bodied animals play a vital role in ecosystems. They influence the abundance and behaviour of other animals, and their activities shape the structure and composition of the habitats in which they occur. Different species have different functional roles in shaping the environment (Lacher et al. 2019), and the contribution of individual species to ecosystem processes has long been a central question in ecology. In terrestrial ecosystems, grazers affect plant growth patterns and vegetation structure by consuming biomass and altering competitive advantage among plant species (Hobbs 1996; Pringle et al. 2023; Trepel et al. 2024). Other physical activities of these large animals such as rooting, trampling and wallowing, reduce vegetation cover and modify local conditions of soil structure (Trepel et al. 2024). Through their movements, they also influence the nitrogen cycle by redistributing nutrients through faeces and urine (Hobbs 1996; Abbas et al. 2012; Pringle et al. 2023) and facilitate seed dispersal by transporting seeds in e.g. fur, hooves and faeces (Janzen 1984; Heinken et al. 2002; Baltzinger et al. 2019). Because of their major influence on large-scale structuring effects in the environment, large ungulates are often referred to as ‘ecosystem engineers’. Ecological engineers are species that cause physical state changes of the biotic or abiotic environment in which they occur, and thereby, directly or indirectly alter the availability of resources to other species (Jones et al. 1994). By modifying and/or creating habitats, they alter ecosystem structure and function and increase complexity and heterogeneity. Environmental heterogeneity is regarded as a key element promoting species diversity across taxonomic groups and scales (Stein et al. 2014). Induced spatial heterogeneity provides an expansion in niche space, thereby creating windows of opportunity for plant colonisation and the coexistence of a greater number of species (Currie 1991; Tews et al. 2004). As severe changes in plant composition could in turn affect ecosystem function and services, e.g. by affecting plant-pollinator interactions (Gilliam 2007), such actions hold the potential to alter the structure and dynamics of whole ecosystems. Ecosystem engineering by large ungulates can even trigger cascading effects on other animal communities by increasing abundance and diversity of smaller animals (Trepel et al. 2024). Plant-animal interactions are thus a fundamental aspect when assessing overall ungulate biodiversity impacts.

Sympatric ungulate species coexist in space and often exhibit complex interactions, which can play an important role in structuring ecological communities (e.g. Schoener 1983; Connell 1983). Sympatric species may compete for access to common depletable resources (Pianka 1976). The influence that species have on one another is commonly described using different terms of competition, which differentiate between direct and indirect forms of interaction. Exploitation competition occurs when two species interact indirectly, whereby the use of a limited resource by one species reduces its availability to the second species. In contrast, interference competition occurs when two species using a common resource interact directly in a way that negatively affects the fitness of one of the species (Birch 1957; Begon et al. 1996). Additionally, sympatric ungulate communities may be indirectly affected by modifications in forage availability resulting from reduced vegetative cover or alterations in habitat structure (Focardi et al. 2006). While interspecific competition often results in exclusion of a species from habitats where they could otherwise exist, sympatric species do not necessarily influence each other negatively. In fact, research findings suggest non-competitive coexistence to be more common than competitive exclusion among ungulate species (Hobbs et al. 1996). The coexistence of species can be facilitated through resource partitioning (Schoener 1974) and by spatial or temporal avoidance, which may minimise competitive encounters (Voigt & Earle 1983; Durant 2000; Hayward & Slotow 2009).

1.1 The wild boar

The wild boar (*Sus scrofa*) has a broad global distribution, which suggests they can easily adapt to a wide range of environmental conditions and habitats (Baskin & Danell 2003). Part of the success of the wild boar establishment has been attributed to its biology. Unlike most ruminating or herbivorous ungulates, which often exhibit selective foraging behaviour (Hofmann 1989; Shipley 1999), wild boar are omnivorous ungulates whose dietary habits can vary considerably over geographical location or seasons (Stegeman 1938; Genov 1981; Baubet et al. 2004). The combination of its opportunistic feeding habits and an exceptional behavioural flexibility gives the wild boar a strong ability to occupy new areas and adapt to anthropogenic changes. Compared to other wild ungulates of similar body size, the wild boar has a high reproductive capacity, with large litter sizes and early puberty considered to be important factors contributing to the high reproductive potential (Malmsten et al. 2017; Mauget 1982; Servanty et al. 2007). A clear association between forage availability and population growth rates have been recognised in central European wild boar populations (Massei et al. 1996; Jędrzejewska et al. 1997; Okarma et al. 1995).

The wild boar is an important component of Europe's native fauna community. It has adapted well to agricultural changes of the continent, that today provide favourable conditions for a rapid population growth and recovery. In many parts of Europe, populations are now recolonising areas from which they were once extirpated. The wild boar colonised Scandinavia at about the same time as humans, after the last ice age. Archaeological finds from around 4,000 B.C. indicate a prehistoric range from Skåne to Uppland (Swedish Association for Hunting and Wildlife Management). Due to extensive hunting and hybridisation with the domestic pigs, the wild boar became regionally extinct in the 18th century. However, low numbers of the species remained in game parks and estates where it was held for recreational hunting and meat production (Danell 2024). After repeated escapes from enclosures, the Swedish Parliament declared the wild boar to be part of the Swedish fauna in 1987. Over the past three decades, the population has been steadily increasing and the wild boar is today re-established in the southern and central parts of the country (Bergqvist et al. 2024). Although the absolute number of wild boar in Sweden is not known, most recent estimates suggest a total population size of at least 300,000 animals (Swedish Environmental Protection Agency 2020).

1.2 Impacts of wild boar

Wild boar management is a controversial issue, given to the numerous and complex aspects that it encompasses. Although wild boar generate positive economic values through hunting and meat supply, the recent rapid increase in densities and range expansion has led to conflicts with human activities due to crop damage, vehicle collisions and disease transmission (Schley et al. 2008; Thurfjell et al. 2015; Podgórski & Smietanka 2018; Gren et al. 2020; Stenberg et al. 2022) and has raised concerns about the potential consequences for local ecosystems (Barrios-Garcia & Ballari 2012). Wild boar management in Sweden is primarily directed for controlling damage, and the national objective is to achieve "a sustainable, controlled and healthy wild boar population, adapted to regional and local conditions" (Nationell förvaltningsplan för vildsvin 2020-2025, Swedish Environmental Protection Agency). As wild boar range over extensive areas, conflicts of interest often emerge between diverse human interests. Stakeholders often have different perceptions and expectations of the management based on their interests. Game management strategies typically seek to improve hunting value through high densities, while efforts to minimise crop damage are also implemented, sometimes within the same estate (Geisser & Reyer 2004; Storie & Bell 2017). While population control is the primary method for mitigating overall negative impacts in Sweden, severe local crop damage has led to the implementation of additional avoidance measures, including supplementary feeding and the use of electric fencing.

1.2.1 Social and economic concerns

The most prominent costs of wild boar, so far, are related to agricultural damage (Schley et al. 2008; Gren et al. 2020). Following the technological advances of the mid-twentieth century, the agricultural revolution since the 1960s transformed the agricultural landscape through intensification and extensive monoculture. The modern agricultural landscape offers a vast abundance of nutritionally rich forage across extensive areas. Wild boar select agricultural crops when available (Thurfjell et al. 2009; Muthoka et al. 2022), and economic losses to farmers are therefore expected to grow as both agricultural intensification and wild boar abundance increase (Gren et al. 2020).

In addition to conflicts in agricultural areas, increasing wild boar numbers in Sweden and other parts of Europe have led to an increase in wildlife-vehicle collisions, resulting in injuries (occasionally fatal) to humans and animals, and damage to property (Thurfjell et al. 2015; Jägerbrand & Gren 2018). High population densities also increase the risk of disease transmission from wild populations to domestic animals and livestock (Podgórski & Smietanka 2018), which has recently been highlighted by the first outbreak of African swine fever (ASF) in the Swedish wild boar population (Chenais et al. 2024).

1.2.2 Ecological concerns

As ecosystem engineers, wild boar directly and indirectly alter the environment. Through their subsurface feeding behaviour, i.e. rooting, they directly modify consumed plant parts, fungi, invertebrates and soil organic matter, while indirectly altering habitat characteristics and the availability of resources for other organisms. Their strong capacity to create, modify or destroy habitats for other species has the potential to induce cascading effects on other taxonomic groups and may alter all components of the surrounding ecosystems (Barrios-Garcia & Ballari 2012). The current understanding of the relationship between wild boar activity and the structure and composition of plant communities is severely limited, despite the important implications this may have for wild boar management and biodiversity as a whole.

With increasing wild boar densities, interspecific interactions become more common. Interference competition between ecologically similar species is likely to increase, as is competition over space use and different resources (Putman & Putman 1996). The impact of wild boar on other ungulates is poorly understood and rarely investigated. However, typical for ecological generalists, it holds strong competitive abilities and is often competitively dominant to sympatric herbivorous species (Oliver & Brisbin 1993; Popova et al. 2017).

1.3 Supplementary feeding

Supplementary feeding of game animals is a common practice throughout Sweden as well as other parts of northern Europe and parts of North America (Putman & Staines 2004; van Beest et al. 2010; Milner et al. 2014). Although winter feeding of roe deer has long been applied in Sweden, supplementary feeding has drastically increased over the last decades, reflecting the increase in wild boar numbers. In Sweden, all feeding of game is conducted on private initiative, with no official feeding programmes in place. Intended effects of feeding of ungulates is typically to maintain or increase population size by providing energy-rich food during periods of normal food shortage, thus buffering the negative impact of seasonally occurring times with poor foraging conditions (Schmidt & Hoi 2002). Feeding may also be designed in a diversionary way with the purpose of redirecting animals away from sensitive areas, thereby reducing the levels of damage caused to particularly agriculture and forestry (Milner et al. 2014; Kubasiewicz et al. 2016).

Wild boar are often subject to diversionary feeding attempting to redirect animals away from economic crops (Calenge et al. 2004; Barrios-Garcia & Ballari 2012). In Sweden, substantial forage quantities are provided every year at feeding sites by farmers, hunters and landowners, particularly aimed to mitigate crop losses (Gren et al. 2020). However, this practice is not always successful in meeting stakeholder objectives, and there is a lack of conclusive empirical studies examining its efficiency in preventing agricultural damage by wild boar (Putman & Staines 2004; Milner et al. 2014). Meanwhile, supplementary feeding has been alleged to promote the spread and increase of ungulate populations (Milner et al. 2014) and it is frequently suggested as the single most important factor contributing to the rapid growth of wild boar populations (Melis et al. 2006; Oja et al. 2014). Various kinds of forage used for supplementary feeding, including maize, cereals and legumes, have been found to constitute a significant part of the wild boar diet (Malmsten 2017), indicating that wild boar in Sweden rely heavily on supplementary feeding.

The unintended and indirect effects of feeding are a topic of ongoing debate and controversy. Many authors point out the complexity of supplementary feeding on species ecology and severe management implications with this practice. A range of unintended and unexpected outcomes may occur, affecting not only the target species but also other trophic levels. Concerns typically regards the sustainability of this management practice considering its potentially undesirable ecological side effects (Milner et al. 2014) and the probability of increased interspecific encounters at feeding sites (Popova et al. 2017; Saldo et al. 2024).

1.4 Expanding wild boar populations

Like in many other wild ungulate populations, wild boar numbers are rising in Sweden and across Europe, with several populations recolonising their former distributional range (Apollonio et al. 2010; Massei et al. 2015). A key challenge to ecologists today is to understand how an expanding wild boar community can affect surrounding landscapes and sympatric species. Understanding the impact on other species is also essential as it has important implications for management and conservation. Current studies on interspecific interactions between wild boar and sympatric species in Sweden are lacking and studies on their effects on other trophic levels are scarce. Moreover, in the light of a more common use of supplementary feeding practices and its extensive utilisation by wild boar, it is necessary to identify how such human-driven ecological manipulations may affect species coexistence and biodiversity.

2. Objectives of the thesis

The overall aim of this thesis is to increase the ecological understanding about the effects and extent of impact of wild boar activities on ecosystem and landscape elements. I also aim to better understand the role of supplementary feeding in mitigating the impact of wild boar in this context. To achieve this aim, I investigated the effects of wild boar spatial and foraging behaviour at different ecological scales in Sweden. More specifically, the objectives of this thesis were to:

1. Investigate how wild boar spatial behaviour is affected by the availability of agricultural land and population density (*Paper I*).
2. Assess the effect of diversionary feeding on wild boar spatial behaviour (*Paper II*).
3. Investigate the level of interference competition between wild boar and roe deer around shared feeding sites (*Paper III*).
4. Investigate how wild boar feeding behaviour impact local plant communities (*Paper IV*).

3. Methods

I evaluated the impacts of wild boar on ecosystem and landscape elements, through a range of studies, which included compilation of long-term monitoring data (e.g. Swedish Infrastructure for Ecosystem Science, SITES) as well as purpose-directed manipulative experiments. The following section provides a general overview of the most important methods. For details see each paper (I – IV).

3.1 Study area

Data was collected across two different geographical ranges; Paper I was conducted across the main distributional range of wild boar in Sweden (55°N – 60°N, 12°E – 18°E; Figure 1) and Paper II – IV was conducted in Grimsö Wildlife Research Area (59°72′N, 15°47′ E; Figure 1), located in the northern edge of the current wild boar distributional range.

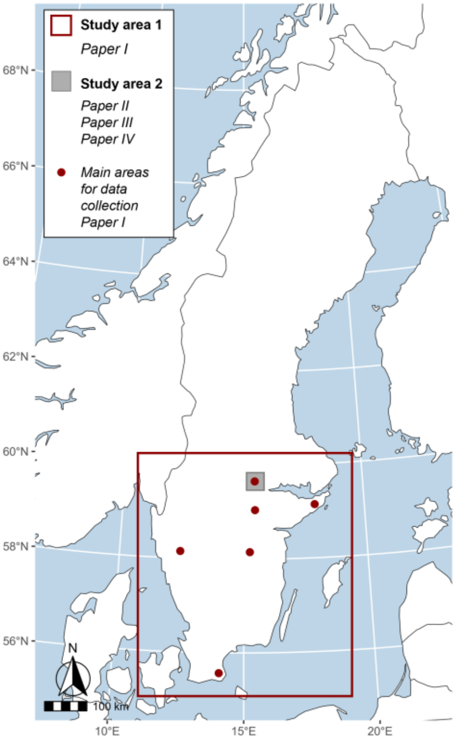

Figure 1. Locations of the two study areas: South-central Sweden (Paper I); unfilled red rectangle, and Grimsö Wildlife Research Area (Paper II – IV); filled grey rectangle. Red points represent the main areas for the collection of wild boar telemetry data used in Paper I.

3.1.1 Study area 1: South-central Sweden (*Paper I*)

The landscape composition varies across the wild boar distributional range in Sweden, with the boreal forest being the dominating habitat in the north and farmland in the south. The duration of the growing season (days with average temperature > 5 °C) varies from 190 to 220 days. Average annual precipitation varies from 500 to 1,100 mm and average snow cover is between 25 – 100 days per year (The Swedish Meteorological and Hydrological Institute, SMHI 2024). There tends to be a longer period of snow-covered ground and a shorter duration of the growing season in the northern part of the range compared to the southern part. Supplementary feeding is common throughout the study area, although it occurs in unknown quantities. Attributed to the larger quantities of agricultural land, landowner structure and higher wild boar densities, the southern part of the range has a greater number of feeding sites per unit area than the northern part.

3.1.2 Study area 2: Grimsö Wildlife Research Area (*Paper II – IV*)

Grimsö Wildlife Research Area comprises 13 000 ha and is located within the southern boreal vegetation zone (Moen 1998) in south-central Sweden with a growing season of 180 – 190 days and 100 – 125 days with snow per year (WMO normalperiod 1991–2020; SMHI 2024). Intensively managed coniferous forests dominate the landscape, interspersed with other habitat types such as wetlands, bogs and mires, agricultural land, lakes, rivers and few human settlements (Angelstam et al. 1985). Four ungulate species occur in the area: moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar. The wild boar has recently colonised the research area, and the first known observation of wild boar was in 2006 (SITES-data unpublished). All four ungulate species population sizes are controlled through hunting.

3.2 Data collection

3.2.1 Capture and monitoring / Telemetry data (*Paper I – III*)

The main method to investigate spatial behaviour in wild boar and sympatric species was through the collection of telemetry data. Wild boar were immobilised with a tranquiliser gun on agricultural fields or close to feeding sites, or by using a blowpipe after being captured in coral traps, and then equipped with a GPS-collar (Figure 2). Roe deer were captured using box traps and equipped with a GPS-collar.

All captures and handling were approved by the Ethical Committee in Animal Research, Umeå Sweden (Paper I: permit A18-04) and Uppsala Sweden (Paper I: permit C80/9, C77/10, 5.2.18-2830/16 and 5.8.18-03524/2018, Paper II: permit 5.2.18-2830/16, 5.8.18-03524/2018 and 23643/2022, Paper III: permit C302/12, C149/2015, 5.8.18-22179/2021, 5.2.18-2830/16, 5.8.18-03524/2018 and 23643/2022) and in compliance with Swedish and European laws and regulations.

Figure 2. A female wild boar equipped with earmarks and a GPS-collar at the Koberg estate in southwestern Sweden. Photo: Ingemar Pettersson

For Paper I, I used telemetry data compiled from several studies conducted between 2004 and 2021, from 102 adult wild boar (16 males and 86 females) equipped with GPS-collars. For Paper II, I used year-round telemetry data from 22 adult wild boar (4 males and 18 females) collected between 2019 and 2024. For Paper III, I used telemetry data from 99 adult roe deer (41 males and 58 females) collected during the winter period (1^{st} December to 31^{st} March) between 2011 and 2023, and telemetry data from 15 adult wild boar (2 males and 13 females) collected during the winter period between 2018 and 2023. Telemetry data was collected or thinned to one location every 1 h for wild boar and 4 h for roe deer to obtain homogeneity among individuals for each species.

3.2.2 Establishment of supplementary feeding (*Paper II and IV*) and plant community data (*Paper IV*)

To investigate the diversionary effect of supplementary feeding on wild boar populations and the secondary ecosystem-level effects of increased wild boar abundance and activity, a manipulative experiment was conducted between 2018 and 2023. This involved introducing supplementary feeding sites in an area where wild boar have not previously been exposed to such practices (the Grimsö Wildlife Research Area). Effects of feeding and increased wild boar abundance were assessed across three time periods, based on feeding conditions: before, during, and after supplementary feeding, and over two different treatments (control and impact). I investigated the direct effects of supplementary feeding on wild boar use of agricultural land (Paper II) and the indirect effects of wild boar feeding activities on plant communities (Paper IV).

Plant community and rooting survey (Paper IV)

Plant communities were repeatedly surveyed at the end of the vegetation season (August – September) during a 5-year period. The study included 23 sites (control and impact) where transects of 150 m were distributed at a longitudinal and a latitudinal direction from the sites with sample plots of 10 m^2 at six different distances from the centre of each site. A plant community survey was conducted at each plot, along with an estimation of rooting disturbance. Wild boar rooting intensity was recorded as one of four categories: absent, low (< 10%), medium (10 – 50%), and high (> 50%).

3.3 Environmental variables

3.3.1 Agricultural land (*Paper I – III*)

To determine wild boar relative use for agricultural land in Paper I, I used CORINE land cover (CLC) data with a 100 m spatial resolution (European Union 2000; 2006; 2012; 2018). 44 CLC classes were reclassified into two main habitat groups: agricultural land and others. To define the boundaries of agricultural lands in the study area for Paper II and to generate the Euclidean distance to nearest agricultural land for each feeding site in Paper III, I used the Swedish Land Cover Map (NMD) with a 10 m spatial resolution. Agricultural land was defined as NMD class: arable land (Nationella Marktäckedata; Swedish Environmental Protection Agency 2018).

3.3.2 Snow depth (*Paper III*)

To correct for a potential impact of snow conditions on the use of feeding sites by roe deer, I collected snow data from the Swedish Meteorological and Hydrological Institute (SMHI) and used daily snow depth (m) from the nearest weather station (Kopparberg D station id 95520).

3.3.3 Wild boar abundance (*Paper I and III*)

Wild boar density proxy (Paper I)

Motivated by a strong correlation between wild boar collisions data (wild boar-vehicle collisions/km^2) and hunting bag (shot wild boar/km^2), hunting bag was assumed to be a reliable proxy for wild boar abundance in Paper I. I obtained hunting bag for each hunting management precinct and hunting season between 2004 and 2021 from the Swedish Association for Hunting and Wildlife Management. I assigned hunting bag to each individual according to the location (hunting management precinct) and time stamp (hunting season) of its first GPS-location (hereafter referred to as 'population density'). For individuals with more than one monitoring period, I used the hunting bag for the first period.

Wild boar abundance proxy (Paper III)

In Paper III, I used wild boar by-catch data in roe deer traps (baited with livestock forage, resembling supplementary feeding sites) to estimate proxies for annual wild boar abundance on two different spatial scales: feeding site- and study area-level. Annual feeding site level wild boar abundance was calculated by dividing the number of caught wild boar individuals each winter by the sampling effort (winter roe deer capture days) for each site, and wild boar abundance at study area level by dividing the total number of caught wild boar individuals each winter in the research area by the total sampling effort (winter roe deer capture days). At study area level, wild boar abundance was further categorised into two groups: 'low' (winters with < 0.1 number of captured wild boar per roe deer capture day) and 'high' (winters with > 0.1 number of captured wild boar per roe deer capture day).

3.4 Data analysis

Most data processing and analysis were performed in R (R Core Team 2024). Generalised linear mixed models (Paper I-II and IV) were calculated using the package *glmmTMB* (Brooks et al. 2017). Generalised additive models (Paper III) were fitted using the package *mgcv* (Wood 2017), and logistic regression models (Paper III) were run in the package *lme4* (Bates et al. 2015). Most results were visualised using the *sjPlot* package (Lüdecke 2023), or the *ggeffects* package (Lüdecke 2018).

3.4.1 Wild boar space use (*Paper I and II*)

I assessed shifts in wild boar habitat use by applying a habitat selection design (e.g. Johnson 1980; Manly et al. 2002) where the sample of use for each wild boar was related to a sample of availability for the same animal. Using a 2 step-approach, I first estimated the individual use of agricultural land (Paper I and II) and use of feeding site (Paper II) for each wild boar, and the availability of agricultural land (Paper I and II) and availability of feeding site (Paper II) for each wild boar at the scale of the individual's home range (i.e. a type III analysis; Manly et al. 2002). Second, I assessed on population-level the sample of use in relation to the sample of availability under different population densities (Paper I) and feeding conditions (Paper II) using generalised linear mixed modes. To exclude other types of behaviour than feeding (e.g. resting), I used wild boar locations exclusively for the main active phase of the day, i.e. between sunset and sunrise.

Wild boar home range size and use of agricultural land in relation to population density (Paper I)

For each wild boar, all available locations were used to calculate a home range using the alpha-concave hull method (Aseedi et al. 2017) with a concave distance of 3 km. For availability data, I generated an equal number of random locations to the true locations, i.e. a ratio of 1:1, within each wild boar home range. Availability was calculated as the proportion of random locations in agricultural land divided by the total number of random locations. To test for differences in selection for agricultural land across different seasons, I defined three different seasons related to the ecology of wild boar in Scandinavia: spring-early summer (main reproductive season; March – June), summer-autumn (crop season; July – October) and winter (November – February; Mauget 1982; Thurfjell et al. 2014; Malmsten et al. 2017). I assigned a random season to all random locations at an equal number to true locations for each season. I assessed the effect of population density on wild boar home range size and relative use of agricultural land separately, fitting 2 separate generalised linear mixed modes.

Wild boar use of agricultural land and feeding sites in relation to different feeding conditions (Paper II)

To define boundaries of feeding sites, I created circular buffer zones with a radius of 150 m around each of the feeders (hereafter referred to as 'feeding site buffer'). For each wild boar, all available locations were used to calculate a home range using the 100% minimum convex polygon method (MCP; Mohr 1947). Availability of agricultural land and feeding site buffers was calculated by estimating the proportional covered area of agricultural land and the proportional covered area of feeding site buffers within the individual home range. I assessed the use of agricultural land by using the GPS-locations of wild boar during the vegetation season (defined to 16th April – 2nd November using the moving temperature average; SMHI 2024), and the use of feeding site buffers by using the GPS-locations of wild boar during the vegetation season and during the winter season (3rd November – 15th April), separately. Consequently, I used 3 different response variables, each fitted in a separate generalised linear mixed model: use of agricultural land during vegetation season, use of feeding site buffers during vegetation season, and use of feeding site buffers during winter season.

3.4.2 Roe deer use of feeding sites (*Paper III)*

To assess roe deer behavioural response to changing wild boar densities, I used GPS-locations of roe deer during the winter period (1st December – 31st March) when low natural food availability attracts roe deer and wild boar to supplementary feeding sites. To define boundaries of feeding sites, I created circular buffer zones with a radius of 150 m around each roe deer trap site (n = 27) within the study area, that were active during the corresponding winter period. To test whether the likelihood of encountering wild boar affected the probability and the timing of roe deer visiting feeding sites, I used a proxy for wild boar abundance at two spatial scales, local feeding site- and study area-scale. The analysis was divided in two parts with different approaches based on the scale of the predictor variable and the expected relationship between predictor and response (linear/nonlinear): i) general temporal pattern over a 24-hour circadian cycle within the research area and ii) local presence at a feeding site.

Roe deer use of feeding sites at the study area scale

To investigate the influence of wild boar abundance on roe deer use of feeding sites at a study area scale, I modelled the probability of roe deer presence within all feeding site buffers combined across the study area by fitting a generalised additive model, using the binomial response variable (0 = outside, 1 = inside) as a function of wild boar abundance and time. Given the expectation that roe deer activity follows a non-linear circadian cycle over the 24-hour day, I used generalised additive models which are well-suited to capturing non-linear relationships in a flexible manner. To account for the large variation in daylight at the study site, I used sun time-adjusted times in the analyses.

Wild boar use of feeding sites at the study area scale

I also modelled the probability of wild boar presence at feeding sites using GPS-locations of wild boar during each winter period from December 2018 to March 2023. The probability of wild boar presence within all feeding site buffers combined across the study area was estimated by fitting a generalised additive model, using the binomial response variable (0 = outside, 1 = inside) as a function of time.

Roe deer use of feeding sites at the local site scale

To investigate the influence of wild boar abundance on roe deer use of a specific feeding site at a local scale, I modelled the probability of roe deer presence within a given feeding site buffer using logistic regression (0 = outside, 1 = inside). In addition to wild boar abundance, I investigated the effect of Euclidean distance to nearest agricultural land and daily snow depth to control for differences in local conditions between sites, as well as for the fact that agricultural crops become progressively less available to roe deer with increasing snow depth.

3.4.3 The effect of wild boar rooting on vascular plant communities (*Paper IV)*

I investigated the effect of wild boar rooting intensity on components of the local plant species diversity and plant community composition using generalised linear mixed models. To assess impacts of rooting disturbance on plant communities, I examined plant characteristics that determine responses to physical disturbance and effects on other species. I used species-specific ecological indicator values, physiological and reproductive traits, and conservation indices for vascular plant species of Sweden according to Tyler et al. (2021). I included traits according to: life form – annual or long-lived perennial; response to disturbance – disturbance dependent or competitive; and seed properties – short-lived or long-lived seeds of the species. Moreover, to assess potential implications of wild boar rooting for other species groups, I included traits according to: pollinator dependence – pollinator independent or insect pollinated; biodiversity relevance – low or high; and nectar production – low or high. I investigated the effect of rooting intensity on overall vascular plant species richness (number of different plant species), species diversity (Shannon-Wiener index) and the count of species sampled that possess each of the ecological traits in the given plot, using generalised linear mixed models and applied a separate model to each response variable (species richness, species diversity or the count of species sampled that possess a certain ecological trait). To control for variation in environmental conditions, all models were constructed to include estimations of forest age and percentage of deciduous trees in close vicinity of the sample units. I tested for significant differences between categorical variables by comparing 95% confidence interval.

4. Results and discussion

4.1 How is wild boar spatial behaviour affected by the availability of agricultural land and population density? (*Paper I)*

My results demonstrate a distinct density-dependency in wild boar spatial behaviour. I found that both female and male home ranges were negatively related to population density, as formerly shown by e.g. Massei et al. (1997). This trend is also observed in other ungulate species, including roe deer (Kjellander et al. 2004) and moose (van Beest et al. 2016) and suggests that the level of intraspecific competition may influence home range size. The total home ranges of wild boar males were nearly three times larger as those of females (49.6 km^2 and 17.3 km^2 respectively). Such sex differences are likely a consequence of the wild boar social and mating system, whereby males attempt to optimise mating opportunities by searching and visiting several spatially separated female groups for females in heat (Singer et al. 1981; Dardaillon 1988). In species where males compete for breeding females during the mating season and female movement is restricted by the limited physical capacity of their offspring during certain times of the year, this usually leads to larger home ranges in males (e.g. Kjellander et al. 2004). While not tested for in this thesis, evidence of sex-based differences in space use, as illustrated by home range size, could indicate that wild boar population demographics are important for understanding the potential consequences for the landscape and associated damages.

The wild boar use of agricultural land was found to be contingent upon its availability, in that wild boar used agricultural land more intensively where it was more available (Figure 3). This response, commonly referred to as a ‘functional response’ (Mysterud & Ims 1998), demonstrates the wild boar's opportunistic feeding behaviour, which has been reported for several European contexts (e.g. Massei et al. 1996; Schley & Roper 2003; Malmsten 2017). Wild boar also adjusted their space use according to wild boar population density. The intensive use of agricultural land by wild boar was further exacerbated in areas with high densities, although contingent upon the availability of agricultural land. In areas rich in agricultural land and with high densities, wild boar are likely to spend more time in agricultural land than would be expected, which is likely to result in a disproportionately high levels of damage to agricultural crops (Figure 3).

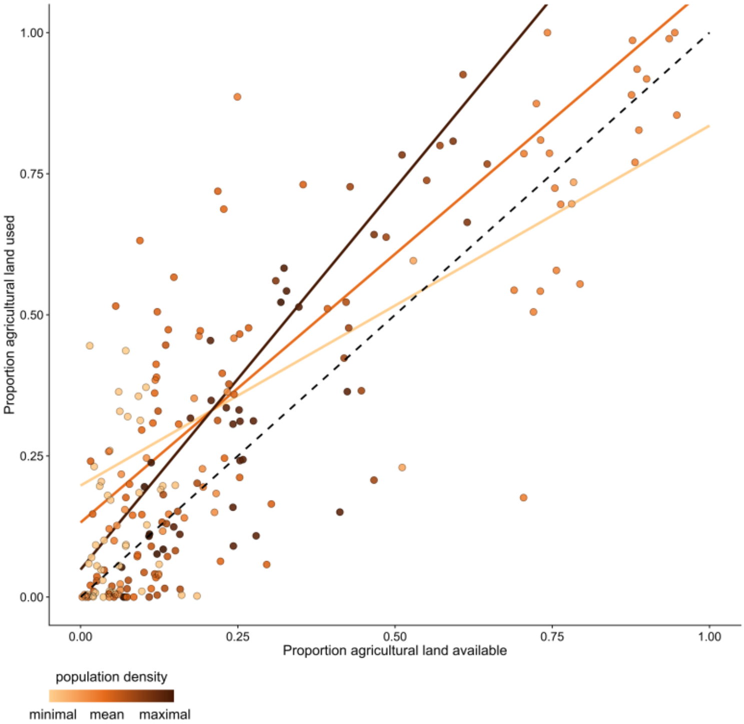

Figure 3. Wild boar use of agricultural land in relation to availability of agricultural land and population density within the home range. Dashed line indicates proportional use as availability changes. Points represent observed values of each individual, repeated for several seasons (n = 211). Lines show predicted values for different population densities: min (0.0045/km^2; light yellow), mean (1.42/km^2; orange), and max (3.23/km^2; dark brown) for season summer-autumn. Shading of points indicates the individual population density within the home range. Data was collected from GPS-locations of collared wild boar (n = 92) in southern Sweden, 2004 – 2021.

Animals are known to adapt their spatial utilisation in accordance with perceived risk, a phenomenon that is often referred to as the ‘landscape of fear’ (Gaynor et al. 2019). This indicates that animal movement patterns are influenced by predation risk. While previous studies have demonstrated that agricultural crops are a highly attractive and selected food source for wild boar (Keuling et al. 2009; Thurfjell et al. 2009; Muthoka et al. 2022), animal behaviour is also affected by the risk of human predation. Consequently, trade-offs between access to high-quality resources and the risks associated with foraging may lead to changes in habitat use (Valeix et al. 2009; Bonnot et al. 2013). Open grasslands and crop fields are relatively insecure environments compared to forested areas which contain more concealed habitats. Thus, in conditions of low competition, wild boar should prefer to forage in more concealed habitats, if available. In addition, I confirmed that wild boar use agricultural land to a greater extent during the summer and autumn months compared to the non-growing season. This seasonal variation likely occurs because agricultural land is most attractive when crops are ripe, as highlighted by several previous studies (Lemel et al. 2003; Keuling et al. 2009; Thurfjell et al. 2009).

4.2 Can wild boar spatial behaviour be manipulated by diversionary feeding? (*Paper II*)

I found no evidence to support the notion that supplementary feeding can be used to redistribute wild boar. In fact, the provision of supplementary food, in the quantities and practices commonly applied by landowners throughout Sweden, did not result in a decreased use of agricultural land by wild boar nor did it lead to any significant changes in the use of areas in the immediate vicinity of where the food was provided. During the vegetation season (16th April – 2nd November), wild boar selected for agricultural land irrespective of whether supplementary food was provided or not, and there was no significant change in the overall use of agricultural land (Figure 4).

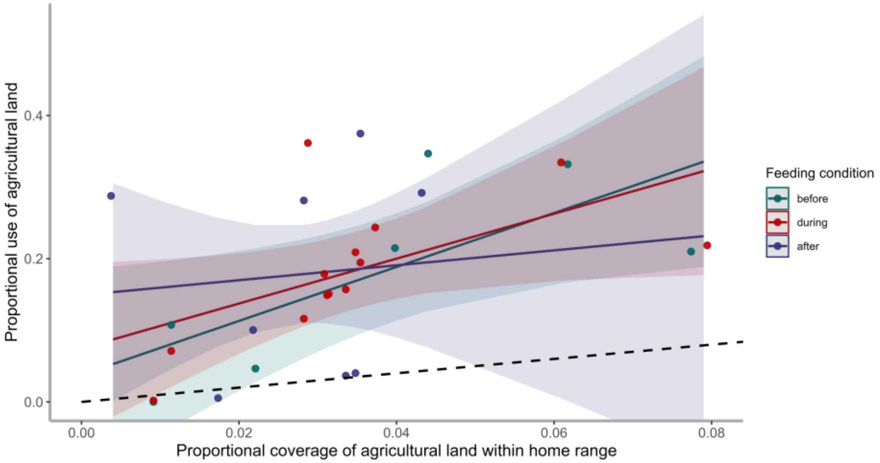

Figure 4. Predicted wild boar use of agricultural land in relation to availability of agricultural land within the home range and under different feeding conditions. Shaded area represents 95% confidence bands. Colour indicated feeding condition: before (green), during (red), and after feeding (blue). Dashed line indicates proportional use (no selection, i.e. intercept = 0, slope = 1) as availability changes. Points represent observed values of each individual wild boar and point colour indicate feeding condition. Data was collected from GPS-locations of collared wild boar (n = 22) in Grimsö Wildlife Research Area, 2019 – 2024.

Although wild boar tended to use feeding sites at a higher extent when food was available, I found no significant difference in the use between periods, either during the vegetation season (16th April – 2nd November) or the winter season (3rd November – 15th April). Wild boar tend to select for agricultural fields when crops are ripe (e.g. Thurfjell et al. 2009; Muthoka et al. 2022). This could explain a limited pull effect of feeding during the vegetation season. However, it is surprising that I found no effect during the winter season when natural and other food resources were low. The consistent use of both agricultural land and feeding sites under different feeding conditions suggests that the attractiveness of supplementary feeding was not strong enough to cause a redistribution of wild boar in this study. Thus, there is a lack of support for that supplementary feeding, when applied in a diversionary design and using current practices, is successful in reducing damage to agricultural land.

4.3 Do wild boar abundance cause sympatric species to alter behaviour in shared feeding sites? (*Paper III*)

Roe deer may avoid wild boar at shared feeding sites by adapting their presence and timing of visits in response to the probability of encountering wild boar. At the local feeding site scale, roe deer chose feeding sites where wild boar abundance was lower (Figure 5A). At the study area scale, roe deer arrived at feeding sites earlier in the day during periods of high wild boar abundance (Figure 6). As a small and solitary species, roe deer are often displaced by other more dominating species in the occurrence of an interaction event (Ferretti 2011; Ferretti & Mori 2020). The most frequent time for wild boar to visit a feeding site was after sunset but before midnight (Figure 6). By arriving earlier, roe deer likely reduce their temporal overlap with wild boar at the feeding sites and increase their access to food (Figure 6). Roe deer was approximately 2.5 times as likely to be at the feeding sites at sunset during periods of high wild boar abundance compared to periods of low wild boar abundance.

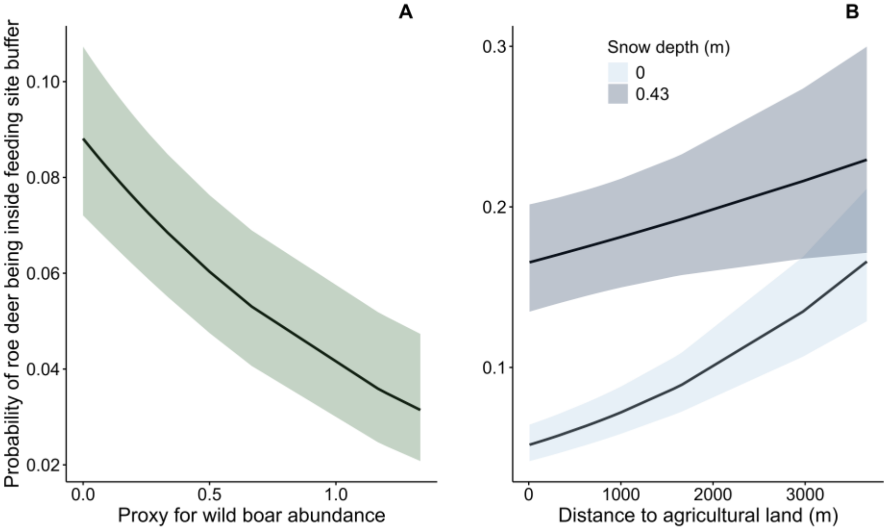

Figure 5. Relationship between roe deer presence at feeding sites and (A) wild boar abundance at the local feeding site scale; and (B) distance to agricultural land and snow depth. Lines represent predicted values with 95% confidence limits (shaded areas). Presence was estimated from GPS-locations of roe deer (n = 94) in Grimsö Wildlife Research Area between 2011 and 2023.

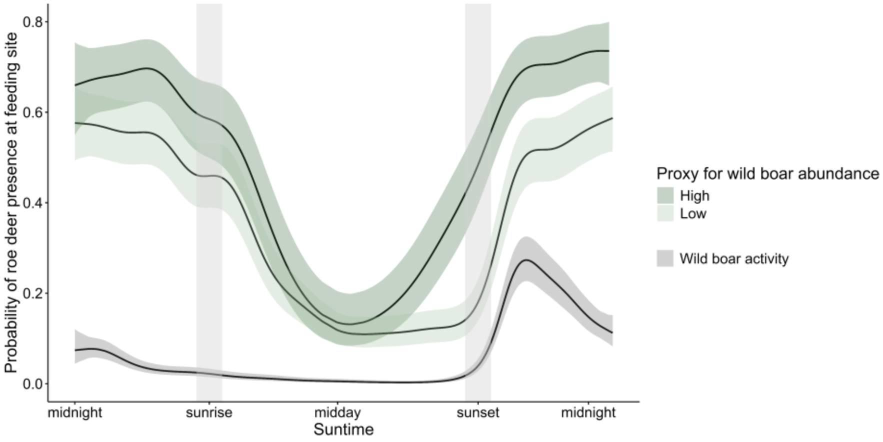

Figure 6. Visual representation of the predicted probability of roe deer presence at feeding sites over the 24-h circadian cycle in relation to wild boar abundance, and predicted probability of wild boar presence at feeding sites over the 24-h circadian cycle at the study area level. Metrics of roe deer presence and wild boar presence were generated by separate models, but outputs are combined in the figure for visual comparison. The time of all observations was standardised along the x-axis to 'sun time' where sunrise and sunset times were determined based on the date and location for each observation. Curves for roe deer presence represent predicted values with 95% confidence limits (shaded areas) for periods of low (light green; Dec 2011 – March 2020) and high (dark green; Dec 2020 – March 2023) wild boar abundance. The equivalent curve for wild boar presence represents predicted values with 95% confidence limits (grey; Feb 2019 – March 2023). Data was collected from GPS-locations of collared roe deer (n = 99) in Grimsö Wildlife Research Area between 2011 and 2023 and wild boar (n = 15) in Grimsö Wildlife Research Area between 2019 and 2023.

The behavioural responses exhibited by roe deer in this study indicate that interspecific encounters may serve to trigger behavioural adjustments that facilitate coexistence with potential competitors. Such actions are likely to have been shaped by the long evolutionary history of coexistence between the two species, prior to the extirpation of wild boar during the 18th century. As two native species that colonised Scandinavia at about the same time, they are expected to have evolved behavioural strategies to minimise competitive interactions. For instance, sympatric species often display resource partitioning, which has presumably evolved as a consequence of past competition (Putman & Putman 1996). Behavioural adjustments tactics may still be costly, however, and an increase in competitor occurrence at feeding sites may force roe deer to be more vigilant, possibly at the expense of reduced food intake, with potential impacts on fitness (Lima 1998).

Moreover, it is widely accepted that interspecific interactions may lead to reduced habitat quality (Focardi et al. 2006) or altered resource utilisation (Hardin 1960). Roe deer may compensate for reduced access to feeding sites by grazing on alternative forage, such as agricultural crops and grassland (e.g. Abbas et al. 2011). This could, in turn, modify the structure and composition of vegetation communities, thereby altering the broader ecological landscape (Partl et al. 2002; Côté et al. 2004).

I found that roe deer used feeding sites more frequently during times when access to natural resources was low. Roe deer were more than twice as likely to use the feeding sites when snow cover was deep and the probability of roe deer presence at feeding sites increased with increasing distance to agricultural land, although this effect was attenuated by increasing snow depth (Figure 5B). The implications of wild boar exploiting roe deer feeding sites are, thus, expected to vary with landscape structure and resource availability, both with regards to roe deer physiology and grazing pressure on alternative resources. This suggests that the impact is potentially high when alternative forage is scarce, e.g. under harsh weather conditions, or in landscapes offering little natural forage or less quality forage. The access to feeding sites is likely less important for roe deer during summer, particularly in landscapes with high availability of agricultural crops and grasslands.

4.4 Can wild boar feeding behaviour impact local plant communities? (*Paper IV*)

Introducing supplementary feeding increased the local wild boar activity, with an overall increase in rooting intensity in the sample units after the food was introduced. Physical disturbance caused by wild boar rooting had an overall positive effect on local vascular plant species richness and species diversity in a young managed boreal forest ecosystem (Table 1). I found that rooting not only affects the number of species in the area in which it occurs, but also has the potential to alter local plant community composition, by causing uneven impacts on species with different ecological traits. Species that were annual, disturbance dependent, or with long-lived seed bank, were positively influenced by rooting while competitive plant species and species with short-lived seed banks were negatively influenced by wild boar disturbance. Additionally, the count of species that were pollinator independent, of high biodiversity relevance, or with low nectar production increased with increasing rooting intensity.

Table 1. All tested response variables and the direction of their relationship (+, -, 0) with rooting intensity, when controlling for forest age and percentage deciduous trees. When controlling for forest age, a significant response to rooting intensity for any response variable is indicated depending on the direction of the estimated response as increased (+), decreased (-) or when no response (0), when the responses differed among rooting intensities (non-overlapping 95% CI), specifically between levels absent-medium, absent-high, and low-high. When controlling for percentage deciduous trees, the reported direction (+, -, 0) of the relationship reflects a significant coefficient ($p < 0.05$).

	Rooting intensity			***Percentage deciduous trees***			
Response variable	*Young forest*	*Middle aged forest*	*Mature forest*	*Absent rooting*	*Low rooting intensity*	*Medium rooting intensity*	*High rooting intensity*
Species richness	+	0	0	0	+	+	+
Species diversity	+	0	0	0	+	0	+
Number of species: Annual	+	0	+	0	+	+	+
Number of species: Long-lived perennial	0	0	0	0	+	+	+
Number of species: Disturbance dependent	+	0	+	0	+	0	0
Number of species: Competitive	0	0	-	0	+	0	0
Number of species: Short-lived seeds	0	0	-	+	+	0	0
Number of species: Long-lived seeds	+	0	+	+	+	0	+
Number of species: Pollinator independent	+	0	0	0	+	+	+
Number of species: Insect pollinated	0	0	0	0	+	+	+
Number of species: Low biodiversity relevance	0	0	0	0	+	+	+
Number of species: High biodiversity relevance	+	0	0	+	0	+	+
Number of species: Low nectar production	+	0	0	0	+	+	+
Number of species: High nectar production	0	0	0	+	+	0	0

The increased levels of vascular plant diversity are likely attributed to the increased environmental heterogeneity caused by rooting. Rooting disturbance enhance spatial heterogeneity in light and soil resources through increased soil turnover and reduced plant cover, thereby promoting species dispersal and recruitment probabilities (Gómez 2004). Exposed soil allows colonisation of new species and enables coexistence of a greater number of species (Currie 1991; Tews et al. 2004). Contrary to the results of this study, wild boar feeding behaviour is often described causing generally negative effects on plant communities (Barrios-Garcia & Ballari 2012). I found the effect of rooting to be particularly pronounced in young forests, however, and in areas rich in deciduous trees (Table 1). The extent of wild boar impacts on the plant community is likely mediated by the type of system in which they occur, thus dependent on both the amount of disturbance and the local conditions.

This study indicates that rooting disturbance affects not only the plant community but might also have cascading effects on higher trophic levels. As rooting disturbance appears to favour species that are independent of pollinators and with low nectar production, it may induce modifications in plant community functional characteristics through decreased nectar availability among the species that are present. Consequently, plant-pollinator interactions may be impacted, ultimately resulting in a reduction in the number of visits made by pollinating insects. Such severe changes in the plant composition could influence ecosystem function and services (Gilliam 2007), which may in turn lead to modifications in the structure and dynamics of entire ecosystems. However, our findings also indicate that the negative impacts on secondary organism groups may be offset by an increased occurrence of other plant species groups, namely species with high biodiversity relevance. This could potentially balance the potential negative effects on overall biodiversity. This study, therefore, highlights the complexity of multitrophic interactions. However, due to the temporal and spatial scale of this study, it is difficult to know what the long-term effects will be on these plant communities or in a different study system.

5. General discussion

This thesis investigates the recolonisation process of the native wild boar in the Swedish landscape from an ecosystem-based perspective. By combining movement data with experimental manipulations and vegetation surveys, I have investigated potential impacts of wild boar at different ecological scales, and by adopting two distinct landscape perspectives: agriculture and forestry.

The wild boar is currently recolonising its native territory. However, the present human-dominated landscape differs considerably from its historical counterpart, particularly regarding the prevalence of intensive and monocultural agricultural practices, which have had a significant impact on the natural environment. While such anthropogenic changes could be good or bad, the high adaptability and resilience of wild boar to environmental fluctuations allows them to exploit the new landscape and thrive. The historical abundance of wild boar in Sweden remains unknown, but due to more favourable conditions, current population levels are likely to exceed those of the past. My results suggest that the selective behaviour of wild boar will continue to have adverse effects on crops and farmland in the future, given no changes in management. Moreover, I would anticipate the impact to be more pronounced in regions where agriculture is intensive and wild boar populations are dense (Paper I).

Forecasting the impacts of wild boar from a forestry perspective is more challenging. Depending on the perspective, the presence of wild boar can have both positive and negative unforeseen effects on forest floral communities. Moreover, there may be additional effect on other trophic levels. This lack of consistency makes it difficult to identify general patterns in how wild boar modify these ecosystems, and it is uncertain whether their effects are large enough to cause substantial impacts on a larger scale.

Modern forestry practices often lead to low environmental heterogeneity and have adverse effects on biodiversity (e.g. Esseen et al. 1997). In landscapes with intensive forest management, wild boar rooting could serve as an ecologically important disturbance element and prove to be an effective and important means of counteracting these negative impacts (Paper IV). A diverse plant community, resulting from wild boar rooting, may also have additional beneficial effects on herbivorous species, as it can support a variety of herbivore dietary selections. Considering that large parts of Sweden are comprised of intensively managed coniferous plantation forests with few natural disturbances, I would anticipate that, at least in the short term, the effects of wild boar will be predominantly positive.

Broad-scale ecological landscape changes could be initiated by wild boars' use of common food sources. This behaviour may increase grazing pressure on alternative resources or induce modified foraging behaviour in sympatric species. Additionally, other ungulate populations may be directly affected by wild boar presence through reduced habitat quality or reduced fitness due to costly responsive behavioural adjustments (Paper III). With more interaction events likely to occur in the future due to increasing ungulate populations (Apollonio et al. 2010), these insights into the coexistence dynamics between wild boar and other species will facilitate predictions of future ecological developments. Consequently, when wild boar utilise shared resources, the negative impacts on subordinate species are likely to be particularly pronounced, especially in conditions where natural forage is limited.

My results demonstrate that density is crucial to the impact of wild boar populations and their foraging behaviour. The abundance of wild boar likely plays an important role in shaping the landscape, particularly concerning crop use, vegetation cover, and plant community composition (Paper I and IV). However, the impact of ungulates should be considered in the context of historical changes (Hobbs 1996). Given the long history of coexistence between wild boar and other species, it is reasonable to expect that the surrounding ecosystem will exhibit a certain degree of resilience to their presence. Through the findings of this thesis, I suggest that any potential negative effects may be partially or fully buffered by behavioural adjustments in populations of sympatric species, and that disturbance activities may even have positive effects on plant diversity.

Feeding sites are an important food source to wild boar (Malmsten 2017). The practice of supplementary feeding is likely to accentuate wild boar impact through concentrating their feeding activities (Paper IV), and to enhance interaction events between sympatric species (Paper III). Considering the growing use of supplementary food in wildlife management and the increasing wild boar population, wild ungulate communities are more likely to rely on supplementary food provision in the future. Should subordinate species respond by intensifying their grazing on alternative forage, it is possible that additional downstream effects on plant communities may be observed, with both positive and negative effects for biodiversity. The extent to which this management practice is applied is therefore likely to play an important part in future impact of wild boar populations.

5.1 Management implications

The lessons learned in this thesis can be used to improve management in several ways. The observed context-dependency in wild boar behaviour (Paper I) indicates that any generalisations about their behaviour should be made with caution and that action plans must be created within the appropriate context to ensure their applicability. Well-founded estimates of space use parameters, e.g. home range size, can be used to inform management practices, particularly for disease control where adaptive management strategies can be applied according to wildlife ecology (Smith et al. 2022). Additionally, my findings provide examples on which conditions that are expected to lead to high damage levels on agricultural fields (Paper I). Considering that the Swedish management system of wild boar is centred around damage control, this knowledge in wild boar spatial behaviour can improve management practices by directing actions to where they would be applied most usefully.

I found no evidence that the commonly used management practice of diversionary feeding in Sweden had any strong redistribution effect on wild boar (Paper II). Due to the known variability in the spatial behaviour of wild boar (Paper I), we can expect regional differences in their responses to similar feeding regimes. Thus, the limited response observed in this study may be attributed to its restricted spatial scale. However, the effectiveness of supplementary feeding as a dissuasive tool to reduce damage to annual crops remains questionable. Diversionary feeding has shown low efficiency also in the scientific literature and only in some rare cases has it been shown to reduce damage to annual crops (Vassant 1994; Calenge et al. 2004). In fact, it seems to be generally accepted that crop damage is not avoided through supplementary feeding. My results support that standpoint. Furthermore, potential negative effects of supplementary feeding can be linked to the unresolved debate about whether feeding improves survival and reproduction. If true, it may even be counterproductive by having a long-term positive effect on population growth and thus risking increased future damage to agricultural land. Additional food provision is likely to exacerbate wild boar impacts on their environment through enhanced local animal traffic and aggregation (Paper IV), but without any strong evidence of mitigating damages on economically valuable areas (Paper II). Wild boar are also likely to utilise feeding sites designed for other species, such as roe deer or fallow deer. As a result, other species may be displaced (Paper III), which could significantly impact deer population dynamics. Thus, it may be economically and ecologically beneficial to reconsider current supplementary feeding practices for wild boar.

While the effectiveness of feeding in reducing the agricultural use of wild boar seems questionable, it may be an effective approach in reducing their home range size (e.g. Olejarz & Podgórski 2024), which may facilitate hunting. Moreover, SOU (2014) reported that approximately 50% of all wild boar killed in Sweden are shot at a feeding site or bait station. Feeding thus remains as an important management tool and has an important role in population control. Nevertheless, changes in feeding practices have the potential to alter the effects of ungulates ecosystem processes, and landowners and policymakers therefore need to consider the important trade-off between short-term benefits and long-term costs of feeding.

5.2 Future perspectives

This thesis addressed the first-order effects of a wild boar recolonisation and, for most of the studies included, at a local scale. Further studies should therefore aim to assess the secondary effects of behavioural adaptations of sympatric species due to increasing wild boar densities, and the long-term effects of wild boar rooting disturbance on plant communities and biodiversity, in order to draw conclusions beyond the local context and for a more comprehensive understanding of how a continued wild boar expansion will affect localised landscapes and ecosystems.

5.3 Concluding remarks

It is likely that wild boar populations will continue to grow and expand throughout Sweden. It is therefore important to consider the profound ecological changes caused by their populations and their impacts. This thesis provides new insights into this subject and suggests that with an inevitable growth in wild boar populations, we face potentially large impacts on habitats and biodiversity. However, due to a strong context dependency, the extent and direction of the effects remain uncertain. I demonstrate that wild boar have extensive and direct impacts on agriculture as well as on faunal and floral communities. Their presence may induce behavioural modifications in other, less competitive ungulates, and their rooting behaviour can alter plant community composition. Furthermore, effects at a broader ecosystem community scale may result from altered resource use by sympatric ungulate communities and potential cascading effects following changes in plant communities and habitats. Future impacts on ecosystems are also likely to be highly dependent on the abundance of wild boar. Finally, it can be concluded that human-driven ecological manipulations, such as supplementary feeding, are likely to accentuate such effects and should therefore be considered in a wider perspective before being applied.

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Popular science summary

> "Om aftonen lämna de sitt stamhåll och begiva sig ut på åkrar och ängar, för att söka sin föda. Om våren och fram på sommaren få de åtnöjas med gräs, örter, maskar och insekter. För att söka dessa uppböka de om natten hela ängar. Längre fram på sommaren infinna de sig på åkrar som bär ärter, havre, rovor o s v och anställa stor förstörelse. Om hösten få de dock sin bästa föda, som består av ek- och bokollon, hasselnötter och vildäpplen. De förtära då även insektslarver och tryffel, som de böka upp under mossan. Om vintern gräver de djupt efter ormbunksrötter och de gå även på åtel, i synnerhet på hästkadaver, som i skogarna är utlagda för räven eller vargen." (Sven Nilsson 1847)

The wild boar is one of the most widely spread large mammals in the world, with a long and sometimes tumultuous history in Swedish nature. The presence of this animal has been documented through rock carvings and other archaeological discoveries dating back to the Stone Age, yet extensive hunting and hybridisation with domestic pigs led to its extinction in the 18th century. Low numbers of the species remained in game parks and estates where they were held for recreational hunting and meat production. Repeated legal releases were followed by decisions for extermination, but numerous escapes in the 1980s led to the parliamentary decision for the species to be allowed to re-establish in the country. Due to a cautious management approach and the species' high reproductive capacity, the wild boar population has grown considerably since then. Although the current number is unknown, the Swedish wild boar population is estimated to be around 300,000 individuals today.

Few species evoke as many emotions as the wild boar. Despite its long history in the country, the return of the wild boar is leading to conflicts with various human activities. The main issue today is found in agricultural landscapes, where landowners can suffer significant economic losses due to wild boar foraging. In recent decades, the landscape has undergone substantial changes, particularly due to the intensification of agriculture and forestry, at the expense of the wild boar’s natural habitat. Lost Nordic experience, hunting traditions and, not the least, limited knowledge of wild boar behaviour have led to uncertainties about how to manage and deal with the problems that may be caused by this species. At the same time, there has been an increase in the use of various preventive management actions, such as supplementary feeding, scaring, and electric fencing. The feeding of wild boar is primarily aimed at diverting them from valuable agricultural land, but there is a lack of management traditions and knowledge, in terms of the effectiveness of this measure and the unintended consequences it may have on the surrounding environment. The feeding behaviour of wild boar is often described as destructive. Due to its rooting activities, the species has a strong potential to affect the environment and the ecosystem it inhabits, both positively and negatively. Apart from the obvious damages that can be easily observed during a walk in the woods, our knowledge of the impact of wild boar on local flora and fauna and the potential effects of their increasing population on our ecosystem, remains quite limited. What could we expect when this shy but sometimes assertive giant reappears in our midst?

The aim of this thesis was to improve the ecological understanding of how the presence and activities of wild boar effect the ecosystem and landscape they inhabit, as well as the role of supplementary feeding in this context. By investigating how wild boar use their surrounding habitats, in the first two studies of this thesis I examine how wild boar population size influences their foraging behaviour and use of agricultural land. What are the most important factors, and can supplementary feeding mitigate the adverse effects that may arise? The last two studies of the thesis investigate how the presence and activities of wild boar affect other animals and plants in the surrounding ecosystem.

The wild boar has successfully adapted to its current environment. However, its return has not gone unnoticed. This thesis shows that the wild boar has a direct impact on its environment. In agricultural landscapes, the damage can be considerable, as wild boar like to consume agricultural crops due to their accessibility and high energy content. However, the extent of this problem appears to be strongly influenced by the specific context and environment in which it occurs, such as the amount of agricultural land and the size of the wild boar population in the area. This knowledge can hopefully help to enhance management practices by directing actions to where they would be most useful. Within the Swedish forest landscape, which is heavily impacted by intensive forestry practices with considerable negative consequences for biodiversity, the wild boar can actually play an ecologically important role. Soil nutrients are redistributed through their rooting behaviour and exposed soil enables establishment of, for example, less competitive plants, leading to increased biodiversity. Altered plant communities can, in turn, affect other trophic levels such as insects, ultimately leading to broader effects on the whole ecosystem. My results show that significant ecological landscape changes can also be initiated by wild boar sharing food resources with other ungulate species, for example through winter or supplementary feeding. I show how feeding contributes to an increase in interactions between wild boar and other animals attracted to such feeding sites. These interactions, in turn, can lead to changes in the behaviour of species that seek to avoid wild boar, by causing them to increase their consumption of different plants than they would have in their absence. I also show how supplementary feeding leads to an increase in the impact of wild boar on surrounding vegetation, although without any clear diversionary effect from agricultural land.

This thesis examines the initial effects of wild boar recolonising the Swedish landscape. The results show that wild boar have a strong ability to influence both their environment and the surrounding ecosystem in a profound way. Due to favourable conditions, it is expected that the wild boar population in Sweden will continue to increase and expand. As a result, significant and continued impacts on ecosystems and biodiversity can be expected. The extent and nature of the impacts (positive or negative) are likely to vary depending on the specific environment, particularly the size of the local wild boar population. Finally, I conclude that supplementary feeding will continue to have a significant influence on the future ecological and economic impact of wild boar, and that a broad perspective needs to be taken before applying this management method.

Populärvetenskaplig sammanfattning

> “Om aftonen lämna de sitt stamhåll och begiva sig ut på åkrar och ängar, för att söka sin föda. Om våren och fram på sommaren få de åtnöjas med gräs, örter, maskar och insekter. För att söka dessa uppböka de om natten hela ängar. Längre fram på sommaren infinna de sig på åkrar som bär ärter, havre, rovor o s v och anställa stor förstörelse. Om hösten få de dock sin bästa föda, som består av ek- och bokollon, hasselnötter och vildäpplen. De förtära då även insektslarver och tryffel, som de böka upp under mossan. Om vintern gräver de djupt efter ormbunksrötter och de gå även på åtel, i synnerhet på hästkadaver, som i skogarna är utlagda för räven eller vargen.“ (Sven Nilsson 1847)

Vildsvinet är ett av de mest utbredda stora däggdjuren i världen, med en lång och stundtals brokig historia i svensk natur. Dess närvaro har dokumenterats genom hällristningar och andra arkeologiska fynd sedan stenåldern, men på grund av omfattande jakt och hybridisering med tamsvin utrotades vildsvinet i det vilda under 1700-talet. Ett fåtal fanns dock kvar på godsen i så kallade jaktgårdar (hägn) där de hölls för jaktupplevelser och köttförsörjning. Återkommande lagliga utsättningar och rymningar följdes av beslut om utrotning, men på 1980-talet resulterade upprepade rymningar i ett riksdagsbeslut om att arten skulle få återetableras i landet. En försiktig förvaltning i kombination med artens höga reproduktionsförmåga har lett till en betydande ökning av den svenska vildsvinsstammen. Även om nuvarande antal är okänt uppskattas den nationella vildsvinspopulationen idag till cirka 300 000 individer.

Få arter väcker så mycket känslor som vildsvinet. Trots sin långa historia i landet innebär vildsvinets återkomst konflikter med flera mänskliga aktiviteter. Den idag främsta problematiken påträffas i jordbrukslandskapet, där enskilda markägare kan drabbas av kännbara ekonomiska förluster till följd av vildsvinens sökande efter föda. Under de senaste decennierna har landskapet genomgått betydande förändringar, framförallt med avseende på intensifieringen av jord- och skogsbruk, på bekostnad av vildsvinens naturliga miljö. Förlorade nordiska erfarenheter, jakttraditioner och inte minst begränsade kunskaper om vildsvinets beteende har lett till en osäkerhet kring hur man bäst förvaltar och hanterar de problem som denna art kan förorsaka. Samtidigt ökar enskilda initiativ till olika avvärjande förvaltningsmetoder, såsom exempelvis utfodring, skrämsel och stängsel. Utfodring av vildsvin syftar i huvudsak till att avleda dem från värdefull jordbruksmark, men det saknas faktabaserad kunskap både när det gäller åtgärdens effektivitet och de eventuella oavsiktliga konsekvenser som detta kan få för den omgivande miljön. Vildsvinets födosöksbeteende (bök) beskrivs ofta som destruktivt. Genom sitt markberedande bök har arten stor potential att påverka den miljö och det ekosystem den befinner sig i, både positivt och negativt. Förutom de rena skador som lätt upptäcks på en skogspromenad vet vi dock mycket lite om hur vildsvinet påverkar det lokala växt- och djurlivet, samt vilka effekter växande stammar kan tänkas ha på våra ekosystem. Vad kan vi förvänta oss när denna vanligtvis blyga men stundtals burdusa bjässe återigen kliver in i vår natur?

Syftet med denna avhandling var att fördjupa vår ekologiska förståelse för hur vildsvinets närvaro och beteende påverkar omgivande ekosystem och landskap, samt att undersöka betydelsen av utfodring i detta sammanhang. Genom att studera hur vildsvin rör sig i de områden där de lever undersöker jag i avhandlingens två första studier hur antalet vildsvin påverkar dess födosöksbeteende och utnyttjande av jordbruksmark. Vilka faktorer är de viktigaste och kan utfodring som syftar till att avleda från jordbruksmark minska de negativa effekter som kan uppstå? I avhandlingens två senare studier behandlas hur vildsvinets närvaro och beteende påverkar andra djur och växter i sin omgivning.

Vildsvinet har på ett framgångsrikt sätt anpassat sig till nuvarande förhållanden. Men dess återkomst sker på inget vis obemärkt. Denna avhandling visar att vildsvinet har direkta effekter på sin omgivning. I jordbrukslandskapet kan det uppstå betydande och kostsamma skador eftersom jordbruksgrödor är en lättillgänglig och energirik föda som vildsvin gärna äter. Problemets omfattning visar sig dock vara starkt kopplat till den specifika miljö där det uppstår, såsom hur mycket jordbruksmark det finns i närområdet och hur stor den lokala vildsvinsstammen är. Förhoppningsvis kan denna kunskap bidra till en förbättrad förvaltningspraxis genom att åtgärder kan sättas in där de gör störst nytta. I det svenska skogslandskapet å andra sidan, där skogsbruket är intensivt och har orsakat betydande negativa konsekvenser för biodiversiteten, kan vildsvinet utgöra ett mycket positivt inslag. Genom böket omfördelas näringsämnen i marken och jorden blottläggs, vilket skapar nya ytor där exempelvis konkurrenssvaga växter kan börja växa, och ge upphov till ökad mångfald. Förändringar i växtsamhällen kan påverka andra delar av näringskedjan, som till exempel insekter, vilket i sin tur kan leda till mer storskaliga effekter i ekosystemet. Mina resultat visar att betydande ekologiska förändringar i landskapet också kan initieras genom vildsvinens nyttjande av födoresurser som delas med andra klövviltsarter, såsom vinter- eller stödutfodring. Jag påvisar hur utfodring bidrar till att antalet möten mellan vildsvin och andra djur ökar genom att de lockas till gemensamma foderplatser. Detta kan resultera i att andra arter ändrar sitt beteende för att undvika vildsvin genom att konsumera och beta mer på andra växter än de skulle göra om det inte fanns vildsvin. Vidare visar jag hur utfodring ökar vildsvinens påverkar på omgivande växtlighet, dock utan att utfodringen i sig har någon tydligt avledande effekt från jordbruksmark.

Denna avhandling behandlar de första, inledande effekterna av en återetablering av vildsvin i det svenska landskapet. Resultaten visar att vildsvinet har en betydande förmåga att påverka både sin miljö och det omgivande ekosystemet på ett mycket märkbart sätt. Till följd av gynnsamma förhållanden förväntas vildsvinspopulationerna i landet fortsätta att växa och sprida sig. Därmed kan vi vänta oss betydande och fortsatta effekter på livsmiljöer och biologisk mångfald. Effekternas omfattning och karaktär (positiva eller negativa) kan dock förväntas variera beroende på den specifika miljön och inte minst den lokala vildsvinsstammens storlek. Slutligen konstaterar jag att utfodringens omfattning kommer att ha en fortsatt stor betydelse för vildsvinets framtida ekologiska och ekonomiska påverkan och understryker därför vikten av att denna förvaltningsmetod beaktas utifrån ett helhetsperspektiv och tillämpas med försiktighet.

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RESEARCH

Density-dependent dinner: Wild boar overuse agricultural land at high densities

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Abstract

The Swedish wild boar (*Sus scrofa*) population has increased rapidly over the last decades, resulting in conflicts with human activities. Particularly, the increase has been challenging for agriculture as wild boar cause damage on crops and grasslands. To predict under what conditions to expect damage and where to prioritize management actions, basic knowledge about wild boar habitat and space use is needed. In this study, we used data from 99 wild boar equipped with GPS-collars, collected over a large temporal scale and throughout their distributional range in southern Sweden. We investigated wild boar home range size and habitat use across gradients of habitat availability and population density. Functional response in habitat use was assessed by estimating the use and availability of agricultural land on individual level and then, on population-level evaluating how use changed with changing availability. Finally, a potential response in habitat use was evaluated in relation to population density, i.e., the interaction between availability and population density. Home range size was negatively related to population density for both male and female wild boar. Wild boar used agricultural land more intensively with increasing population density and when other habitat types were less available. Our findings show that wild boar spatial behavior is highly context dependent and may vary considerably due to landscape characteristics and local conditions. Wild boars tend to overuse agricultural land at high densities which has strong implications for wildlife management. It is therefore important to consider local conditions when predicting space and habitat use by wild boar. Overall, this study provided a better understanding of the drivers of wild boar distribution and space use in agro-forested mosaic landscapes and how this knowledge can improve management practices.

Keywords Spatial behavior · Habitat use · Population density · Wild boar · *Sus scrofa*

Introduction

From being extirpated in the eighteenth century, the Swedish wild boar (*Sus scrofa*) population has increased rapidly since the 1970s, when some individuals escaped from enclosures in which they were held for recreational hunting and meat production (Truvé and Lemel 2003). Today, the population has re-established in the main parts of southern and central Sweden. The current population size is estimated to be over 300,000 animals and the reported annual hunting bag was more than 112,000 animals in 2023 (Swedish Association for Hunting and Wildlife Management). Wild boar can demonstrate high reproductive rates, adaptability, and opportunistic feeding habits (Massei et al. 1996; Schley and Roper 2003; Fonseca et al. 2011; Malmsten 2017). In Sweden, and other parts of Europe, this has led to a rapid range expansion and population increase as well as conflicts with human activities

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due to crop damage, vehicle collisions and disease transmission (Thurfjell et al. 2015; Gren et al. 2020; Stenberg et al. 2021). Agricultural fields are known to be a preferred habitat for wild boar (Thurfjell et al. 2009; Muthoka et al. 2022) and are used at a higher extent during summer than during the rest of the year (Sweden: Lemel et al. 2003, Thurfjell et al. 2009; Germany: Keuling et al. 2009). The challenge to agriculture has been of particular interest due to crop damage and severe economic losses for farmers. The modern agricultural landscape, providing a high abundance of nutritious feed over large areas, represents an interface for conflict between humans and wildlife. Farmers' economic losses are expected to grow as both intensification of agricultural activities and wild boar abundance increase (Gren et al. 2020). Moreover, the risk of disease transmission between wild boar and pig farms have been accentuated due to the first case of *Salmonella enterica* subsp. *enterica*, serovar Choleraesuis in more than 40 years (Ernholm et al. 2022), and the recent outbreak of African swine fever (ASF) in the Swedish wild boar population (SVA 2023). Due to such conflicts, the management of wild boar has, as in other parts of the world, become an issue of national concern in Sweden, and an increased understanding of the wild boar distribution in agro-forested mosaic landscapes is crucial.

A common contemporary approach to monitor and map animal movements is the tagging of animals with GPS telemetry collars. By spatially locating individuals with high precision at a given time, this technique allows to investigate distributional variation in relation to landscape characteristics and local conditions (Cagnacci et al. 2010). A well-established and frequently used method of describing animal distribution is to estimate home range sizes. Animal spatial behavior is shaped by both social and environmental factors; forage availability and competition level are well known to effect space use (e.g., Tufto et al. 1996; van Beest et al. 2016). Home range size is by theory predicted to decrease with increasing food abundance (Ford 1983), and generally, higher-quality habitats are associated with smaller home ranges. Adjustment of home range size to resource levels has been demonstrated in a wide range of mammalian species (Ims 1987; Boitani et al. 1994; Lucherini and Lovari 1996; McLoughlin and Ferguson 2000; Schradin et al. 2010; Bjorneraas et al. 2012) and wild boar home range has shown to be negatively correlated to increasing resources as in years with tree seed mast (Bisi et al. 2018) and around baiting areas (Keuling et al. 2008b). The "density-dependent hypothesis" predicts that changes in home-range size are inversely related to population density (Massei et al. 1997). Increased local animal density increases the competition (Focardi et al. 2006), why competition is considered a main mechanism promoting density dependence. A reduction of home range size at high density has been confirmed in several species (roe deer: Kjellander et al. 2004; wild boar: Massei et al. 1997; moose: van Beest et al. 2016). In wild boar, inter-sexual differences in spatial behavior patterns are related to differences in reproductive strategies between males and females (Kurz and Marchinton 1972; Singer et al. 1981; Boitani et al. 1994; Cavazza et al. 2023; Miettinen et al. 2023). Females form family groups that can include several generations of adults and offspring, while adult males live isolated from the herd outside the rut period (Podgorski 2013). Although the territorial behavior in wild boar is poorly understood, male wild boar are reported to be less territorial than females, interacting more frequently with individuals of both sexes and with larger home ranges that overlap both sexes (Kay et al. 2017; Schlichting et al. 2022). Furthermore, due to their greater body size and advantageous physical characteristics (Spitz et al. 1998), males could be expected to be more resilient to interference competition.

Animals are known to adapt their spatial utilization according to perceived risk, often referred to as the "landscape of fear" (Gaynor et al. 2019). This suggests that animal movement patterns are influenced by predation risk. Although agricultural fields provide high energetic gain, it could also be a dangerous environment for wild boar considering that 20% of the annual hunting bag in Sweden is shot in crop fields (Swedish Association for Hunting and Wildlife Management 2017). However, the avoidance of risky areas (e.g., hunting areas) by wild boar is a debated issue, and is likely to vary at the local and individual scale (Tolon et al. 2009; Said et al. 2012; Brogi et al. 2020, 2022). Hence, context-dependency of animal spatial behavior is complex and behavioral decisions animals make often result in trade-offs between opposing needs, such as forage and safety (Brown et al. 1999).

While home range models may serve an important descriptive purpose, these models describe space use based solely on spatial location, and it is of ecological interest also to understand the causal processes of animal movement and distribution patterns. Analyzing a species' distribution across habitats, i.e., habitat use, links individual animals to their environment by connecting behavior to resource availability (Johnson 1980) and habitat use is most commonly studied by comparing the use of a given habitat in relation to the availability of that habitat in the surrounding landscape (Boyce and McDonald 1999; Manly et al. 2002; Johnson et al. 2006). Although the availability of suitable habitats and resource abundance are proven central determinants for habitat use patterns (Mysterud and Ims 1998; Pellerin et al. 2010; Boyce et al. 2016; Holbrook et al. 2019), the use-available relationship is often more complex. Individuals may change their preference of a particular habitat as a function of its availability. Hence, the use of a given habitat may be conditional on the availability of that habitat (Holbrook et al. 2019). This phenomenon was first termed "functional response" by Mysterud and Ims (1998) and its importance has been demonstrated widely since (Godvik et al. 2009; Bjorneraas et al. 2012; Holbrook et al. 2017; Avgar et al. 2020; Oeser et al. 2023). In addition to adjustment in habitat use due to habitat availability, adaptive shifts in distribution may also be due to site-specific conditions in different populations (e.g., William et al. 2018). Avgar et al. (2020) showed that density dependence may provide a mechanistic explanation for the context-dependent outcomes often reported in habitat use analysis and empirical support for density-dependent habitat selection is growing (Mobæk et al. 2009; van Beest et al. 2014, 2016).

Functional responses have most commonly been studied by assessing how the use of a given habitat changes with its availability (Holbrook et al. 2019), but the number of studies linking variation in functional response to site-specific conditions is growing. Due to an expected increase in Swedish wild boar densities in areas recently recolonized, it is important to understand also how the species adjusts their space use under different population levels. Knowledge on the spatial behavior of wildlife is also crucial in order to predict, prevent, and manage diseases at the wild-domestic interface (Pascual-rico et al. 2022, Podgorski and Smietanka 2018). Management practices aiming to mitigate human-wildlife conflicts in agricultural landscapes require science-oriented and ecologically reliable information to be effective. However, such essential information is still not very well examined, and the knowledge of context dependencies and plasticity in wild boar space use is very limited.

Aims

In this study, we used wild boar telemetry data collected between 2004 and 2021 and throughout the species' distributional range in southern Sweden, allowing us to investigate two aspects of wild boar spatial behavior across gradients of habitat availability and population density. The aim was twofold: (1) investigate the influence of population density and availability of agricultural land on wild boar home range size, and (2) investigate the influence of population density and availability of agricultural land on wild boar use of agricultural land.

Based on the literature, we predict that wild boar home range size will (P1a) decrease at high population density (Massei et al. 1997), (P1b) the decrease in home range size due to population density will be more pronounced in females (Spitz et al. 1998; Kay et al. 2017; Schlichting et al. 2022), (P2a) home range size will decrease at high availability of agricultural land (Ford 1983), and (P2b) the decrease in home range size due to availability of agricultural land will be more pronounced in females (Podgorski 2013). In the context of landscape of fear, and the relatively high mortality risk associated with agricultural land, we predict that (P3) wild boar use of agricultural land (in relation to availability) will increase at high population density.

Material and methods

Study area

We conducted this study within the main distributional range of wild boar in Sweden (55°–60° N, 12°–18° E, Fig. 1). The landscape composition varies across the study area, with the boreal forest being the dominating habitat in the north and farmland in the south. The duration of the growing season (days with average temperature > 5 °C) varies from 190 to 220 days. Average annual precipitation varies from 500 to 1100 mm and average snow cover is between 25 and 100 days per year (SMHI 2022). There tends to be a longer period of snow-covered ground and a shorter duration of the growing season in the northern sites compared to the southern sites. Supplemental feeding is common throughout the study area, although of unknown quantities.

Capture, collars, and positional data

In this study, we used multiple telemetry datasets (e.g., Thurfjell et al. 2009; Muthoka et al. 2022) collected between 2004 and 2021, from 99 wild boar (16 males and 83 females) equipped with GPS-collars. The animals were immobilized with a tranquiliser gun (Dan-inject model JM, Dan-inject, Kolding, Denmark) from a vehicle on agricultural fields or close to feeding stations, or a blowpipe (Dan-inject model Blow 125) after being captured in coral traps. Wild boars were immobilized using one of the following anaesthetizing combinations and adjusted for their body size: 10 mg medetomidine + 20 mg butorphanol + 500 mg ketamine (Kreeger and Arnemo 2007; Thurfjell et al. 2009); 15–30 mg romifidine + 300 mg zolazepam-tiletamine; or 5–6 mg medetomidine + 300–400 mg zolazepam-tiletamine. After immobilization, wild boars were equipped with one of the following GPS/GSM collars: Vertex Plus 2D or 3D; Vertex Lite 2D; or GPS Pro Light 3D (Vectronic Aerospace GmbH). Telemetry data was collected or subsampled to one location every 1 h and for a maximum of 365 days to obtain homogeneity among individuals.

Population density and space use

We obtained hunting bag for each hunting district and hunting year between 2004 and 2021 from the Swedish Association for Hunting and Wildlife Management, game monitoring. Hunting bag statistics are commonly used as a proxy for assessing the relative abundance of animals in several species (Apollonio et al. 2010; Putman et al. 2011). However,

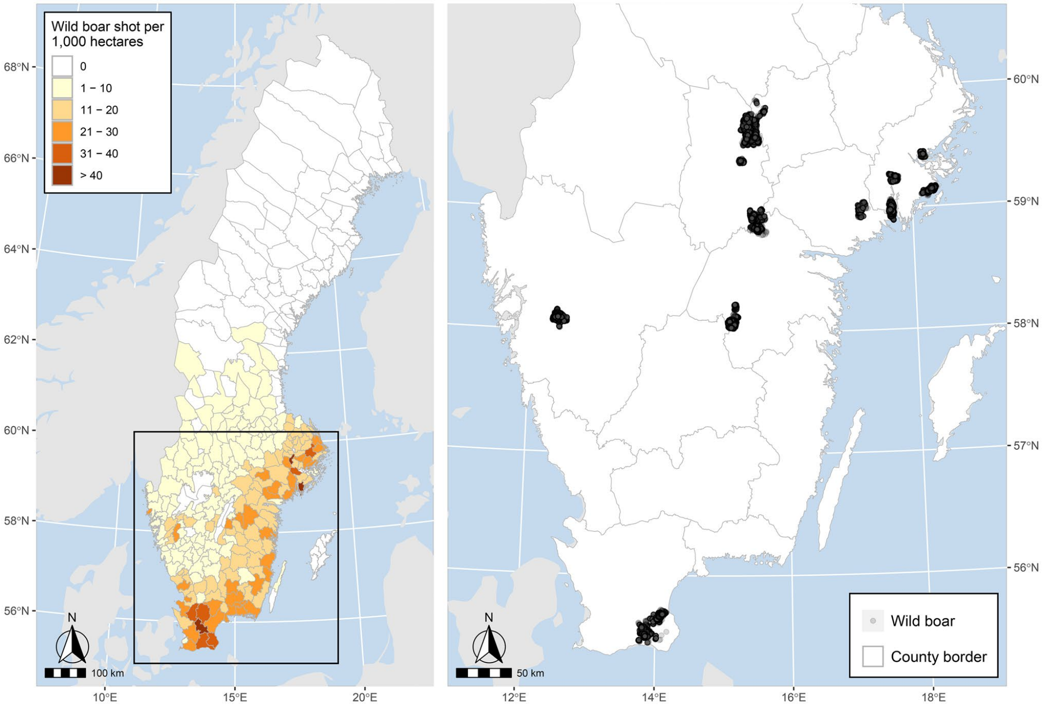

Fig. 1 Hunting bag estimates for each hunting district in the study area for hunting year 2020/2021 (left), illustrating the large density variation across the study area. A hunting bag was used as a proxy for population density and assigned to each individual wild boar according to the location (hunting district) and time stamp (hunting year) of its first GPS location. The study area in southern Sweden with GPS-locations from 99 collared wild boar between 2004 and 2021 (right)

since this approach has formerly been criticized for not being fully reliable (Focardi et al. 2020), we collected wild boar-vehicle collision data for each county and hunting year represented among wild boar location data and conducted a complementary calibration study. Collisions data was compiled to match hunting year (July 1 to June 30). Motivated by the strong correlation between wild boar collisions data (wild boar-vehicle collisions/km^2) and hunting bag (shot wild boar/km^2) ($r = 0.89$, df = 100, $p < 0.0001$; Fig. S1), also demonstrated by Massei et al. (2015) and Neumann et al. (2020), hunting bag (shot wild boar/km^2) was assumed to be a reliable proxy for wild boar abundance and will hereon be referred to as "population density." We assigned hunting bag to each individual animal according to the location (hunting district) and time stamp (hunting year) of its first GPS-location. For individuals with more than one monitoring period, we used the hunting bag for the first period.

To determine wild boar habitat use, we used CORINE land cover (CLC) data with 100 m spatial resolution, which has 44 categorized land cover and land use classes in total (European Union 2000, 2006, 2012, 2018). We reclassified the CLC classes into two habitat groups: agricultural land and others. Agricultural land was defined as all subclasses of the CLC category agricultural area (Kosztra et al. 2017): areas principally occupied by agriculture, arable land, fruit and berry plantations, pastures, meadows, and other permanent grasslands under agricultural use. All remaining land cover classes were grouped as others. We assigned land cover data to each individual according to the year for its first GPS-location and the closest corresponding year of the CLC data.

Both day and night location data from 83 female and 16 male collared wild boar (mean locations per individual = 4081, range = 304–8697) were used to compute an alpha-concave hull with a concave distance of 3 km in order to estimate home range used by each wild boar (Asaeedi et al. 2017). We estimated the use of agricultural land by calculating the proportion of true locations in agricultural land divided by the total number of true locations. We assessed available resources by generating an equal number of random locations to true locations, i.e., a ratio of 1:1, within the individual home range. This design ensured that availability was measured in the area known and in reach to each animal, and thus representing a type III analysis (Manly et al. 2002). Availability was calculated as the proportion of random locations in agricultural land divided by the total number of random locations. Seven individuals were omitted from the dataset before estimating habitat use due to a complete absence of agricultural land in their home range. The range of variables used in the statistical analysis is provided in Table 1. We used a two-stage approach (Fieberg et al. 2010): first, estimating the use of agricultural land and availability of agricultural land per individual and season; and second, on population-level assessing how the sample of use changed with the sample of availability (Holbrook et al. 2019).

As the hour of sunset is known to trigger the onset of activity (Boitani et al. 1994; Lemel et al. 2003; Thurfjell et al. 2014), each used location was assigned a daylight value (day = 1, night = 0) according to its sunrise and sunset (Schlyter 2021). We used night-time data from 76 female and 16 male collared wild boar (mean locations per individual = 1979, range = 110–4201) to analyze habitat use as wild boar are predominantly nocturnal (Boitani et al. 1994; Lemel et al. 2003; Keuling et al. 2008a; Podgorski et al. 2013; Thurfjell et al. 2014; Brivio et al. 2017).

We defined three different seasons related to the ecology of wild boar in Scandinavia: spring–early summer (reproductive season; March–June), summer–autumn (crop season; July–October), and winter (November–February; Mauget 1982; Thurfjell et al. 2014; Malmsten et al. 2017). To account for differences in habitat use across different seasons, all random locations were assigned a random season at an equal number to true locations for each season. This allowed us to test for the change in use while holding availability constant. Individuals with fewer than 10 days of data or 100 recorded locations per season were removed from the dataset before estimating habitat use.

Statistical analysis

We investigated variables influencing wild boar home range size ($\log_{10}$) by using a generalized linear mixed model with a Gaussian error term in the R package *glmmTMB* (Brooks et al. 2017). We investigated the effects of population density (shot wild boar/km^2), availability (proportion of random locations in agricultural land), and sex (females coded as 0 and used as reference value, males coded as 1), including the interactions "population density * sex" and "availability * sex," while controlling for monitoring days ($\log_{10}$).

We investigated variables influencing wild boar use of agricultural land by using a generalized linear mixed model with a Gaussian error term in the R package *glmmTMB*. We investigated the effects of population density and availability of agricultural land, including the interaction "population density * availability," while controlling for season. Intersexual differences were excluded from the analysis due to the limited sample size of males. Animal ID was treated as a random factor to account for the dependency of repeated seasons within individuals (Zuur et al. 2010). For both analyses, we used Akaike information criterion, corrected for small sample sizes (AIC_C), to compare the relative strength of candidate models by calculating the ΔAIC_C (Akaike 1974), and performed AIC_C model selection on candidate models (Tables 2 and 4). To assess model quality and to further ensure that models fulfilled assumptions, models were screened using the package *performance* (Lüdecke et al. 2021). Figures were produced using the package *ggplot2* (Wickham 2016). For data analysis, we used R version 4.2.2 (R Core Team 2022).

Results

Home range size

The mean estimated alpha-concave hull home range size for individuals monitored for a minimum of 14 days was for males 49.6 km^2 (95% CI 24–75) and for females 17.3 km^2 (95% CI 14–20). The best predictive model explaining home

Table 1 Mean value and range for the variables used in the analyses

Variable	Unit	Mean	Range
Population density	Shot wild boar/km^2	1.42	0.0045–3.23
Availability	Proportion of random locations in agricultural land	0.24	0–0.95
Monitoring days	Days	242	14–365
Sex	Female = 0, male = 1		
Season	Spring–early summer: March–June Summer–autumn: July–October Winter: November–February		

Table 2 Competitive models on the effects of population density, availability, sex, and monitoring days on wild boar home range size ($\log_{10}$)

Response	Corresponding predictions	Formula[a]	df	AIC_C	ΔAIC_C
Home range size	P1a, P1b, P2a, P2b	Population density * Sex + Availability * Sex + Monitoring days	8	26.5	0.0
	P1a, P1b	Population density * Sex + Monitoring days	6	26.9	0.38
	P1a, P2a, P2b	Availability * Sex + Population density + Monitoring days	7	27.2	0.61
	P1a, P2a, P1b	Population density * Sex + Availability + Monitoring days	7	27.9	1.38
	P1a	Population density + Sex + Monitoring days	5	30.9	4.39
	P1a, P1b, P2a	Availability + Population density + Sex + Monitoring days	6	32.3	5.74
	P2a, P2b	Availability * Sex + Monitoring days	6	59.8	33.26
	0	Sex + Monitoring days	4	65.0	38.44
	P2a	Availability + Monitoring days + Sex	5	67.1	40.61

[a] Interactions include both main effects and interactions

range size included the predictors availability of agricultural land, population density and sex, and the interaction between availability of agricultural land and sex, and the interaction between population density and sex (Table 2). We found a strong negative effect of population density but a weaker effect of availability of agricultural land on home range size (Fig. 2, Table 3). Male home ranges were in general larger than female home ranges. Both females and males showed an overall decrease in home range size with increasing population density. The effect of population density was more pronounced in male home range size than female home range size (Fig. 2). Males showed a decrease in home range size with increasing availability of agricultural land, while female home ranges increased with increasing availability of agricultural land, although the effect of availability of agricultural land was not as strong (Table 3).

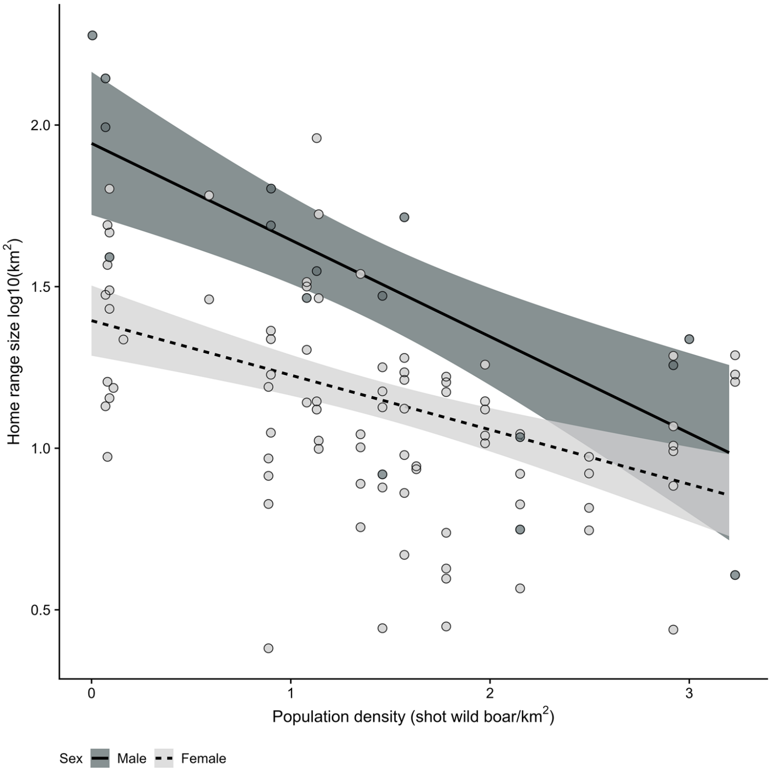

Fig. 2 Home range size for male and female wild boar in relation to population density index (shot wild boar/km^2). Points represent individual observed values for males (dark gray) and females (light gray). Lines show predicted values with 95% confidence limits (shaded areas) for males (solid line) and females (dashed line). Data was collected from GPS-locations of collared wild boars ($N=99$) in southern Sweden, 2004–2021

Table 3 Summary of model coefficients predicting wild boar home range size ($\log_{10}$) for the highest ranked model based on AIC_C

Predictor	Estimate (± SE)	*z* value	*p* value
Intercept (female)	0.518 (±0.171)	3.030	0.002
Population density	−0.169 (±0.033)	−5.142	<0.001
Availability	0.186 (±0.109)	1.707	0.088
Sex male	0.711 (±0.127)	5.613	<0.001
log10(monitoring days)	0.360 (±0.074)	4.897	<0.001
Population density * sex male	−0.130 (±0.075)	−1.740	0.082
Availability * sex male	−0.710 (±0.364)	−1. 954	0.051

The reference category for "Sex" was "Female"

Use of agricultural land

The best predictive model explaining wild boar use of agricultural land included the predictors availability of agricultural land and population density as well as the interaction between these two variables (Table 4). We found that wild boar increased their use of agricultural land with increasing availability of agricultural land (Fig. 3, Table 5). Moreover, wild boar used agricultural land more intensively with increasing population density, and when the availability of agricultural land was high. We found an overuse of agricultural land at high wild boar densities, an underuse of agricultural land at low densities, and a proportional use of agricultural land (in relation to availability) at intermediate densities (Fig. 3). Additionally, wild boar showed a higher use of agricultural land during summer–autumn than in other seasons (Table 5).

Discussion

In this study, we show that high wild boar densities lead to an overuse of agricultural land. We found that wild boar home range size was negatively related to population density for both male and female wild boar, thus confirming our prediction that home range size will decrease at high population density (P1a). We found no support for that this negative relationship between home range size and population density should be more pronounced for females (P1b). On the contrary, we found the effect of population density to be more pronounced in male home range size. Males showed a decrease in home range size with increasing availability of agricultural land, thus partially confirming our prediction that home range size will decrease at high availability of agricultural land (P2a). However, we found no support for this in female home range size, nor for our prediction that the negative relationship between home range size and availability of agricultural land should be more pronounced for females (P2b). Wild boar adjusted their use of agricultural land in relation to availability of agricultural land and population density, supporting our prediction that wild boar will increase their use of agricultural land (in relation to availability) at high population density (P3).

Home range size

Wild boar exhibited smaller home ranges at higher densities (Fig. 2). This is in support of our prediction and suggests that the level of intraspecific competition may influence home range size. It is also in line with previous literature on wild boar spatial behavior (Massei et al. 1997), as well as in other ungulate species (roe deer: Kjellander et al. 2004; moose: van Beest et al. 2016). This knowledge can be used to inform management policies, particularly for disease control where adaptive strategies can be applied according to wildlife ecology (Smith et al. 2022). Realistic home range sizes are crucial when assessing contaminated areas or potential rate of disease transmission. Contrary to our prediction, population density was more important for male home range size than for female home range size. Keuling and Massei (2021) concluded that recreational hunting caused changes in wild boar home range size. In this study, we used hunting bag as a proxy for population density. As hunting bag also reflects hunting pressure, the more pronounced effect in male home range size could be due to the higher hunting pressure on males. The observed behavior in males may also been affected by age. Cederlund and Sand (1994) showed that size of male moose home ranges was strongly dependent on age, in contrast to that of females. Due to unknown animal age

Table 4 Competitive models on the effects of population density, availability, sex, and season on the use of agricultural land by wild boar

Response	Corresponding predictions	Formula[a,b]	df	AIC_C	ΔAIC_C
Use of agricultural land	P3	Availability * Population density + Season	8	−212.6	0.00
	0	Availability + Season	6	−209.9	2.70
	P3	Availability + Population density + Season	7	−207.9	4.74

[a] Interactions include both main effects and interactions

[b] Animal ID was included as a random effect in all models

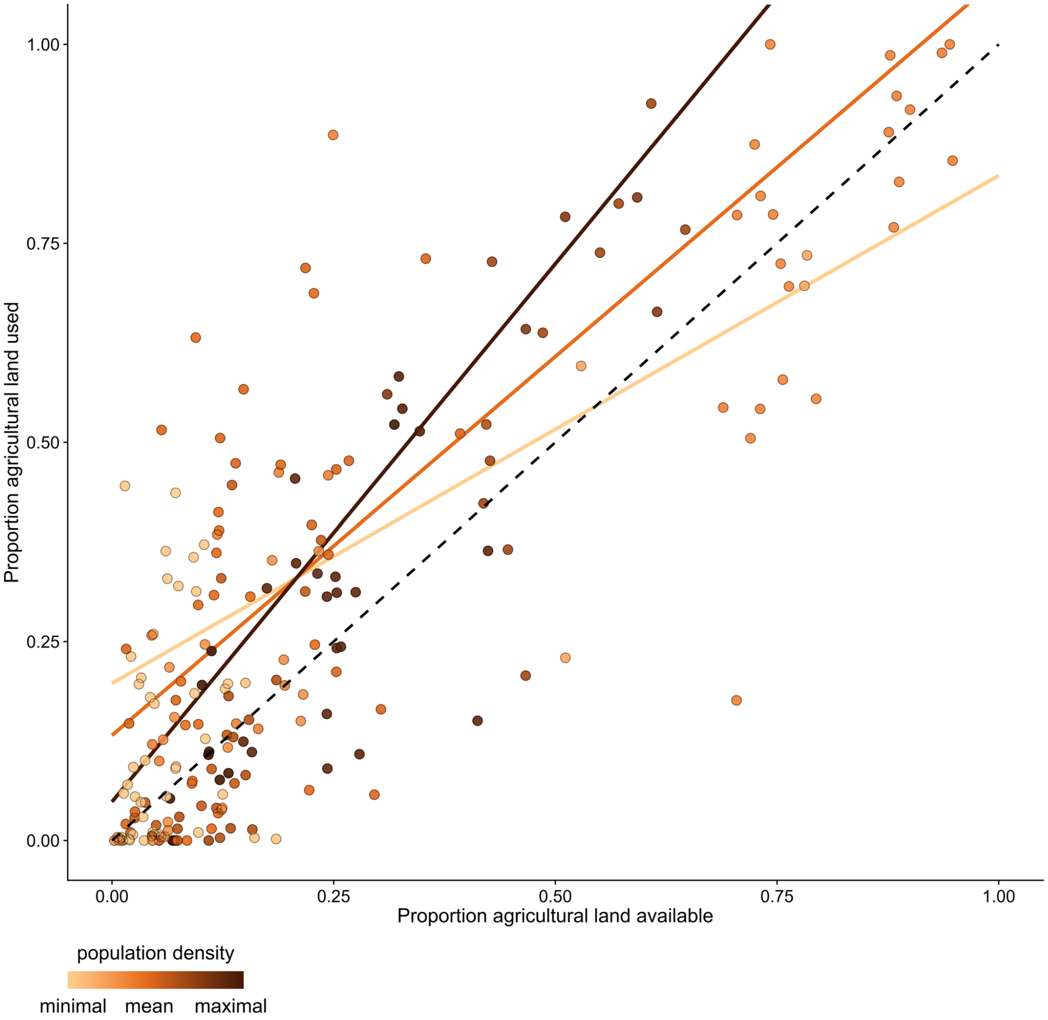

Fig. 3 Wild boar use of agricultural land in relation to availability of agricultural land and population density within the home range. Dashed line indicates proportional use as availability changes. Points represent observed values of each individual, repeated for several seasons ($N = 211$). Lines show predicted values for different population densities: min (0.0045/km^2; light yellow), mean (1.42/km^2; orange), and max (3.23/km^2; dark brown) for season summer-autumn. Shading of points indicates the individual population density within the home range. Data was collected from GPS-locations of collared wild boars ($N = 92$) in southern Sweden, 2004–2021

in our sample, besides being adults, we could not correct for this in the analysis.

Theory on food exploitation suggests that when food supply decreases, home range size should increase due to increased activity, a relationship that has been demonstrated in the wild boar literature (Singer et al. 1981; Boitani et al. 1994; Massei et al. 1997; Bisi et al. 2018). Although the availability of agricultural land alone does not provide a complete understanding of an area's food supply, agricultural crops are highly nutritious and could therefore be considered a high-quality resource. We found that male home range size was negatively affected by the availability of agricultural land. For females, however, this relationship was more complex, and it is possible that the effect of population density may mask or override the effect of availability of agricultural land. Moreover, animal spatial behavior is often

Table 5 Summary of model coefficients predicting wild boar use of agricultural land for the highest ranked model based on AIC_C

Predictor	Estimate (± SE)	*z* value	*p* value
Intercept (spring–early summer)	0.086 (±0.032)	2.698	0.007
Population density	−0.046 (±0.021)	−2.251	0.024
Availability	0.637 (±0.112)	5.678	<0.001
Season summer–autumn	0.111 (±0.022)	5.092	<0.001
Season winter	−0.006 (±0.023)	−0.247	0.805
Population density * availability	0.221 (±0.083)	2.670	0.008

The reference category for "Season" was "Spring–Early summer"

subjected to a food/cover trade-off (Mysterud and Ims 1998; Brown et al. 1999); thus, once the need for food is saturated, other factors, such as shelter, may become more important. In summary, our results suggest that home range size is context dependent and affected by a complex combination of multiple conditions, such as food availability, access to cover, and level of competition.

Our results support previous findings on that males of wild boar have larger home ranges than females (Kurz and Marchinton 1972; Singer et al. 1981; Boitani et al. 1994). This is a probable consequence of the wild boar social- and mating system through males trying to optimize mating opportunities by searching and visiting several spatially separated female groups for females in heat (Singer et al. 1981; Dardaillon 1988). In species where males compete for breeding females during the mating season and female movement is restricted by the limited physical capacity of their offspring during certain times of the year, this usually leads to larger home ranges in males (e.g., Kjellander et al. 2004).

Use of agricultural land

Wild boar use of agricultural land was influenced by the amount of agricultural land available (Fig. 3), confirming the importance of resource availability in habitat use patterns (Mysterud and Ims 1998; Pellerin et al. 2010; Boyce et al. 2016; Holbrook et al. 2019). Wild boar demonstrate an opportunistic feeding behavior, and its diet reflects local environmental conditions (Schley and Roper 2003), why we could expect the species to utilize resources in relation to availability and abundance. Population-density effects on spatial behavior are not well described in the wild boar literature, but have been demonstrated in several other ungulate species (e.g., moose: van Beest et al. 2014), and the importance of considering density-dependent changes in habitat selection in a theoretical framework was shown by Avgar et al. (2020). We found that the effect of population density on wild boar use of agricultural land was conditional on the availability of agricultural land. Wild boar adjusted their use of agricultural land in relation to population density, with an underuse of agricultural land at low densities and an overuse at high densities, and with a stronger effect of density at high availability of agricultural land (Fig. 3). Theory on density-dependent habitat selection predicts that animals exhibit a specialized behavior when densities are low and a more generalized behavior during high densities to reduce competition for resources. In this perspective, an increased use of a habitat type due to increased competition would suggest that it is not the most preferred habitat. Although previous studies suggest that agricultural crops are highly attractive and are selected for by wild boar (Keuling et al. 2009; Thurfjell et al. 2009; Muthoka et al. 2022), the observed response may be explained by that animal behavior is also influenced by human predation risk. Trade-offs between access to high-quality resources and risk-taking may result in adjustments in habitat use (Valeix et al. 2009; Bonnot et al. 2013). Agricultural land is due to its openness, a relatively unsafe environment. Under low competitive conditions, wild boar should prefer to forage in more concealed habitats, if available. The quality of an otherwise poor area can be artificially increased by providing supplementary food (Muthoka et al. 2022) and wild boar are known to modify their spatial behavior around feeding sites (Keuling et al. 2008b). In the Swedish context, artificial feeding sites are often placed in areas of high cover, and thus, when available, provides easy access to high energetic gain under safe conditions. Such local food sources, however, are likely to be monopolized quickly and therefore lack the capacity to sustain dense populations. Agricultural areas are harder to monopolize due to its larger size. This provides a potential explanation for the observed overuse of agricultural land at high densities: strong competitive conditions push wild boar towards high-risk forage areas, i.e., agricultural fields. A similar behavior was shown by van Beest et al. (2016) who demonstrated an increased selection for riskier habitat in elk with increasing animal density. Furthermore, we found a stronger effect of population density when availability of agricultural land was high. In this study, we focus on the use and availability of a single habitat type: agricultural land. As the selection for a given habitat is conditional on other habitat types being available to the individual, an increase in the proportional availability of agricultural land indicates a decrease in the proportional availability of other, "safer," habitat types, and consequently, an increased competition in these areas. Competition may act on different limited resources, where food may be one and safety another. It is likely that the observed functional responses in wild boar habitat use reflect the competitive conditions for cover rather than the competitive conditions for food, or possibly a combination of both resources.

We confirmed a seasonal variation in wild boar use of agricultural land, previously demonstrated by several studies (Lemel et al. 2003; Keuling et al. 2009; Thurfjell et al. 2009). Wild boar overused agricultural land during late summer and early autumn while demonstrating a proportional use in relation to its availability during other seasons. This seasonal variation is likely due to that agricultural land offers different food items throughout the year and is most attractive during periods when crops are ripe.

Conclusions

Wild boar spatial behavior is highly context dependent and may vary considerably due to landscape characteristics and local conditions. In this study, we show that we can expect adjustments in habitat use due to both habitat availability and population density. High wild boar densities are expected to lead to disproportionally high damage levels on agricultural fields which has strong implications for management. Realistic and achievable goals increase the chances of farmers and hunters agreeing on management practices and our results imply that, in many cases, it may in fact be enough to reduce wild boar density to moderate levels to reduce crop damage. We demonstrate the importance of identifying the level of plasticity in wild boar spatial behavior due to population-level characteristics. Applying static space use models not considering density may thus lead to inaccurate inferences with ecological and management consequences. Still, this observed plasticity in wild boar use of agricultural land and its consequences for crop damages requires further research to better assess the consistency in our observed overuse at high densities. This study provided a better understanding of the drivers of wild boar distribution and space use in agro-forested mosaic landscapes and showed that improved knowledge in wildlife spatial behavior can enhance management practices by directing actions to where they operate most usefully.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-024-01766-7.

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Author contribution P. Kjellander, H. Thurfjell, S. Widgren, H. Kim, and E. Augustsson developed the study design. P. Kjellander, H. Thurfjell, S. Widgren, H. Kim, J. Malmsten, and J. Månsson provided data. Data were analyzed by E. Augustsson, H. Thurfjell, H. Kim, H. Andrén, and L. Graf. E. Augustsson led the writing of the manuscript and drafted the initial version. All authors revised the manuscript, contributed with supportive information, and gave final approval for publication.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All wild boar captures and handling were approved by the Ethical Committee in Animal Research, Umeå, Sweden (permit A 18-04), and Uppsala, Sweden (permit C 80/9, C 77/10, C 5.2.18-2830/16, and 5.8.18-00845/2017), and in compliance with Swedish laws and regulations.

Competing interests The authors declare no competing interests.

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Supplementary Information for: Density-dependent dinner: Wild boar overuse agricultural land at high densities

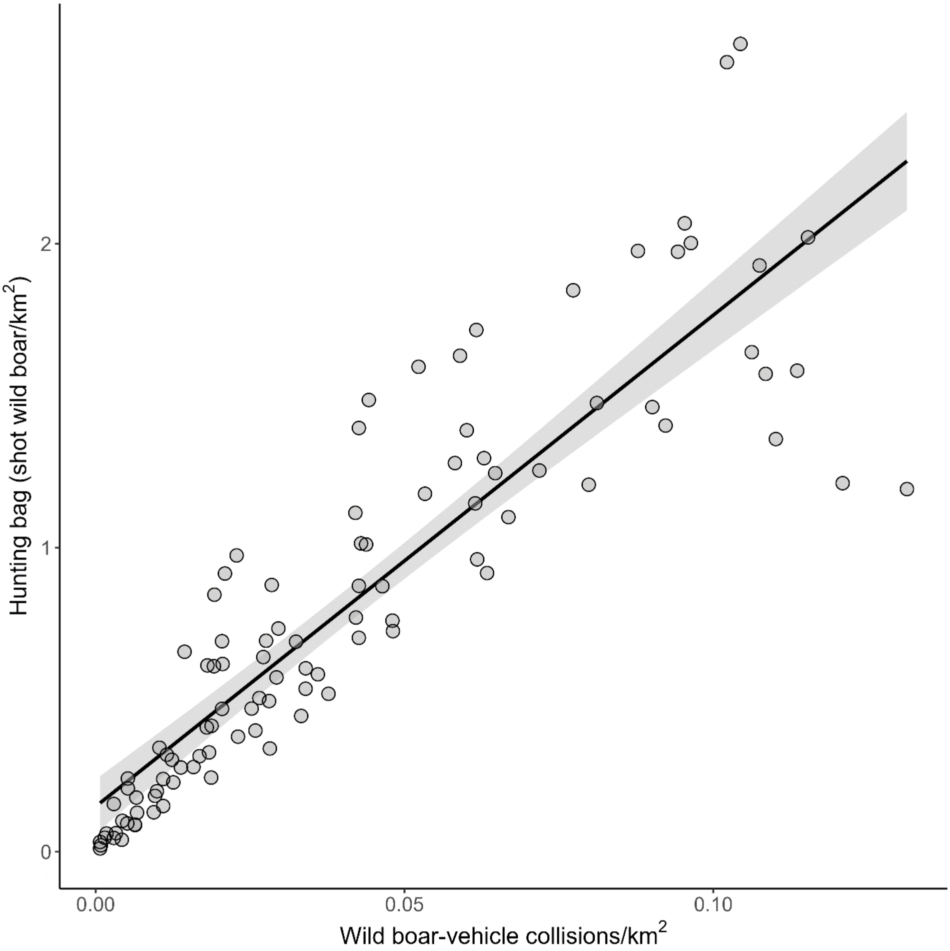

Fig. S1. Correlation plot (r = 0.89, df = 100, p < 0.0001) between hunting bag (shot wild boar/km²) and wild boar collision (wild boar-vehicle collisions/km²) for each hunting year between 2004 and 2021 and county with GPS-collared wild boar. Shaded area represents 95 % confidence limit.

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The wild boar is currently recolonising its native territory. This thesis examines the initial effects of wild boar at different ecological scales in the human-dominated Swedish landscape. The findings suggest that if wild boar populations continue to increase, significant and continued impacts on habitats and biodiversity can be expected, resulting in both positive and negative consequences. Additionally, human-driven ecological manipulations, such as supplementary feeding, are likely to amplify these effects.

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